UPLAND BOREAL FOREST

NORTHWEST OF THUNDER BAY, ONTARIO:

ECOLOGY AND APPLICATIONS TO SILVICULTURE

By

(C) Jeffery C. G. Goelz

A thesis submitted in partial fullfillment

of the requirements for the degree of

Master of Science in Forestry

Lakehead University

School of Forestry

July, 1984

ABSTRACT

Goelz, Jeffery C.G. 1984. Upland boreal forest northwest of Thunder Bay, Ontario: Ecology and applications to silviculture. 169 pp.

Additional Key Words: geomorphology, indirect gradient analysis, land classification, ordination, phytosociology, silvicultural recommendations, site index, succession, synecology.

Multivariate phytosociological methods were used to investigate the ecology of upland boreal forest stands. The ecological information was used to derive silvicultural recommendations. The boreal forest stands did not form tight associations. Species were distributed individualistically; most species have broad, overlapping, environmental tolerances. Most of the variability among stands was attributed to the environment and to species precedence on a site. Geomorphology and moisture regime were related to community composition. *Pinus banksiana* dominates sandy glaciofluvial deposits. *Picea mariana* achieves moderate abundance on glaciofluvial deposits which are moister due to finer soils or to topographic position. *Picea mariana* may also dominate shallow moraines. Deeper moraines were dominated by mixedwoods composed of all species common to uplands in the study area. Succession is of minimal importance; other factors override successional trends.

While plant communities were related to landforms, the landforms are much more discrete than the plant communities. Therefore, landforms were used to derive silvicultural recommendations. Land types were identified by combining or dividing simple geomorphological features. The seven land types were associated with trends of community composition and of productivity. Silvicultural recommendations were derived for each of these land types. These recommendations were primarily determined by potential hardwood competition and productivity.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

During my tenure at Lakehead, I received financial support from two Canadian Forestry Service Bursaries, two Lakehead University Graduate Assistantships, and 1 1/2 Canadian Forestry Service Summer Supplements. These funds were allocated by the graduate studies committee, School of Forestry, Lakehead University. Field work was funded through the Canadian Forestry Service block grant to the School of Forestry.

Derek Dool, of Great Lakes Forest Products, Pat Corbett, of the Ontario Ministry of Natural Resources, Thunder Bay district, and Brian Vermeersch, of the Ontario Ministry of Natural Resources, Ignace district, helped me locate areas which haven't been cut over or burned. Grant Cottam and Ed Beals, University of Wisconsin-Madison, offered some suggestions on sampling and analytical methodology. Claude Garton, Lakehead University Herbarium, identified some species. Paul Betts and Jim Youngblut were my research assistants during different parts of the field season. Bob Pollard, Ontario Ministry of Natural Resources, Sioux Lookout district, arranged accomodations at the Savant Lake silvicultural camp.

The following people, all faculty, staff or students at Lakehead University, gave me various aid: Frances Bennett-Sutton, Ralph Birston, Ian Burgess, John Connor, R.J. Day, Jack Flowers, Karen Foster, Helen Huk, Joanne Kavanaugh, A.J. Kayll, Tom Krickl, Dan Lenthall, Frank Schnekenberger, Michael Stoehr, Craig Sutherland, Gil Vanson.

My graduate committee, Crandall Benson, Willard Carmean, and Rob Farmer, gave me their perspectives. Their viewpoints are greatly appreciated. Rob Farmer, my major advisor, encouraged me to satisfy my intellectual curiosity, although my thesis is outside his research interests.

1. INTRODUCTION

The North American Boreal Forest crosses the continent from interior Alaska to Newfoundland in a belt over 800 km wide. Within this belt there are distinct differences in vegetation across relatively short distances in both latitude and longitude (Larsen, 1980; La Roi, 1967; La Roi and Stringer, 1976). This study will characterize one part of the variability within the boreal forest.

The intent of this study is to use quantitative phytosociological techniques to attain the following objectives:

1) To identify and describe the major plant communities in the area.

2) To determine the factors that affect community composition, structure and dynamics.

3) To obtain information about species distribution and performance across environmental and temporal gradients.

4) To determine relative stand productivity (in terms of site index) and relate productivity to site and community characteristics.

5) To derive silvicultural recommendations by synthesizing the ecological environment with the management environment.

2. LITERATURE REVIEW

2.1. UPLAND BOREAL FOREST COMMUNITIES

A comprehensive review of the boreal forest is given by Larsen (1980). Boreal forest stands across a longitudinal gradient were studied by La Roi (1967) and La Roi and Stringer (1976). The southern boreal forest border has been studied by Buell and Niering (1957), Maycock and Curtis (1960) and Gregory (1979). Hurley and McIntosh (1964), Damman (1964), Davis (1966), Delaney and Cahill (1978) and Foster (1984) have studied eastern subalpine and maritime boreal forest. Bellefleur and Auclair (1972) and Cogbill (1982) studied Quebec boreal forest in both the Great Lakes - St. Lawrence and the true boreal regions of Rowe (1972). Carleton and Maycock (1978, 1980, 1981) and Carleton (1982a, b) have investigated the boreal forest south of James Bay. The boreal forest of Manitoba, Saskatchewan and Alberta has been studied by Moss (1953), Ritchie (1956), Mueller-Dombois (1964), Groenewoud (1965), Swan and Dix (1966), Dix and Swan (1971), and Purchase and La Roi (1983). Viereck, et al (1983) and Yarie (1983) studied boreal forest vegetation of interior Alaska. My review will be restricted to upland conditions in the closed boreal forest zone; tundra and open woodlands will not be discussed.

2.1.1. Fire and Succession

Fire has a large influence on the structure of the boreal forest (Lutz, 1960; Rowe, 1961; Kayll, 1968; Rowe and Scotter, 1973; Day and Woods, 1977; Woods and Day, 1977a;b;c; Larsen, 1980; Carleton and Maycock, 1980; Alexander and Euler, 1981; Cayford and McRae, 1983; Rowe, 1983). The boreal forest consists of a mosaic of predominantly even-aged stands due to fire history and, to a lesser extent, topographic conditions.

Fire is such an important process that it has been questioned whether succession has any meaning in the boreal forest (Rowe, 1961; Dix and Swan, 1971; Carleton and Maycock, 1978; 1980; Larsen, 1980; Cogbill, 1982). Few stands survive longer than 140 years (Dix and Swan, 1971; Maclean and Bedell, 1955), and the fire rotation is on the order of 60 to 100 years (Woods and Day, 1977c; Cogbill, 1982; Rowe, 1983). The fire interval varies from region to region and varies with topography and soils within a region (Rowe, 1983; Foster, 1983). Foster (1983) calculated a fire rotation of 500 years for southeastern Labrador, an area with slow forest growth and with a cool wet climate. Within this area, lichen woodlands and birch forests had a fire rotation of less than 100 years.

The classical concept of the climax (Clements, 1936) is untenable for the boreal forest, if not elsewhere (Drury and Nisbet, 1973; Horn, 1974). All boreal tree species except balsam fir (*Abies balsamea*) are well adapted to regenerate after fire (Rowe, 1961). Balsam fir is the only upland boreal tree species able to reproduce successfully under its own canopy (Rowe, 1961; Dix and Swan, 1971; Carleton and Maycock, 1978; 1980) and typically it requires a disturbance by spruce budworm or blow-down to reach the canopy (Sprugel, 1976). Apparently balsam fir is more tolerant in its seedling stage than sapling or tree stage (Maycock and Curtis, 1960). The concept of the climax as a pattern of various-aged stands across the landscape (Whittaker, 1953) could be applied to the boreal forest. However, this pattern is a result of fire regimes and not an intrinsic property of the vegetation.

Individual boreal forest stands change through time due to differing growth rates and longevity of the component species. It is pointless to argue whether one should call this succession or stand development (Wierman and Oliver, 1979; Oliver, 1978; 1981; Bicknell, 1982). There is only a difference of scale.

Carleton and Maycock (1980; 1981) and Maycock and Curtis (1960) found that boreal species do not form tight communities. Carleton and Maycock could find no discrete clusters when they tried to classify understorey communities. Overstorey and understorey species appeared together primarily due to similar site requirements. Many herb species seemed indifferent to changes in the canopy. Understorey species tend to resprout after a fire which leads to a greater uniformity than the overstorey which may change after a fire. Some overstories were associated with a greater understorey species richness. This occurred on sites with an import of water and nutrients from lateral seepage. The species richness was greater because of a more favorable site and perhaps an increase in the range of microsites which would increase the number of available niches. Carleton and Maycock's (1980; 1981) evidence tends to support the individualistic nature of plant communities (Gleason, 1926).

Attempts to classify upland boreal forests have delineated a few broad groups and a few extremely local associations (Moss, 1953; Ritchie, 1956; Groenewoud, 1965, among others). Associations that exist only in one locality are merely a curiosity. Groenewoud's (1965) classification of white spruce communities derived two very specific associations which only occurred on gley-soils near lakes and one very general catch-all white spruce association. The gley-soils communities were identified by the presence of <u>Equisetum arvense</u> or <u>Equisetum pratense</u> The general type was characterized by feather moss and various amounts of herbs. Groenewoud's results are typical. Other investigators merely studied more of the landscape and described more associations. Such studies apply some phytosociological methods, but the derived units do not have a true ecological basis. The studies are more mensurational than ecological. Swan and Dix (1966) stated that although the primarily monodominant stands they encountered could probably be readily classified, such a classification would not be based on any real distinct differences. The classification would be based on artifacts of stochastic processes on species distribution and would not represent the results of competition or a strict plant-environment response.

2.1.2. Soils and Environment

Soils and environment also influence the structure of individual boreal forest stands. Jack pine (Pinus banksiana) predominates on fresh to dry sandy soils (Moss, 1953; Mueller-Dombois, 1964; Swan and Dix, 1966; Carleton and Maycock, 1980; Purchase and La Roi, 1983; Cayford and McRae, 1983), although Ritchie (1956) found jack pine predominating on clays after fire. Ritchie's study area was near the northern limit of closed boreal forest and only black spruce (Picea mariana) and jack pine were abundant. On shallow ground moraine black spruce and jack pine dominate (Maclean, 1960; McClain, 1981; Pierpoint, 1981; Jeglum, 1982). The finer upland soils will be forested by a mixedwood composed of Aspen (Populus tremuloides), paper birch (Betula papyrifera), balsam fir, the spruces and jack pine with the various components determined by age, soils, climate and stochastic events (Moss, 1953; Maclean, 1960; Mueller-Dombois, 1964; Swan and Dix, 1966; Carleton and Maycock, 1978; 1980; Day and Harvey, 1981; McClain, 1981; Pierpoint, 1981). La Roi (1967) and La Roi and Stringer (1976) found two discontinuities in spruce communities across Canada. One discontinuity was south of James Bay. Balsam fir was greatest to the east and gradually became less important to the west. Aspen and white spruce (Picea glauca), were most abundant to the west and less important to the east. Another discontinuity was located near Lake Winnipeg. To the west of Lake Winnipeg balsam fir was negligible and aspen was also less important. White spruce was of much higher importance to the west of Lake Winnipeg. Understorey species had similar geographic distributions. These differences are controlled by climate (La Roi, 1967; Larsen, 1980); precipitation decreases from east to west.

Bellefleur and Auclair (1972) used principal components analysis to help explain the variation in the Quebec boreal forest. They found that biotic (tree species) and abiotic (site and climate) variables were strongly correlated and they stated that abiotic variables gave a better indication of the patterns of variability than the tree species themselves in distinguishing major ecological relations. However, their study was a biased test of the hypothesis. They used forest inventory data from a large part of Quebec. Some of their data were from the Great Lakes - St. Lawrence region (Rowe, 1972) and some were from the boreal region. Since climate varies greatly over their study area, climate should, and does, have a large effect. One of their main findings was simply that lowlands are different than uplands. Given this simple dichotomy of uplands and lowlands, site characteristics should have a large effect. The only vegetation data they used were presence or absence of tree species. No understorey species were considered and no quantitative values for tree species were used - only presence or absence. Boreal tree species are known to have wide environmental tolerances (Farmer, Knowles and Parker, 1983) so mere presence or absence of a species has little or no ecological value. For example, aspen, birch, balsam fir, black spruce and jack pine may all be present in stands varying from dry outwash sands to moist, loess-covered moraines. Quantitative values for these tree species would give considerable information pertaining to the characteristics of a stand. Since any tree species may be present in almost any stand, presence-absence data gives little information. Furthermore, their environmental variables tended to be mutually exclusive while their vegetation data were not; only one type of soil could be present in a stand, but several species could be present. Expectedly, Bellefleur and Auclair (1972) found that their vegetation data did not explain the variation as well as their environmental data.

2.2 APPLICATION OF ECOSYSTEM STUDY TO FORESTRY

Forest stands vary due to soils, physiography, climate and species presence, abundance and growth characteristics. There must be some basis for dealing with this variation to determine appropriate management decisions. Since these factors comprise an ecosystem, it seems logical to base management on the characteristics of the ecosystem (Nelson, Harris and Hamilton, 1978). Either the entire ecosystem or some part of the ecosystem may be considered (Barnes, 1983). Although only one part of the ecosystem may be used, it is hoped that the one factor will adequately describe ecosystems. Different factors may perform better or worse in different areas. A single factor will not work well when the factor varies little in the study area, or when the factor has no consistent relationship with other components of the ecosystem. Methods must be judged empirically; one method should not be universally applied merely because it was successful somewhere else. Often the plant community is considered in isolation of the other components. I have attempted to use plant communities in this manner. Therefore, I mainly discuss the use of plant communities rather than the entire ecosystem. Hills' (1952; 1960; 1961) system in Ontario and the British Columbia system (Klinka, et al., 1980a; b; Klinka, Feller and Lowe, 1981) have both claimed to be holistic. However, Hills' system is primarily based on physiography and soils, after an initial stratification by climate, and the British

Columbia system is based on vegetation after an initial stratification by climate.

Classification systems can be formulated at a broad, policy and regional planning level or at a specific land management level (Frayer, Davis and Risser, 1978). The scale used to look at the landscape is tied into the purposes of the classification (Rowe, 1971). I will concentrate on the scale suitable for individual silvicultural and forest management decisions - the forest stand. Some studies use a scale larger or smaller than a stand. If the scale deviates in either direction the classification has less utility for forestry (Nelson, Harris and Hamilton, 1978). Management decisions may be derived for one specific purpose (such as site quality or wildlife habitat) or for many diverse considerations.

2.2.1. The Classification Procedure

The classification procedure attempts to formulate a model of the landscape. This model must be descriptive and predictive. The classification units must be recognizable in the field and the units must have characteristic responses which give them some utility other than as a curiosity. The proper application of ecosystem study to forestry requires three steps. Many studies do not satisfy one or more of these steps.

1) Identification of Objectives

A classification of any kind is subjective and it is imperative that the investigator designs his study to satisfy specific goals (Rowe, 1971; 1980; Barnes, 1983). One must not classify and then try to find some use for the classification. The goals must be incorporated into each subsequent step. Classification must be viewed as a means rather than an end point (Nelson, Harris and Hamilton, 1978). One should not classify for the sake of classification.

2) Development of a Scheme to Delineate Useful Units.

There are two general ways that a classification scheme can be set up. One common method is the subjective delineation of community types (or associations, forest types, habitat types, ecosystem types, etc.) based on what the investigator thinks is important, field sampling and some subjective, largely non-quantitative data manipulation, and previous studies of the area's vegetation (Cajander, 1926; Heimburger, 1934; Spilsbury and Smith, 1947; Loucks, 1962; Mueller-Dombois, 1964; Losee, 1965; Daubenmire and Daubenmire, 1968; Franklin and Dyrness, 1973; Pfister, et al., 1977; Coffman, Alynak and Resovsky, 1980; Klinka, et al., 1980a; b; Klinka, Feller and Lowe, 1981; Steele, et al., 1981; Barnes, et al., 1982; Corns, 1983; *inter alia*). Although it is subjective, the classification scheme can work successfully if the objectives are considered when devising the methodology. There is a large risk of bias if the methodology is subjective. If sampling is only done in stands which the investigator feels are typical of a preconceived type, then the classification is based on circular reasoning. Abrupt differences among habitat types will appear in the mind of the investigator, but not in the real world. Such a classification is largely esoteric.

A second method is to use multivariate techniques to obtain a classification (Jeglum, et al., 1982; Jones, et al., 1983; Yarie, 1983). The study of plant communities is greatly facilitated through the use of quantitative phytosociological techniques (Whittaker, 1962; 1978a; Mueller-Dombois and Ellenberg, 1974; Havel, 1980a; Gauch, 1982). However, they have not been used extensively for applied forest research in North America (Havel, 1980a; b). The information derived from these techniques may not be greatly different from that derived from more subjective methods, but it will be less dependent on the investigator's knowledge and inherent biases. Multivariate methods simply speed the process of analysis. They are not a panacea. Subjective decisions must still be made. Whittaker (1960) states, "Quantitative techniques can, when ineptly or mechanically used, obscure important ecological relations." The studies cited above, which used multivariate techniques, are strong evidence supporting Whittaker's warning. These elegant techniques can seduce one to believe that a classification, by itself, is a suitable objective.

3) <u>Validation of the Model</u>

Once a method is developed to delineate units it must be shown that the units have some predictive value (Daubenmire, 1976; Frayer, Davis and Risser, 1978; Nelson, Harris and Hamilton, 1978). The model is valid if it satisfies the objectives of the study and is of use to forest management. There should be a predictable relationship of the vegetation types with soil, topography or climate (Daubenmire, 1976). Specific rates or patterns of tree growth should be related to the units. The units should have some unique characteristics which determine the suitability for various silvicultural practices (Nelson, Harris and Hamilton, 1978). Ideally, the validation should be based on an independent data set.

If the model does not prove valid, then a modification of the objectives or methods is indicated. Perhaps the objectives were unreasonable or the methods ill-suited to attain them. If vegetation types alone poorly predict responses to management alternatives, then soils, landform or climate should be incorporated. The process must be iterative. Methods must be revised until objectives are attained or abandoned. It is important that the end product result from a test of different models rather than be an example of blind faith in some particular method.

Validation is seldom performed as an integral part of the classification process. More often the classification is developed, then validation degenerates into a search for some meaning or use for the classification. The classification may be merely a botanical exercise rather than a useful model if it does not have a sound basis.

Coffman and his coworkers (Coffman and Hall, 1976; Coffman and Willis, 1977; Coffman, Alynak and Resovsky, 1980; Kotar and Coffman, 1982; 1984) have tried to validate their habitat classification system after it was constructed. They found their habitat types to be strongly related to yield, soils, and landforms. This validates their classification. The classification has meaning. Whether or not the classification is a better predictor than other models remains to be determined.

An example of an invalid classification is shown in Figure 2.2.1.1., from Jeglum, et al., (1982). In this case, validity is based on whether a unit has a predictable relationship with appropriate management. Each point represents a vegetation type which they identified using the TWINSPAN computer program (Hill, 1979b). The lines represent 'operational groups' which were subjectively delineated on the basis of vegetation types and soil properties. The authors purport that the operational groups describe and delineate variability which is useful for forest management purposes. Most vegetation types are on the border of an operational group; they appear in two

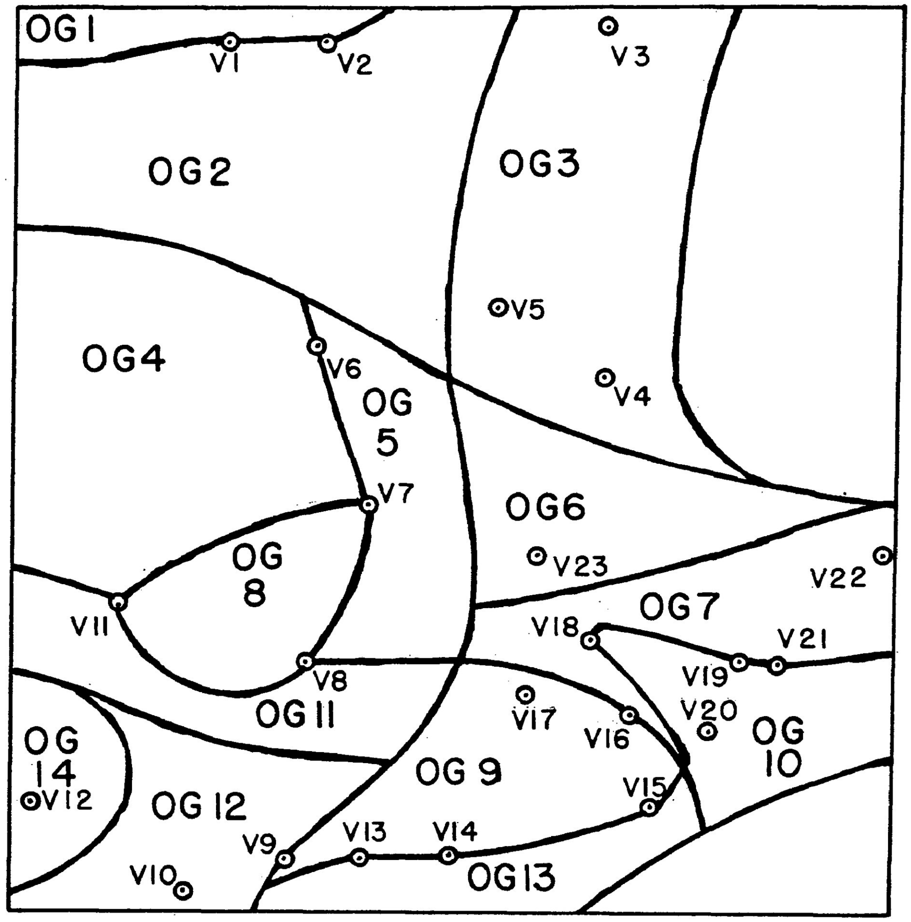


Figure 2.2.1.1. Ordination of vegetational types (V1, V2, V3, etc.) and outline of operational groups (OG1, OG2, OG3, etc.) of the Claybelt Forest Ecosystem Classification (from Jeglum, et al., 1982). Points indicate vegetational types and operational groups are delineated by the lines.

or more operational groups. If the operational groups comprise units useful for determining management practices, then the vegetational types do not. Several vegetation types appear in two or three operational groups. This does not mean that two or three different management regimes are suitable for a given vegetation type. It means that the vegetation types alone cannot be used to determine management. This is why the authors revised vegetation types into operational groups. The vegetation types were not adequate predictors of appropriate management; the vegetation types were invalid. The authors may have been wise to discard or revise the vegetation types before subjectively determining operational groups. As the classification stands, the original TWINSPAN vegetation classification is the prime determinant for allocating stands to operational groups.

2.2.2. What Do You Get and Is It Good Enough?

The result of a classification is the delineation of a number of units. The units may be named community types, habitat types, ecosystem types, operational groups, et cetera. These units can be identified in the field or by remote sensing (Nelson, Harris and Hamilton, 1978). The vegetation component of the unit may be ground flora (Cajander, 1926; Heimburger, 1934; Linteau, 1953; 1955;

Westveld, 1954), present vegetation (Barnes, et al., 1982; Jeglum, et al., 1982; Corns, 1983), or hypothetical climax vegetation (Daubenmire and Daubenmire, 1968; Franklin and Dyrness, 1973; Pfister, et al., 1977; Coffman, Alynak and Resovsky, 1980; Klinka, et al., 1980a). The concept of climax in the boreal forest has already been questioned. The use of hypothetical climax vegetation is pointless since climax vegetation seldom if ever occurs in the boreal forest.

These units may be single or multi-purpose. Most investigators hope that their classification will find general application for several uses. Barnes (1983) lists the types of useable information that can be derived from ecosystem classification. If nothing else, a classification allows stratification of the landscape. It is hoped that these units have more utility than simply allowing impressive multi-color maps to be made (Moon, 1984). Nelson, Harris and Hamilton (1978) warn, "With our attention focused on convenience and orderliness achieved through classification, we sometimes fail to check its validity in the application at hand."

Franklin and Dyrness (1973) succeeded in dividing Oregon and Washington, a large, very heterogeneous area, into less than 350 habitat types. Ponderosa pine (Pinus ponderosa Laws.) commonly occurred in about one-fifth of these habitat types. Yarie (1983) divided 365 forest inventory plots from a 36,000 sq. km area of Alaska into

54 different forest communities. Barnes, et al. (1982) divided a 6,950 ha experimental forest in Upper Michigan into 21 different site units. Corns (1983) found 16 community types in a 17,500 sq. km area in Alberta which crossed four of Rowe's (1972) forest regions. Some of Corns' community types differed only in age. The forest ecosystem classification in the clay belt of Ontario (Jeglum, et al., 1982; Jones, et al., 1983) identified 14 operational groups although the investigators have lamented that this went against their previous biases of "splitting" rather than "lumping" (Jones, et al., 1983).

How many classes must be delineated to adequately represent the study area? Apparently there are differences of opinion in addition to differences in heterogeneity of study areas. The problem arises from the classification process itself. Communities are not discrete entities. There is continuous variation across gradients of moisture, nutrient availability, topography, succession and natural or man-made disturbances (Curtis and McIntosh, 1951; Whittaker, 1956; 1960; Bray and Curtis, 1957). Classification of communities is arbitrary and does not adequately represent the variability of the real world (Nelson, Harris and Hamilton, 1978). Classification of plant communities is not an accurate model. A straight-line regression can be fit to the sigmoid growth pattern of a tree. It will give some general information concerning the growth of the tree, but the model will not be precise enough for most uses. A plant community classification may likewise not be precise enough.

A forest manager needs some tool to delineate units which require different treatment (Nelson, Harris and Hamilton, 1978). If communities, per se, should not be classified, then something else must be used. Landforms or soil, used alone or in combination with vegetation may produce more discrete and meaningful units.

Landforms are one basis for delineating units. Landforms are stable and they obviously have characteristics important to forest management (Rowe, 1971). Landforms alone will not give enough information for management purposes, but they are a good start (Rowe, 1962; Leak, 1978; 1980). In Section 4.4., I have used landforms as the primary criterion for delineating units. Formal soil surveys could also be used. Soil surveys tend to be retrospective; soils are mapped and then the mapping units are interpreted for specific purposes. Most soil surveys perform poorly for forestry applications (Grigal, 1984). Soil surveys do have potential; however, the interpretation portion of the survey must be based on considerable data. Ideally, the interpretation should be included into a feedback loop which refines the mapping process. FLaPS (Gehrels, 1982), the productivity based soil survey carried out in the Northeastern Region of the Ontario Ministry of Natural Resources, shows potential to overcome most of the shortcomings of other soil surveys.

Historically, FLaPS didn't originate as a soil survey _per se_.

Although plant communities should not be classified, individual plant species are much more discrete and may be classified into, say, moisture preference classes or continuous moisture preference values. The presence and abundance of species can provide additional information. Mere species presence and abundance determines potential competitors. Furthermore, overstorey and understorey species respond to environmental factors important to silviculture. These responses can be detected and used to refine stand description and delineation. This use of individual species follows Rowe (1956). Silvicultural practices are determined by the silvics of the individual species. A knowledge of the species' silvics and of the physical site largely determines appropriate silviculture.

2.2.2. Community Classifications Near Study Area.

Maclean (1960) distinguished nine different mixed-wood communties in section B.9, B.8 and B.4 of Rowe (1972). They were based solely on dominant understorey vegetation. These community types were not related to forest management.

Mueller-Dombois (1964) classified the forest habitat types in southeast Manitoba and derived applications for forest management. The 14 habitat types were based on landform and vegetation. Jack pine communities were present on upland sands; mixedwood communities occurred on fresh to moist till, alluvium or beach deposits and black spruce communities dominated the lowlands. Mueller-Dombois attempted to ensure that the habitat types were significant for management purposes. Although he used subjective methods to classify his stands, he seems to have succeeded fairly well. He identified relative productivity, considered choice of species for regeneration and the difficulty of regeneration for the different habitat types. He also discussed improvement of habitats through silvicultural practices and mentioned engineering aspects of the habitat types. A field key and air-photo key were developed (Mueller-Dombois, 1965) for identifying the habitat types. The habitat types have been put to practical use, at least in research (Cayford, 1966).

Losee (1965) developed a preliminary classification of an experimental forest in the southeastern portion of my study area. Braun-Blanquet (1932) methodology was used to distinguish eight site types. Average site indices and common understorey species were listed. The modal descriptions probably do not represent the true variability of these site types. They have not been applied to management.

3. MATERIALS AND METHODS

3.1 STUDY AREA

The locations of the sixty sampled stands are given in Figure 3.1.1. Most stands are in the Upper English River (B.11) section of Rowe (1972). A few stands are near the border of the B.11 and the adjacent Superior (B.9) section.

3.1.1. Surficial Geology

The surficial geology is described by Zoltai (1965). The area is dominated by the Dog Lake, Hartmann and Lac Seul end moraines and the Kaiashk interlobate moraine and the outwash plains associated with these moraines. There is a large area covered by loess which has no counterpart in the surveyed portions of northern Ontario. This loess is relatively shallow, generally 10 to 60 cm. It appears on top of moraines and outwash. Ground moraine dominates the northern portion of the study area and is also present in the south covered by varying thicknesses of loess. There are no extensive lacustrine deposits in the area. Glacial Lake Agassiz covered the northwestern portion of the study area, but its main effect was in washing the ground moraine. Only isolated deposits of lacustrine clay

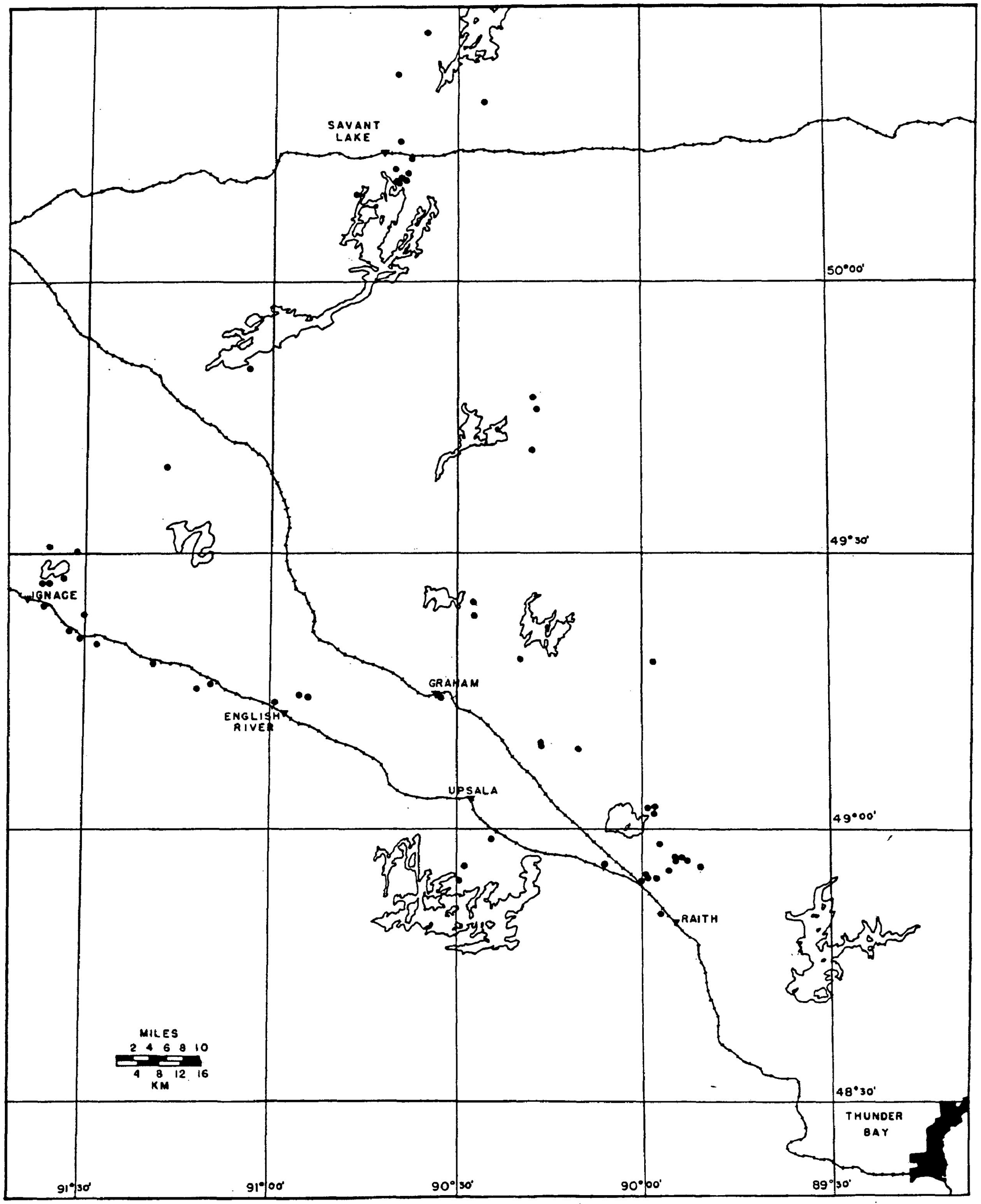


Figure 3.1.1. Location of sampled stands.

or sand are present in the area.

3.1.2. Climate

The study area lies within site region 3W of Hills (1960). This is described as being driest of the humid sections of Ontario. Chapman and Thomas (1968) have named the area the "Height of Land Climatic Region". They state that the region has greater ranges in daily temperature and a shorter frost-free period than might be expected for its latitude. They also state that precipitation is higher than the more western parts of northwest Ontario. Climatic data are given in Table 3.1.2.1.

3.2. SELECTION OF STANDS

Within the study area, stands were selected which satisfied the following requirements: 1) are upland stands; 2) consist of boreal tree species; 3) are closed crown forests; 4) were regenerated naturally; 5) are greater than 40 years old; 6) are relatively undisturbed; 7) have homogenous tree strata and topography; 8) are greater than 2 ha. Upland stands are defined as occurring on mineral soils, being free of surface water, and excluding alluvial areas. Aspen, jack pine, paper birch,

Table 3.1.2.1. Average weather data for Upsala (9yr) and Ignace (10yr), Ontario.

Station	Jan. Temp.	July Temp.	Ann. Precip.
Upsala	-17.9C	17.4C	754.6mm
Ignace	-19.4C	18.5C	822.7mm

black spruce, white spruce, balsam fir, balsam poplar (Populus balsamifera) and tamarack (Larix laricina) are considered to be boreal species. Balsam poplar and tamarack are both uncommon on uplands. Neither species were encountered in the tree stratum. Several of the sampled jack pine stands had previous surface fires, but this is typical of much of the type (Cayford and McRae, 1983; Carleton, 1982b). Stands which were partially cut were excluded.

Stands were chosen to represent as much of the variability of communities in the study area as possible. They were not chosen randomly. Random sampling tends to be very wasteful because of oversampling common communities and undersampling rare ones (Gauch, 1977; 1982; Whittaker, 1978). Stands were not chosen on the basis of how well they represented some preconceived community type. Rather, an effort was made to sample as many different communities as possible which satisfied the previous requirements.

3.3. SAMPLING METHODS

3.3.1. Vegetation

A 0.1 ha (20X50m) plot was used to sample a stand. Trees (>2.5cm d.b.h.) were tallied by 5cm diameter classes. Each tree was assigned a Kraft's tree crown class (Daniel, Helms and Baker, 1979). Shrubs (>.5m tall, <2.5cm d.b.h.) were counted within a 4m wide transect down the center of the plot. Herb and seedling percent cover was recorded in 25 one sq. m plots laid out at one meter intervals along the center. The number of tree seedlings in each sq.m plot was also determined. Non-vascular species growing on woody detritus or stone were not sampled. All species present in the 0.1 ha sample, but absent in the shrub or herb plots were recorded. This sampling routine is essentially the same as that developed by Robert Whittaker and used by him and his students (Whittaker, 1960; 1978a; Whittaker and Niering, 1965; Peet and Christensen, 1980; Westman and Peet, 1982; and many others). Standardization of sampling methods allows comparisons to be made to work done in other areas (Rice and Westoby, 1983).

The objective of sampling the vegetation is to adequately characterize a stand. A stand could be sampled by a number of plots or points or by one larger plot. Point sampling methods (Bitterlich, 1948; Cottam and

Curtis, 1949; 1956; Grosenbaugh, 1952; Cottam, Curtis and Hale, 1953; Cottam, 1955) have inherent assumptions about the distribution of trees. Since the characteristics of the tree diameter distribution is of interest in this study, point sampling could not be used. A number of randomly distributed plots is the best way to characterize a stand (Grant Cottam, personal communication). This could not be used. It would require: 1) identification of the stands on aerial photographs; 2) an initial survey to determine whether the stand was suitable for sampling; 3) random location of twenty or more plots in the field. It was not possible to sample enough stands in this manner during one field season. Therefore, I chose to sample a stand with one 0.1 ha plot. Mueller-Dombois and Ellenberg (1974) give a recommended sample size of 0.02 to 0.05 ha for forest vegetation. This is based on obtaining adequate representation of species composition. I had to go one step further than species composition. I had to obtain an adequate representation of stand structure. Therefore, I chose the standard 0.1 ha plot of Whittaker (1978b). Since stand structure is so important in determining appropriate silviculture (Day, 1972) it is important that any applied ecological study be based on suitable data, although some studies which purport to be applicable to forest management use plots as small as 0.01 ha (Jeglum, et al., 1982; Jones, et al., 1983).

Nomenclature follows Gleason and Cronquist (1963) for herbs and trees, Soper and Heimburger (1982) for shrubs, Crum, Steere and Anderson (1973) for mosses and Hale and Culberson (1970) for lichens. Individuals of *Actaea rubra*, *Actaea alba* and individuals which could not be definitely identified as belonging to either taxa were found. They were all lumped into *Actaea*, spp. *Salix*, spp. includes one specimen of *Salix pyrifolia* and other unidentified salixes. Poaceae and several other specimens were identified by Claude Garton, curator of the Claude Garton Herbarium, Lakehead University.

3.3.2. Site Characteristics

A soil pit was dug in an undisturbed area near the center of each plot. The pit was dug to the C horizon or bedrock and the profile described (Soil Survey Staff, 1960; 1975). Slope percent, slope position, aspect, topography, geomorphology, drainage and the OMNR soil moisture regime (Belisle, 1980) were recorded. Soil samples were taken for later pH determination. pH was determined with a 1:2 soil:water mixture and a glass electrode pH meter. Additional notes on the stand and site were made.

One to four trees suitable for site index determination (Carmean, 1975), for each species were cored at d.b.h. to determine age. Height was measured for these trees and site index was determined using site index curves (Carmean and Hahn, 1981 for balsam fir and white spruce; Carmean, 1978 for paper birch and aspen; Lenthall, Daniel, Preliminary polymorphic site index curves for jack pine in the Thunder Bay area, unpublished; Grant, 1984 for black spruce). Intermediate and suppressed trees were also cored or sawn at 50 cm to gain insight into the age structure of the stand.

3.4. ANALYTICAL METHODS

The raw data were converted into relative dominance, relative density and relative frequency values. These values were combined into an importance value for each stratum: herb, shrub and tree. Tree stratum importance value is the average of relative dominance and relative density. Shrub stratum importance value is the relative density. Herb stratum importance value is the average of relative dominance and relative frequency. The importance value data were subjected to several multivariate techniques.

Multivariate phytosociological techniques were used to interpret the effect of many factors (every species is a variable) changing simultaneously. Standard statistical analysis of variance cannot be used. Multivariate techniques compress the variability of many dimensions (too many to comprehend) into a few dimensions which express most of the variability and can be more easily interpreted.

One cannot attribute a statistical significance to the outcome of the multivariate techniques I used. The scientific method can be broken into two stages: hypothesis generation and hypothesis testing. This study will generate plausible hypotheses based on the data set. Some of these hypotheses can be tested by other studies. Testing other hypotheses would require replicating the world. In either case the generation of objective, plausible hypotheses obtains useful knowledge about the characteristics of the boreal forest.

The use of several phytosociological methods is better than restricting analyses to one method (Gauch, 1977; 1982; Whittaker and Gauch, 1978). Different methods may reveal different information about the data set (Orloci, 1978a). Revising the data set by eliminating species or stands or transforming the data can also reveal additional information (Peet, 1980). The analysis of phytosociological data requires the development of a strategy to derive as much information from the data set as possible (Gauch, 1982). Many ordinations and classifications were performed. Few of them will be reported since the others show no new information, only recapitulate the information derived from previous attempts. The strategy becomes iterative. One attempt may encourage some refinement of the data set or method. The data set or method can be varied in an almost infinite number of ways. The investigator must try enough different ways until he is satisfied. Two general techniques were used, ordination and classification.

3.4.1. Ordination

Ordination is a procedure in which the stands are placed in one or more dimensions according to their similarity. Stands which are similar will be placed close together while stands which are dissimilar will be far apart. The result of an ordination is a one, two or three (or theoretically many more) dimensional "map" which expresses the variability between stands.

This expression of the variability is used to determine which factors are associated with differences between stands. The method of interpreting these effects is called gradient analysis. In indirect gradient analysis the ordination "map" is formed by using characteristics of the vegetation. Stand characteristics (environmental factors, age, site index, importance values of individual species, etc.) are then superimposed on the ordination.

Three multivariate methods were used to ordinate the stands for indirect gradient analysis:

3.4.1.1. Wisconsin Polar Ordination (Bray and Curtis, 1957, as modified by Beals, 1960; 1965; 1973; and Cottam, Goff and Whittaker, 1978; with suggestions by E.W. Beals, personal communication).

Polar ordination is comparative. Percent similarity (Sorensen, 1948) is used to compare all stands to two endpoint stands. The placement of a stand along an axis is due to its relative similarity to the endpoint stands.

Wisconsin Polar Ordination is not affected by non-normal distribution, outliers, or discontinuities which are frequent in ecological data (Beals, 1973; Whittaker and Gauch, 1978; Cottam, Goff and Whittaker, 1978).

3.4.1.2. Detrended Correspondence Analysis (Hill, 1973; 1974; 1979a; Hill and Gauch, 1980).

Detrended Correspondence Analysis (DECORANA) can handle large data sets, but is affected by outliers and discontinuities in the data set (Hill and Gauch, 1980; Hill 1979a; Gauch, 1982).

Detrended Correspondence Analysis (DECORANA) is an eigenvector technique which is conceptually related to weighted averages (Gauch, 1982). Random scores are assigned to species. Sample scores are the weighted average (by importance value) of species scores. New species scores are derived from weighted averages of sample scores. Iterations continue until the scores stabilize. The final scores are independent of the initially assigned species scores (Hill, 1979a). DECORANA ordinates species and samples simultaneously.

3.4.1.3. <u>Principal Components Analysis</u> (Goodall, 1954; Gauch, 1977; Orloci, 1978a; b).

Given an n-dimensional space where stands are positioned in each dimension by the importance value for an individual species, Principal Components Analysis derives an axis which expresses as much variation as possible while passing through the centroid. This eigenvector technique is somewhat analogous to linear regression. A second axis is constrained to be orthogonal to the first and to account for the maximum remaining variance. Unfortunately, the variability in ecological data is neither linear nor orthogonal.

Principal Components Analysis (PCA) is about the worst method commonly used with vegetation data because of its linear assumption, inability to handle data sets with large beta-diversity or many zero values, and its distortion of coenoclines and coenoplanes (Gauch and Whittaker, 1972; Beals, 1973; Gauch, et al., 1977; Orloci, 1978b). It was used only to compare methods.

3.4.2. Classification

Classification techniques can only show differences among stands. It is much more difficult to explain the reasons for these differences by merely using a classification technique. Gradient analysis is used for that purpose. Classification techniques are only used when one wants to have a purely objective method of classifying stands. However, subjectivity must be used to determine whether the classification means anything in an ecological sense, or whether the classification is merely an artifact of some fluke of the data set. Two classification techniques were used.

3.4.2.1. Cluster Analysis (Mueller-Dombois and Ellenberg, 1974; Spatz and Siegmund, 1973)

Cluster Analysis is a polythetic, agglomerative, hierarchical classification technique. Sorensen's (1948) similarity index was used as a basis for the cluster analysis. Stand pairs of maximum similarity are combined. These stands are averaged to create a new, synthetic stand. This synthetic stand is replaced into the similarity matrix and the two previous stands are deleted. The new similarity index matrix is scanned for the two stands which have the next highest similarity index. These stands are likewise combined. When a synthetic stand is combined with another stand, a weighted average is used to derive a new synthetic stand. For example, if a synthetic stand composed of three individual stands was combined with another individual stand, the synthetic stand would have a weight of three and the individual stand would have a weight of one. The algorithm repeats itself until all stands have been combined. I wrote a FORTRAN program which performs cluster analysis and allows data transformations.

3.4.2.2. Indicator Species Analysis (Hill, Bunce and Shaw, 1975; Hill, 1979b).

Indicator Species Analysis (TWINSPAN) classifies stands and identifies "indicator species". In this context, "indicator species" are species which differentiate stand groups without necessarily indicating anything about the productivity, nutrient or moisture regimes of the stand. The product of this classification is a usable, dichotomous key to communities using indicator species.

TWINSPAN: 1) ordinates the stands by reciprocal averaging; 2) identifies species associated with both ends of the axis; 3) refines the ordination by using differential species; 4) makes a dichotomy; 5) identifies indicator species and 6) determines whether the indicator species give the same dichotomy as the differential species

(Hill, 1979b). This multivariate technique resembles a Braun-Blanquet (1932) hand arranged matrix.

4. RESULTS AND DISCUSSION

General summary information about each of the sixty sampled stands is shown in Tables 4.1, 4.2, 4.3 and 4.4. The two most important species in each stratum, and their importance value, are listed. Site index of the tree species is shown when site index could be determined. Stand age (d.b.h. age of dominant species), landform type and OMNR moisture regime value is given.

4.1. COMMUNITY COMPOSITION

4.1.1. Community Classification

4.1.1.1. Tree Stratum

A cluster analysis using only tree stratum data is shown in Figure 4.1.1.1.1. Several more or less distinct clusters can be seen. There is a large group dominated by jack pine, another large group dominated by mixedwood

Table 4.1. The importance value and, where applicable, the site index (in brackets) for the two most important species in the tree stratum of each stand. Site index equals meters in height at a base age of fifty. Species are indicated by the following code: Po= _Populus tremuloides_ ; Pj= _Pinus banksiana_ ; Sb= _Picea mariana_ ; Sw= _Picea glauca_ ; Bw= _Betula papyrifera_ ; B= _Abies balsamea_ ; As= _Acer spicatum_ ; Ac= _Alnus viridis_ ssp. _crispa_ ; Pp= _Prunus pennsylvanica._

Stand No.	Species and Importance Values
1	Po 62.9(23.5); As 30.2
2	Pj 75.5(19.0); Sb 19.0(17.5)
3	B 36.2; Po 34.2(23.8)
4	Po 87.9(19.2); As 6.3
5	Sb 49.1; Po 26.3(16.2)
6	Pj 31.3(20.2); As 30.3
7	B 78.6; Sw 7.4
8	Pj 70.8(19.7); Ac 14.7
9	Pj 69.2(20.1); B 11.1
10	Pj 79.3(18.6); Sb 16.6(16.5)
11	Pj 71.3(19.0); B 12.0
12	Pj 52.3(19.0); Sb 40.8
13	Pj 98.2(18.8); Sb 1.8
14	Pj 93.8(18.5); Sb 5.5
15	Po 46.4(19.8); B 34.8
16	B 50.0(16.8); Po 25.0(19.2)
17	Bw 24.8(20.4); As 24.5
18	Po 48.6(20.4); Sb 42.7
19	Pj 83.2(18.1); Po 8.2(18.6)
20	Pj 61.9(18.5); Sb 38.1(16.6)
21	Bw 58.3(16.8); B 36.1
22	Sb 92.1(12.5); Po 7.2(10.7)
23	Po 31.0(19.8); Sw 24.7(15.3)
24	Pj 38.1(20.8); B 23.2
25	Pj 88.8(19.0); Po 4.3(15.6)
26	Po 38.7(17.7); B 36.0
27	Bw 63.1(13.4); Po 11.2(16.8)
28	B 41.0; Sb 25.3(12.5)
29	Pj 99.4(17.6); Pp 0.6
30	Pj 96.1(13.9); Sb 2.9
31	Pj 86.4(17.0); B 5.4
32	B 39.7(14.6); Sb 26.2(17.4)
33	Pj 58.3(17.7); Sb 30.1(15.8)
34	Pj 96.2(18.4); Sb 3.9
35	Pj 61.0(19.4); Po 20.9(13.7)
36	Pj 74.5(21.0); Bw 20.7
37	Po 53.7(18.9); Pj 30.7(19.6)
38	Bw 81.1(16.2); As 11.1

Table 4.1. (continued)

Stand No.	Species and Importance Values
39	Pj 66.5(19.8); B 24.6
40	Pj 93.3(15.3); Sb 6.4
41	Pj 89.1(16.7); Bw 6.4(16.2)
42	B 54.7; Po 26.1(22.9)
43	Pj 55.3(18.3); Sb 35.4(14.0)
44	Sb 52.1(14.0); Pj 33.3(15.5)
45	B 68.8(13.1); Sb 21.6(16.2)
46	Pj 86.8(17.3); Po 5.2(15.9)
47	B 52.0(14.9); Bw 27.1(13.7)
48	Pj 88.7(17.7); Sb 5.8
49	Sb 66.2(13.8); Pj 33.9(15.3)
50	Pj 90.8(17.9); Sb 9.2
51	B 41.8(14.3); Po 38.5(18.0)
52	Pj 95.0(16.4); Sb 4.1
53	Sb 53.5(13.7); Pj 46.3(13.3)
54	Pj 98.3(14.6); Sb 1.7
55	Po 53.9(14.9); Sb 15.6
56	Sb 98.3(10.5); Bw 1.3
57	Po 56.2(18.3); B 26.5
58	Pj 88.4(13.0); Sb 11.6
59	Sb 73.1(16.0); Pj 16.5(17.0)
60	Sb 46.3(16.0); Pj 23.2(17.0)

Table 4.2. The importance values for the two most important species in the shrub stratum of each sampled stand. Abbreviations were formed with the first four letters of the genus and the first four letters of the specific epithet. Abbreviations and full names are listed in the appendix.

Stand No.	Species and Importance Values
1	ACERSPIC 88.2; CORYCORN 10.8
2	LEDUGROE 56.8; SALIBEBB 17.4
3	ACERSPIC 87.2; POPUTREM 12.8
4	CORYCORN 83.7; ACERSPIC 6.0
5	DIERLONI 56.6; CORNSTOL 13.1
6	ACERSPIC 97.4; ABIEBALS 0.7
7	ACERSPIC 89.7; ABIEBALS 6.4
8	LEDUGROE 50.0; ALNUVIRI 15.5
9	DIERLONI 31.8; LEDUGROE 28.1
10	ALNUVIRI 59.1; AMELHUMI 13.8
11	RUBUSTRI 53.5; AMELHUMI 13.7
12	LEDUGROE 71.3; ABIEBALS 8.8
13	VACCMYRT 47.0; LEDUGROE 34.9
14	LEDUGROE 59.6; ROSAACIC 22.8
15	DIERLONI 39.6; CORYCORN 38.5
16	ACERSPIC 88.0; POPUTREM 6.8
17	ACERSPIC 66.5; CORYCORN 22.6
18	LEDUGROE 77.9; SALIBEBB 5.2
19	SALIBEBB 75.1; ALNUVIRI 11.6
20	ALNUVIRI 62.1; LEDUGROE 27.1
21	ACERSPIC 90.2; ABIEBALS 9.8
22	LEDUGROE 52.7; VACCMYRT 25.7
23	ACERSPIC 74.7; CORYCORN 17.7
24	CORYCORN 39.2; ALNUVIRI 27.4
25	DIERLONI 73.8; PRUNPENN 4.8
26	ACERSPIC 83.7; DIERLONI 8.9
27	ACERSPIC 69.7; CORYCORN 28.1
28	ABIEBALS 50.0; ACERSPIC 31.6
29	ALNUVIRI 77.5; VACCMYRT 8.4
30	SALIBEBB 43.1; LEDUGROE 26.5
31	ALNUVIRI 37.4; VACCMYRT 26.1
32	ACERSPIC 62.4; BETUPAPY 22.6
33	SORBDECO 25.7; DIERLONI 22.9
34	LEDUGROE 37.5; SALIBEBB 23.3
35	ALNUVIRI 42.8; CORYCORN 31.5
36	LEDUGROE 59.2; ALNUVIRI 17.0
37	CORYCORN 59.6; POPUTREM 16.4
38	ACERSPIC 74.7; DIERLONI 12.5
39	DIERLONI 50.0; ALNUVIRI 36.4
40	LEDUGROE 46.3; ALNUVIRI 20.9
41	VACCMYRT 60.0; BETUPAPY 21.8

Table 4.2. (continued)

Stand No.	Species and Importance Values
42	ALNUVIRI 63.9; TAXUCANA 15.3
43	PICEMARI 35.7; DIERLONI 14.3
44	ALNUVIRI 38.5; PICEMARI 23.1
45	ALNUVIRI 63.6; ACERSPIC 9.1
46	PICEMARI 41.0; VACCMYRT 17.9
47	ACERSPIC 76.8; BETUPAPY 12.6
48	ALNUVIRI 52.1; VACCMYRT 36.3
49	LEDUGROE 67.2; PICEMARI 27.6
50	LEDUGROE 97.3; SORBDECO 0.5
51	ACERSPIC 96.3; ABIEBALS 3.1
52	VACCMYRT 52.2; ALNUVIRI 21.7
53	PICEMARI 100.0
54	VACCMYRT 80.0; PICEMARI 20.0
55	ALNUVIRI 49.5; DIERLONI 19.5
56	LEDUGROE 98.0; BETUPAPY 2.0
57	ACERSPIC 84.1; CORYCORN 11.2
58	VACCMYRT 42.9; SALIBEBB 33.3
59	BETUPAPY 66.7; POPUTREM 33.3
60	LEDUGROE 53.3; BETUPAPY 26.7

Table 4.3. The importance values for the two most important species in the herb stratum of each sampled stand. Species names have been abbreviated with the first four letters of the genus and the first four letters of the specific epithet. Abbreviations and full names are given in the appendix.

Stand No.	Species and Importance Values
1	ASTEMACR 12.8; MITENUDA 11.6
2	PLEUSCHR 31.2; CORNCANA 6.7
3	MITENUDA 13.5; MAIACANA 12.5
4	CLINBORE 13.6; LYCOOBSC 12.3
5	PLEUSCHR 18.4; ARALNUDI 9.1
6	ASTEMACR 11.1; MAIACANA 9.9
7	RHYTSPP. 27.8; MNIUSPP. 11.4
8	PLEUSCHR 25.6; ARALNUDI 6.6
9	PLEUSCHR 32.9; MAIACANA 8.4
10	PLEUSCHR 25.1; MAIACANA 9.8
11	CORNCANA 17.4; PLEUSCHR 15.4
12	PLEUSCHR 45.7; MAIACANA 8.2
13	PLEUSCHR 38.4; VACCMYRT 8.9
14	PLEUSCHR 42.5; MAIACANA 8.7
15	CLINBORE 10.1; DIERLONI 10.0
16	LYCOOBSC 11.9; ARALNUDI 9.6
17	CLINBORE 11.2; STREROSE 9.2
18	CORNCANA 16.2; MAIACANA 7.8
19	PLEUSCHR 28.8; CORNCANA 9.2
20	PLEUSCHR 30.8; POLYSPP. 10.4
21	ARALNUDI 22.0; ASTEMACR 20.9
22	PLEUSCHR 39.3; PTILCRIS 12.4
23	ASTEMACR 10.5; CORNCANA 10.3
24	ARALNUDI 11.3; PLEUSCHR 11.2
25	PLEUSCHR 32.8; CORNCANA 14.7
26	ARALNUDI 10.2; ASTEMACR 9.7
27	ARALNUDI 11.4; LYCOOBSC 10.2
28	PLEUSCHR 38.0; LYCOOBSC 16.0
29	PLEUSCHR 40.2; MAIACANA 10.6
30	PLEUSCHR 43.4; VACCMYRT 11.8
31	PLEUSCHR 35.0; CORNCANA 10.4
32	PLEUSCHR 22.6; CLINBORE 10.3
33	SPHASPP. 22.6; PLEUSCHR 22.6
34	PLEUSCHR 32.8; LYCOCOMP 12.4
35	PLEUSCHR 25.6; DICRSPP. 10.1
36	PLEUSCHR 30.3; CORNCANA 10.0
37	PTERAQUI 15.9; CLINBORE 13.2
38	CLINBORE 15.3; LYCOOBSC 14.3
39	PLEUSCHR 28.0; DICRSPP. 9.1
40	PLEUSCHR 38.4; CORNCANA 10.1
41	PLEUSCHR 35.8; CORNCANA 7.4

Table 4.3. (continued)

Stand No.	Species and Importance Values
42	ASTEMACR 10.5; PLEUSCHR 10.4
43	PLEUSCHR 35.1; MAIACANA 7.7
44	PLEUSCHR 40.6; DICRSPP. 13.4
45	PLEUSCHR 38.6; DICRSPP. 9.2
46	PLEUSCHR 32.6; DICRSPP. 10.5
47	PLEUSCHR 19.6; CORNCANA 11.2
48	PLEUSCHR 30.8; VACCMYRT 13.1
49	PLEUSCHR 41.4; PTILCRIS 10.8
50	PLEUSCHR 25.8; LEDUGROE 14.7
51	ACERSPIC 22.2; LYCOOBSC 18.4
52	PLEUSCHR 26.7; CLADRANG 14.0
53	PLEUSCHR 52.8; DICRSPP. 18.1
54	PLEUSCHR 37.2; CLADRANG 16.9
55	DIERLONI 11.0; CORNCANA 9.4
56	PLEUSCHR 41.4; CHIOHISP 14.5
57	ASTEMACR 11.0; ACERSPIC 8.6
58	PLEUSCHR 35.7; VACCMYRT 17.9
59	PLEUSCHR 36.0; PTILCRIS 24.4
60	PLEUSCHR 41.6; PTILCRIS 9.4

Table 4.4. Summary of site conditions for each sampled stand. Age was determined at breast height. A code for the OMNR moisture regime (Belisle, 1980) follows: 0=moderately dry; 1=moderately fresh; 2= fresh; 3=very fresh; 4= moderately moist; 5=moist; 6=very moist.

Stand No.	Age	OMNR Moisture Regime	Geomorphology
1	74	5	end moraine + loess
2	58	3	outwash
3	58	6	end moraine + loess
4	65	2	end moraine + loess
5	71	5	end moraine
6	79	6	loess
7	105	6	loess
8	60	1	outwash
9	60	0	kame
10	63	1	outwash
11	69	0	dunes
12	76	5	ground moraine + loess
13	67	1	outwash
14	66	1	outwash
15	69	2	end moraine + loess
16	59	2	ground moraine + loess
17	130	2	end moraine
18	72	6	outwash + loess
19	54	1	outwash
20	52	3	outwash
21	73	6	ground moraine + loess
22	77	2	ground moraine
23	84	3	ground moraine + loess
24	62	3	end moraine + loess
25	65	3	ground moraine
26	85	2	end moraine
27	43	1	end moraine
28	92	2	ground moraine
29	67	1	outwash
30	67	0	end moraine
31	64	0	outwash
32	63	4	end moraine
33	55	5	ground moraine
34	62	2	outwash
35	99	1	end moraine
36	66	1	ground moraine
37	65	1	end moraine
38	57	1	end moraine
39	92	2	outwash
40	59	0	outwash
41	67	0	outwash
42	93	5	lacustrine clay
43	93	1	outwash
44	102	0	ground moraine
45	56	1	ground moraine
46	66	1	outwash
47	74	2	end moraine

Table 4.4. (Continued)

Stand No.	Age	OMNR Moisture Regime	Geomorphology
48	61	0	ground moraine
49	58	4	outwash of esker
50	60	1	esker delta
51	75	2	ground moraine
52	64	1	esker delta
53	60	1	esker delta
54	57	1	esker delta
55	70	3	ground moraine
56	119	0	ground moraine
57	69	3	ground moraine
58	64	1	valley train
59	64	1	ground moraine
60	59	0	ground moraine

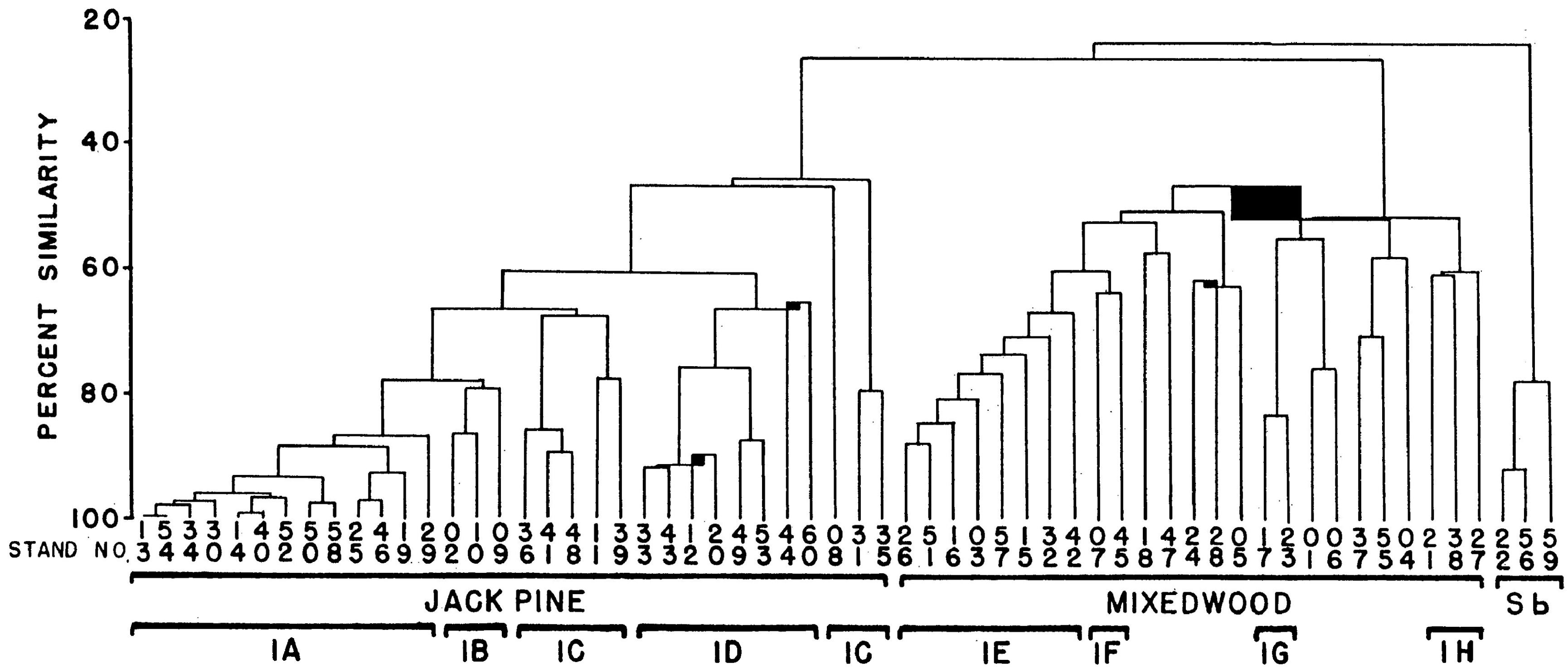


Figure 4.1.1.1.1. Tree stratum cluster analysis. Species present in fewer than four stands were eliminated. Importance values were subjected to a Wisconsin double standardization. Sorensen's (1948) index of similarity was used.

stands and a small, distinct group of black spruce dominated stands. The jack pine group was divided into four, more specific, groups. Table 4.1.1.1.1. shows average importance values for these groups. Stands in group 1A are almost pure jack pine. All group 1B stands have greater than ten percent black spruce. Group 1C stands are dominated by jack pine and have a hardwood or balsam fir component. Group 1D stands are evenly mixed jack pine-black spruce stands.

The mixedwood group didn't have very distinct subgroupings. Table 4.1.1.1.2 shows average importance values for the four subgroups and for the mixedwood stands which don't fit into any group. All group 1E stands have a balsam fir importance value of greater than twenty-five percent and less than fifty-five percent. Both group 1F stands have balsam fir importance values of greater than sixty-five percent. Both group 1G stands have importance values for white spruce of greater than nineteen percent and importance values for balsam fir of less than 7.5 percent. Group 1H stands all have importance values for paper birch exceeding fifty-five percent. Other mixedwood stands are random assemblages of all species. There were no pure stands. Two stands which superficially appeared to be pure aspen had tall shrubs which exceeded 2.5 cm d.b.h. and had scattered paper birch. In this thesis, mixedwood stands are considered to include all stands with a large component of hardwoods, balsam fir or white spruce. Black

Table 4.1.1.1.1. Average importance values for the conifer groups derived from the tree stratum cluster analysis.

Species	Group 1A	1B	1C	1D	Sb
Abies balsamea	.51	5.00	6.32	3.18	-
Betula papyrifera	.20	.23	7.62	3.81	2.58
Picea glauca	.20	1.77	.36	.38	-
Picea mariana	4.77	15.43	2.88	45.29	87.78
Pinus banksiana	92.92	74.65	76.01	45.53	5.92
Populus tremuloides	1.36	2.78	3.27	1.73	3.60
Acer spicatum	-	-	.04	-	-

Table 4.1.1.1.2. Average importance values for mixedwood groups derived from the tree stratum cluster analysis.

Species	Group 1A	1B	1C	1D	Other
Abies balsamea	39.95	73.70	6.15	14.23	13.19
Betula papyrifera	12.45	7.58	17.65	67.45	7.46
Picea glauca	2.30	4.48	21.98	4.90	3.98
Picea mariana	7.62	10.80	.23	.11	14.99
Pinus banksiana	1.11	-	8.56	1.40	12.62
Populus tremuloides	34.96	-	19.58	3.72	39.98
Acer spicatum	1.04	3.30	25.53	7.05	6.69

spruce and jack pine may be present, but they do not dominate the stand. There are no real discrete ecological differences among the mixedwood stands.

The tree strata classification does show several distinct clusters. There is a distinct separation of jack pine from mixedwood stands. There are several distinct subgroupings within the jack pine group. The subgroupings of the mixedwood stands are more arbitrary and indistinct. These results are explained by the dominance of jack pine. Distinct clusters are expected when stands are dominated by one or two species and when there are few species in the data set. Although all species were present in almost all of the groups, the most distinct groups were dominated by one or two species.

4.1.1.2. Shrub Stratum

A cluster analysis of shrub stratum data is shown in Figure 4.1.1.2.1. Several distinct groupings can be seen. Table 4.1.1.2.1. gives average importance values for all shrub stratum species present in 10 or more of the sampled stands. These averages over-exemplify the differences among groups; there is considerable variability within each group for all but the most abundant species. Fairly distinct groups are evident since most stands are dominated by a single species. Group 2A is dominated by *Acer*

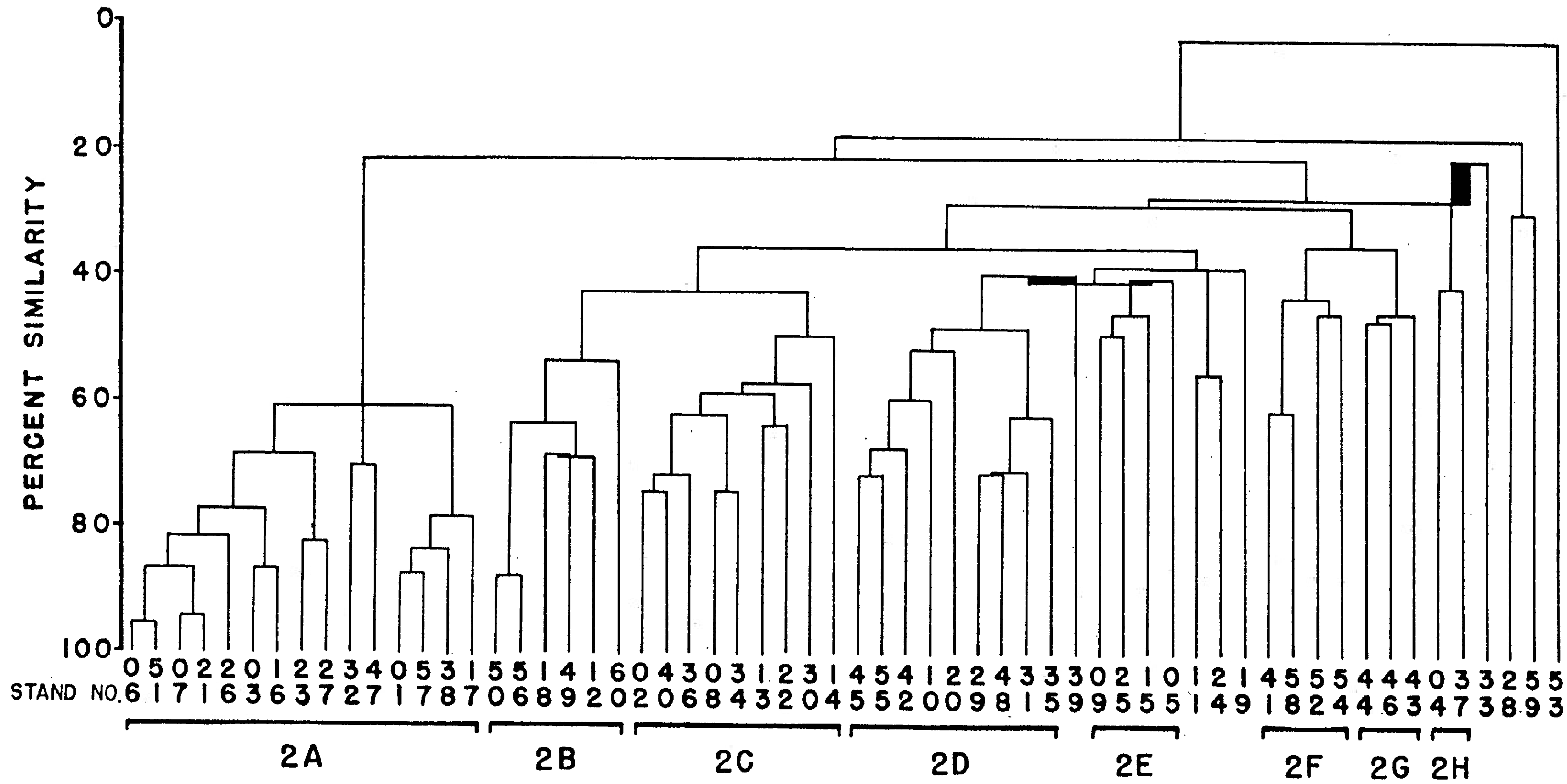


Figure 4.1.1.2.1. Shrub stratum cluster analysis. Species present in three or fewer stands were eliminated. Importance values were subjected to a Wisconsin double standardization. Sorensen's (1948) index of similarity was used.

Table 4.1.1.2.1. Average importance values for groups derived from the shrub stratum cluster analysis.

Species	2A	2B	2C	2D	2E	2F	2G	2H
Acer spicatum	81.97	.22	.20	1.58	-	-	-	3.13
Corylus cornuta	6.68	-	.08	5.86	11.53	-	-	71.65
Abies balsamea	3.56	4.55	.29	1.32	7.28	1.38	8.87	-
Ledum groenlandicum	-	77.50	47.06	4.37	7.03	-	-	-
Salix Bebbiana	-	1.18	11.42	3.91	.40	8.33	1.27	.48
Amelanchier humilis	.03	.06	2.29	3.63	1.73	-	-	3.35
Alnus viridis ssp. *crispa*	.02	-	10.17	56.41	-	5.43	12.83	6.40
Picea mariana	.09	7.03	1.69	.38	1.78	11.25	33.27	-
Vaccinium myrtilloides	-	1.03	15.27	9.16	.13	58.78	9.13	1.60
Rosa acicularis	.03	.42	4.00	.42	4.40	-	-	-
Populus tremuloides	1.56	.58	.07	.39	2.68	1.38	6.00	8.28
Diervilla Lonicera	2.29	1.31	5.84	6.95	50.45	-	9.03	2.10
Prunus pennsylvanica	.02	-	-	1.66	1.98	-	-	.08
Sorbus decora	.19	.09	.11	.34	.60	1.08	2.73	-
Betula papyrifera	2.52	5.23	.29	.21	1.20	10.88	8.90	.65

spicatum; group 2B is dominated by Ledum groenlandicum. Ledum is also the most abundant species in group 2C, but Salix Bebbiana , Alnus viridis ssp. crispa and Vaccinium myrtilloides are also common. Alnus viridis ssp. crispa dominates group 2D; Diervilla Lonicera dominates group 2E; Vaccinium myrtilloides dominates group 2F; Picea mariana is most abundant in group 2G; Corylus cornuta dominates group 2H. Group 2C is obviously intermediate between 2B and 2D.

4.1.1.3. Herb Stratum

Figure 4.1.1.3.1 is a cluster analysis of the herb strata. The groupings are rather obscure. There is a large, general, group dominated by feather moss. Species with high importance and fidelity are: the mosses Pleurozium schreberi, Ptilium crista-castrensis , and Dicranum, spp. and the vascular plants, Ledum groenlandicum, Vaccinium myrtilloides, Vaccinium angustifolium, and Chiogenes hispidula. Within this general group is a more specific group, 3A. Rubus pubescens and Rosa acicularis , in addition to the other species in the feather moss group, are common in group 3A. The surface soils of group 3A are slightly moister than typical of other stands in the feather moss type.

There is also a large mixedwood herb group.

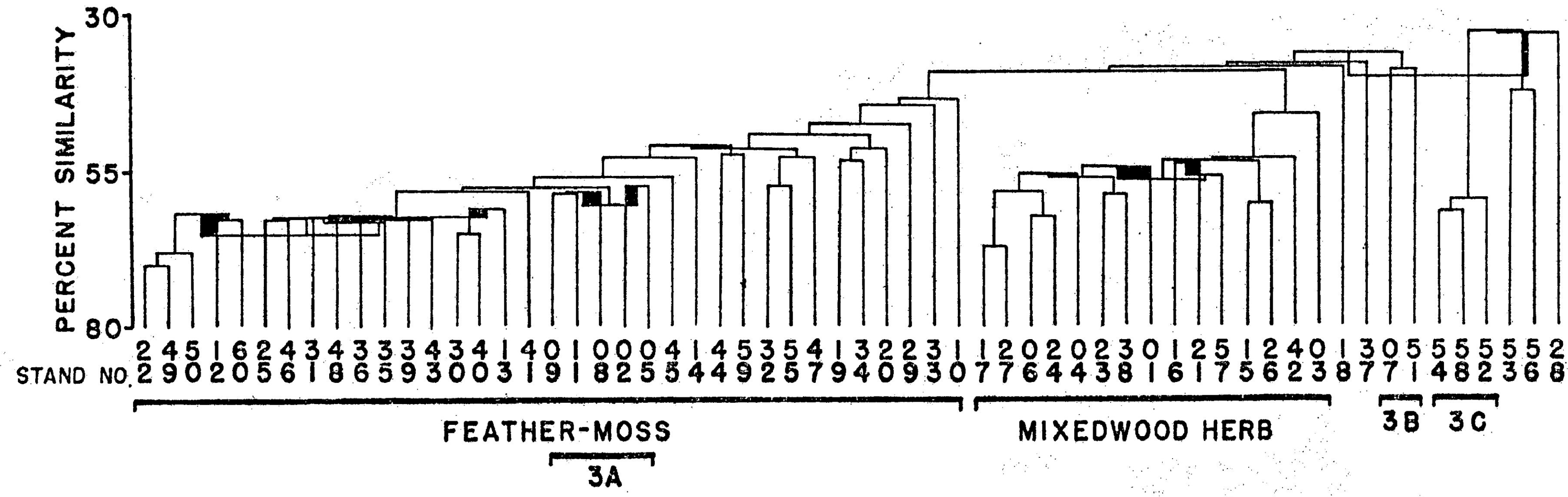


Figure 4.1.1.3.1. Herb stratum cluster analysis. Species present in three or fewer stands were eliminated. Importance values were subjected to a Wisconsin double standardization. Sorensen's (1948) index of similarity was used.

Characteristic species include Streptopus roseus, Mitella nuda, Acer spicatum, Mertensia paniculata, Lycopodium obscurum, Aster macrophyllus, Viola renifolia, Galium triflorum, Rubus pubescens, Abies balsamea, and Osmunda cinnamomea. No meaningful sub-groups could be distinguished within this broad group.

Both stands in group 3B are fairly moist stands with a large balsam fir component in the overstorey. Characteristic species include: the ferns, Athyrium Filix-femina and Gymnocarpium Dryopteris ; the mosses Mnium, spp. and Rhytidiadelphus , spp. ; Abies balsamea seedlings and Carex , spp.

Group 3C is the most distinct group derived from the herb cluster analysis. The most characteristic species are the reindeer mosses Cladina rangiferina and Cladina alpestis. Other common species include Pleurozium schreberi, Dicranum, spp., Vaccinium myrtilloides and Vaccinium angustifolium. While Cladina rangiferina and Cladina alpestris are commonly present in stands with a feather moss ground cover, this group was unique in the high importance values of these reindeer lichens. Cladina alpestris had an importance value of greater than 5.0 for all three stands while not exceeding 0.5 in any other. Cladina rangiferina had importance values of 14.0 or higher in the three stands but was less than 2.2 in all others. Black and Bliss (1978) found these two species to be characteristic of later succession after fire in the

Northwest Territories. They found Cladina mitis to be the reindeer moss which appeared first. Fire scars were only noted in one of the three stands. All three stands had basal areas in excess of 25 sq. m/ha. The reindeer moss seems to be a characteristic of the site rather than a response to a fire-caused opening of the stand. These stands occurred on lake-washed sands from a valley train and from a large delta complex.

The cluster analysis of herb data failed to show distinct groupings. 106 species were used in the analysis. Many of these species have wide environmental tolerances and appear almost everywhere. Cornus canadensis, Maianthemum canadense, Aralia nudicaulis, Linnaea borealis, Coptis trifolia, Trientalis borealis, Diervilla Lonicera, Clintonia borealis and Lycopodium clavatum are most notorious for this behavior. Discrete groups were not found in the cluster analysis because they do not exist in the field.

4.1.1.4. All Strata Combined

Figure 4.1.1.4.1. is the result of a cluster analysis performed on all strata combined. Rare species (present in three or fewer stands) were deleted. There are two main groups, a conifer dominated group and a mixedwood group.

Within the general conifer group there are two

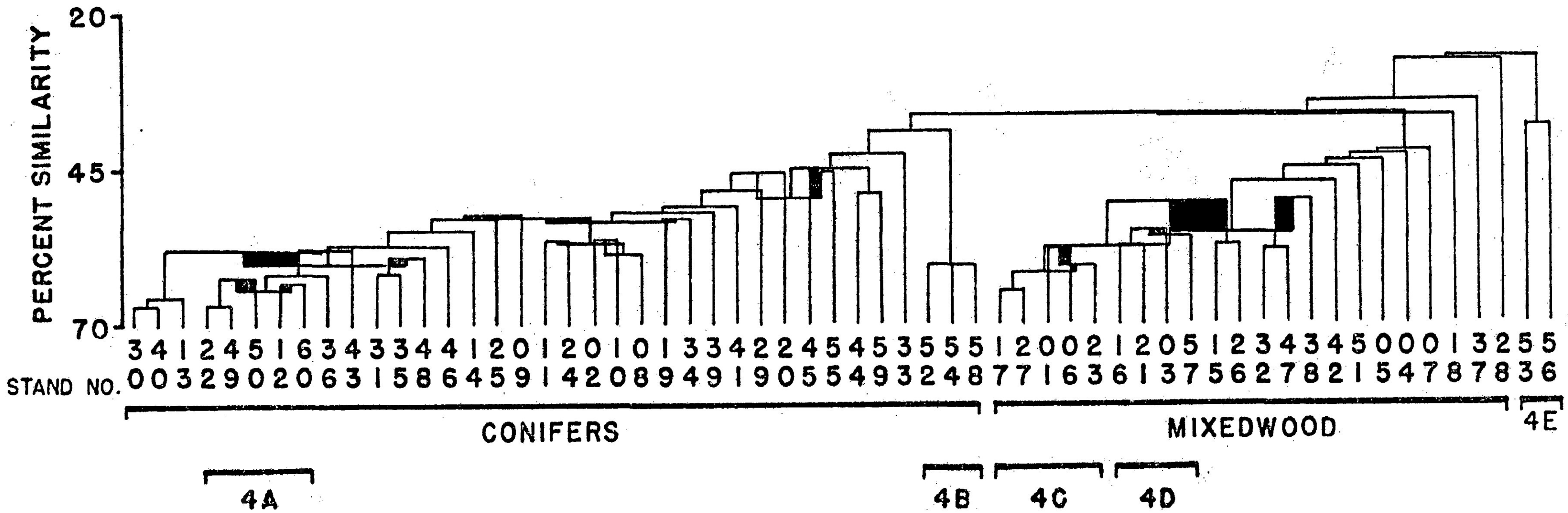


Figure 4.1.1.4.1. Cluster analysis of all strata combined. Species present in three or fewer stands were eliminated. Importance values were subjected to a Wisconsin double standardization. Sorensen's (1948) index of similarity was used.

subgroups. Group 4A is characterized by a large component of black spruce in the canopy, Ledum dominating the shrub layer, and a feather moss dominated herb layer. Group 4B consists of a jack pine dominated overstorey, a Vaccinium myrtilloides dominated shrub layer and a characteristic Cladina dominated herb layer. Group 4E contains two conifer dominated stands which were separated from the main body of coniferous stands. These two stands had dense shade from black spruce in the overstorey which eliminated many of the common understorey species. This made the stands distinct enough to separate them from the other coniferous stands. No other meaningful distinct group could be found within the conifer group. Three stands (24, 45, 55) classified as mixedwood by the tree strata cluster analysis were included in the conifer group in the total data cluster analysis. 45 and 55 had a feather moss dominated herb layer and an Alnus viridis ssp. crispa dominated shrub layer. These herb and shrub strata tend to be associated with conifer stands. Although decidedly mixedwood, stand 24 had a higher importance value for jack pine than any other tree species. Feather mosses were present in the herb layer and alder was present in the shrub layer.

There were two, only slightly more specific, subgroups within the mixedwood group. 4C consisted of mixedwood stands with few balsam fir, while 4D consisted of mixedwood stands which had balsam fir tree strata importance values in excess of twenty-five percent. Although the cluster analysis may show these groups as discrete, the remaining mixedwood stands would fit within or between these two groups.

4.1.1.5. Overstorey-Understorey Combinations

The co-occurance of herb, shrub and tree strata groups derived from the cluster analyses is shown in Table 4.1.1.5.1. Tree X shrub, tree X herb, and shrub X herb combinations are given. Several different shrub groups appear beneath stands belonging to the same tree group. There is high specificity of some shrub groups to certain general overstorey types. The *Acer spicatum* group (2A) and the *Corylus cornuta* group (2H) are confined to mixedwood overstories. The *Ledum groenlandicum* dominated groups (2B, 2C) are associated with coniferous overstories. The almost pure *Ledum* group (2B) is associated with an overstorey with a high black spruce component. The *Vaccinium myrtilloides* group (2F) is associated with a jack pine overstorey. The black spruce group (2G) is associated with coniferous stands with some black spruce in the overstorey. The *Alnus viridis* ssp. *crispa* group (2D) shows some specificity to coniferous stands, but also appears in mixedwood stands. The *Diervilla Lonicera* group (2E) appears beneath both coniferous and mixedwood canopies.

Table 4.1.1.5.1. Co-occurance of tree, shrub and herb groups derived from cluster analyses. The numbers indicate the number of stands, out of 60, in which particular groups of two strata both appear. Example: 6 stands had a tree stratum belonging to group 1E and a shrub stratum belonging to group 2A.

SHRUB STRATUM	TREE STRATUM									
	1A	1B	1C	1D	1E	1F	1G	1H	Sb	other
2A	-	-	-	-	6	1	2	3	-	3
2B	1	-	-	3	-	-	-	-	1	1
2C	5	1	2	-	-	-	-	-	1	-
2D	1	1	3	1	1	1	-	-	-	-
2E	1	1	-	-	1	-	-	-	-	1
2F	3	-	1	-	-	-	-	-	-	-
2G	1	-	-	2	-	-	-	-	-	-
2H	-	-	-	-	-	-	-	-	-	2
other	1	-	2	2	-	-	-	-	1	2

HERB STRATUM	TREE STRATUM									
	1A	1B	1C	1D	1E	1F	1G	1H	Sb	other
Feather-moss	10	1	6	7	1	1	-	-	2	2
3A	-	2	2	-	-	-	-	-	-	1
Mixed herb	-	-	-	-	6	-	2	3	-	4
3B	-	-	-	-	1	1	-	-	-	-
3C	3	-	-	-	-	-	-	-	-	-
other	-	-	-	1	-	-	-	-	1	3

HERB STRATUM	SHRUB STRATUM								
	2A	2B	2C	2D	2E	2F	2G	2H	other
Feather-moss	2	4	7	8	1	1	3	-	4
3A	-	-	2	-	2	-	-	-	1
Mixed herb	11	-	-	1	1	-	-	1	1
3B	2	-	-	-	-	-	-	-	-
3C	-	-	-	-	-	3	-	-	-
other	-	2	-	-	-	-	-	1	2

The tree X herb combinations are even more general. A feather moss dominated herb layer occurs beneath conifer stands and occasionally beneath mixedwood stands with a high coniferous component. The feather moss group with Rubus pubescens and Rosa acicularis (3A) is associated with black spruce in the overstorey. The mixedwood herb group appears solely under mixedwood stands. Group 3B, characterized by ferns and mosses, Carex, spp. and balsam fir seedlings, is found beneath stands with a large proportion of balsam fir in the overstorey. Group 3C is the Cladina , spp. dominated group and is found beneath jack pine stands.

The only strong specificities in shrub X herb combinations are the association between Acer spicatum (2A) and the mixed herb group and the association between Vaccinium myrtilloides (2F) and the Cladina , spp. dominated group (3C).

4.1.1.6. Discussion and Conclusions on Cluster Analyses

The cluster analyses for tree and shrub strata show that these strata can be classified into more or less discrete groups. This is expected when the data set consists of few species or when few species are dominant.

There are problems with even the simple tree stratum data. The jack pine dominated stands were divided into four groups. Three of these groups were based on importance of jack pine and black spruce. One group is predominantly jack pine (1A). Another group has approximately equal importance values for jack pine and black spruce (1D). The third group (1B) is intermediate between group 1A and 1D. These groups form a gradient rather than discrete groups. Black spruce importance values range from 0 to 11.6 in group 1A, from 10.7 to 19.0 in group 1B and from 30.1 to 66.1 in group 1D. The high dominance of one or two species cause these groups to appear distinct although there is no distinct ecological boundary between them.

The mixedwood stands formed no distinct groups. The groups are arbitrarily delineated. The mixedwood stands typically have four or more tree species with importance values all under sixty percent. This heterogeneous mixture defies classification. A cover type classification could adequately describe any given stand at a particular point in time, but this would be based on mensurational rather than ecological principles.

The shrub stratum cluster analysis must also be questioned. While there are more shrub species than tree species, the shrub stratum in any individual stand tends to be dominated by one species. Therefore, fairly distinct clusters were indentified. These clusters may not have much ecological significance. Many of the shrub groups appear under several canopy types and in largely different habitats. One species tends to dominate because of the sprouting ability of the shrub species after a fire. In a 0.1 ha area, one species may gain dominance merely because it had precedence over other species. Among the conifer stands, the amount of _Ledum groenlandicum_ , _Alnus viridis_ ssp. _crispa_, _Vaccinium myrtilloides_ and _Diervilla Lonicera_ is due only in part by environmental tolerances and competition. The shrub species present before the fire largely determine which species will be present after fire. These species can sprout quickly and rapidly reproduce vegetatively or sexually. Dominance may be obtained by mere presence. Carleton and Maycock (1981) have stressed the importance of sprouting by boreal understorey species.

The cluster analyses of the herb stratum and of all strata combined have displayed few discrete groups. Both data sets have many species. Many of these species have wide environmental tolerances which preclude the differentiation of discrete groups. Species of high fidelity are rare or non-existant. The only groups which could confidently be called discrete are two very large, general groups, the conifer dominated and the mixedwood stands, and the more specific jack pine-_Vaccinium myrtilloides_-_Cladina_ stands (2F, 3C and 4B) on deltaic sands or valley trains. Mueller-Dombois (1964) found similar results in southeastern Manitoba. Jack pine dominated on sandy soils and mixedwoods dominated on finer soils. This led Mueller-Dombois to base his habitat type classification on geomorphology rather than strict vegetation types.

4.1.1.7. <u>TWINSPAN Classification</u>

The result of a classification using TWINSPAN is given in Figure 4.1.1.7.1. Fifty species are listed. TWINSPAN selected thirty-six of these species as indicator species. The other fourteen species were chosen based on high fidelity to one of the TWINSPAN groups. A numeric code was used for importance values. A key is given below:

CODE	IMPORTANCE VALUE
1	>0 to 2.0
2	>2 to 5.0
3	>5 to 10.0
4	>10 to 20.0
5	>20.0

Unlike cluster analysis, the length of the lines do not indicate the degree of similarity. TWINSPAN is divisive. It divides the data into smaller and smaller groups until it reaches a user-specified level of division. Each division has an associated eigenvalue which indicates the amount of variation between the two groups. The eigenvalues do indicate certain information about the data set, but are not necessary for general interpretation of

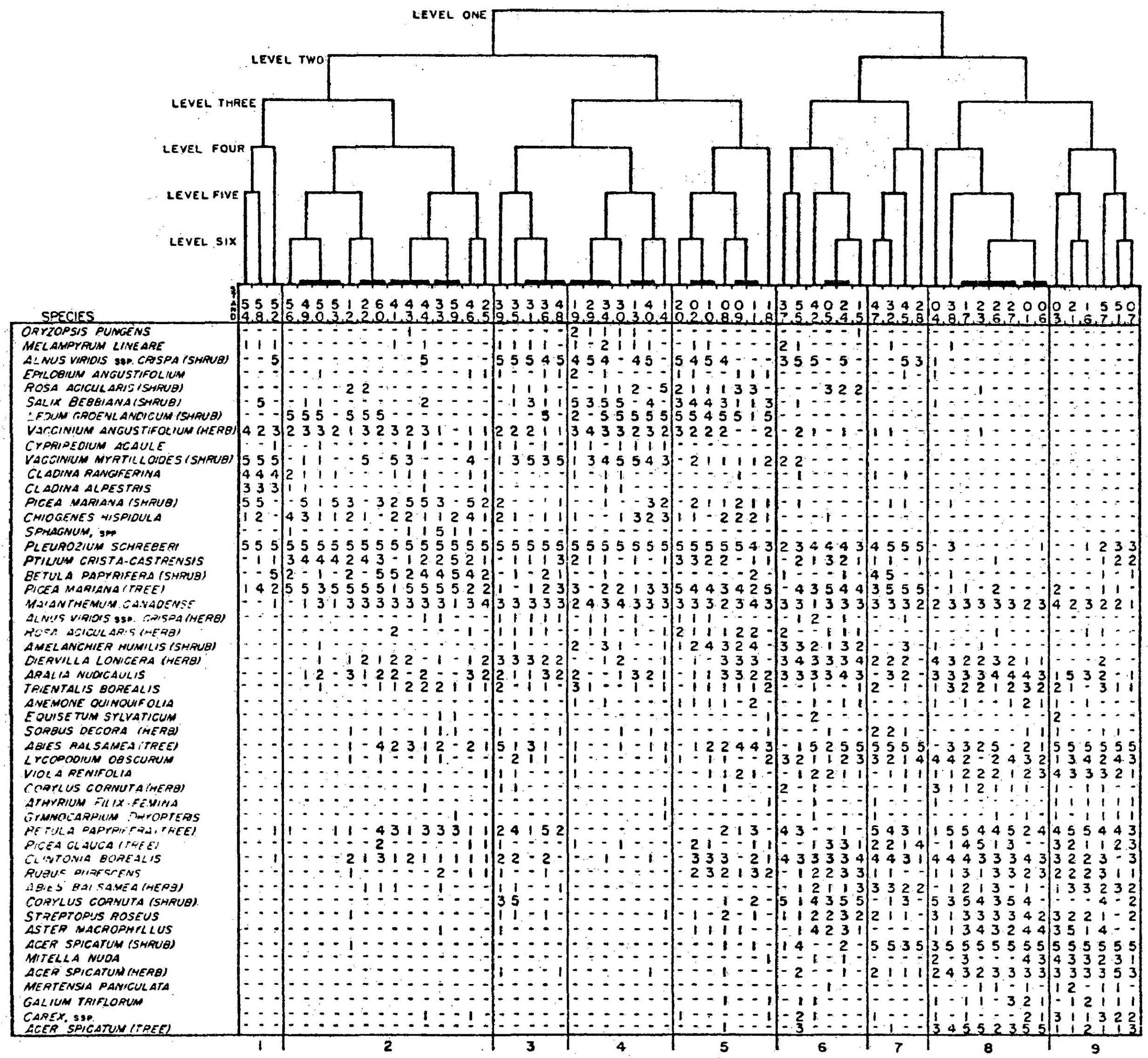


Figure 4.1.1.7.1. TWINSPAN classification. Thirty-six of the listed species were chosen as indicator species by the TWINSPAN classification. The remaining fourteen species were chosen based on fidelity to one of the TWINSPAN derived groups.

the classification.

Nine relatively meaningful groups based on the TWINSPAN hierarchy could be identified. These consist of the results at level three (eight groups) with one of these groups divided at level four to give a total of nine groups.

Group one is the jack pine, Vaccinium myrtilloides, Cladina group identified by the cluster analyses. Group two is a large group of mixed conifer stands dominated by black spruce and jack pine with some hardwoods and balsam fir. Group three consists of jack pine stands with a minor component of balsam fir, paper birch, or both. Group four contains stands which are predominantly jack pine. Stand 19 seems to be misclassified since it has a moderate aspen component. Group five consists of stands dominated by jack pine with a moderate black spruce and balsam fir component. Stand 18 is a misclassified mixedwood stand. Group six contains mixedwood stands with a high proportion of aspen and a small component of jack pine, black spruce, or both. Group seven consists of mixedwood stands with a large balsam component and some black and white spruce. Group eight stands are aspen and birch dominated mixedwoods. Group nine consists of mixedwood stands with a high proportion of balsam fir.

These general groupings are similar to the results of the cluster analyses. Stands which TWINSPAN grouped together are close to each other in the cluster analyses.

TWINSPAN tends to over-exemplify the differences between groups. This is a result of the divisive, hierarchical methodology. Divisions after the first have relatively low eigenvalues. The level one division, which separates conifer dominated stands from mixedwood stands, has an eigenvalue of .416, while the two level two divisions have eigenvalues of .183 and .217. This indicates that the subsequent divisions may not represent very great differences.

TWINSPAN chooses indicator species which are used to allocate stands to one side of a dichotomy or another. This key is used for stands in the data set and can also be used to classify other, independently sampled, stands. The TWINSPAN program identified three stands (5%) as misclassified by the indicator species. Six stands (10%) were classified as borderline. In other words, fifteen percent of the sampled stands may have been assigned to the wrong side of the dichotomy. A greater percentage of an independent data set would be misclassified.

Several of the species identified as indicator species were unfortunate or inaccurate choices. Such ubiquitous species as Maianthemum canadense, Diervilla Lonicera, Aralia nudicaulis, Trientalis borealis, and Clintonia borealis were chosen as indicator species by TWINSPAN. Streptopus roseus was used as an indicator species to separate stand 14 from stands 13 and 40. These stands were dominated by jack pine. Streptopus roseus is common in mixedwood stands but is seldom encountered in pine stands. Such fortuitous occurances do not indicate any characteristic difference between stands.

Classification is predisposed on some actual, discrete differences among groups of stands. Figure 4.1.1.7.1. demonstrates a gradient of change rather than discrete differences. Since only indicator species are included in the figure, the differences appear to be more discrete than they actually are. Nonetheless, the only discrete separation is between mixedwood stands and jack pine - black spruce dominated stands. Again, the jack pine, _Vaccinium myrtilloides_, _Cladina_ group is distinct from all other stands.

4.1.2. Ordinations

Since community change across a gradient is continuous rather than discrete, ordination should reveal additional information about the structure of the data set.

4.1.2.1. Polar Ordinations

Figure 4.1.2.1.1. shows the results of a polar ordination. Species with less than four occurances in the data set were deleted. A Wisconsin double standardization

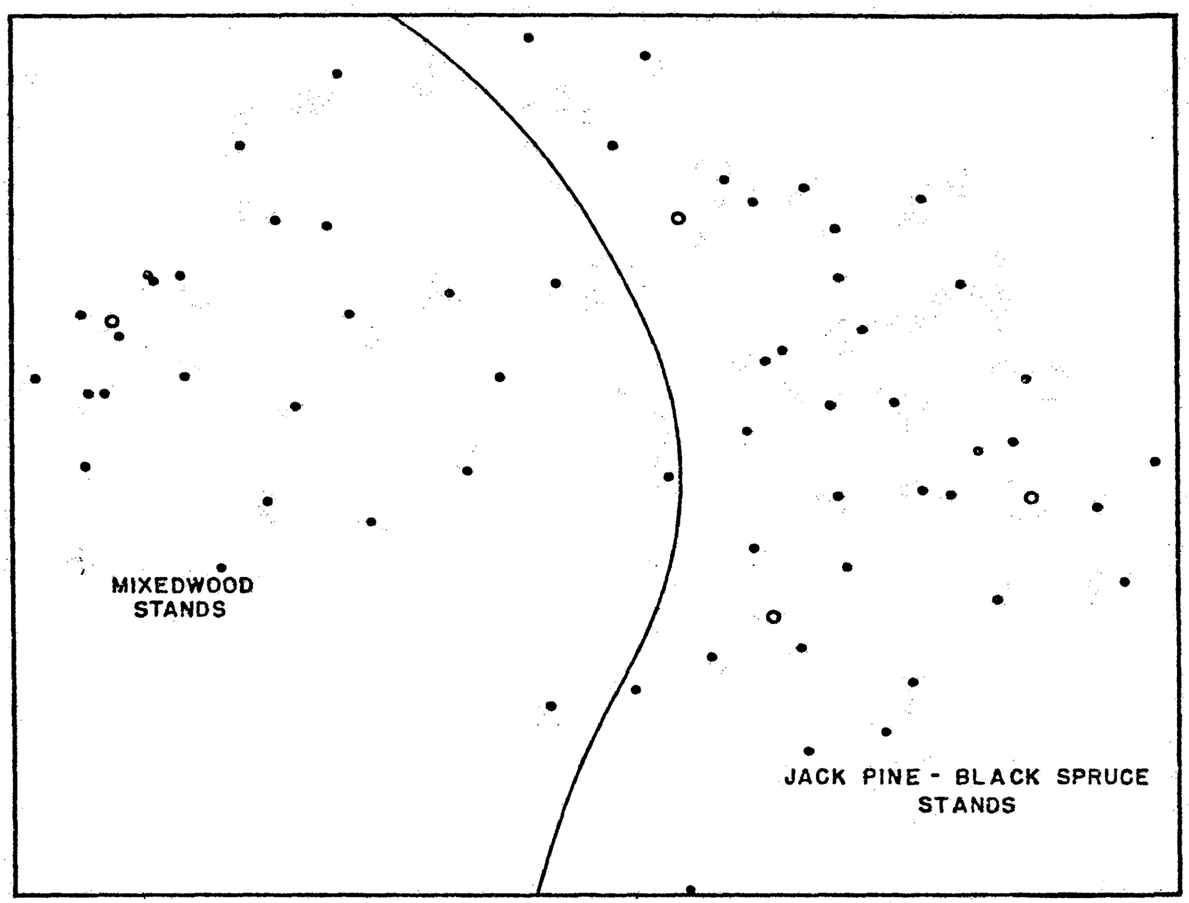


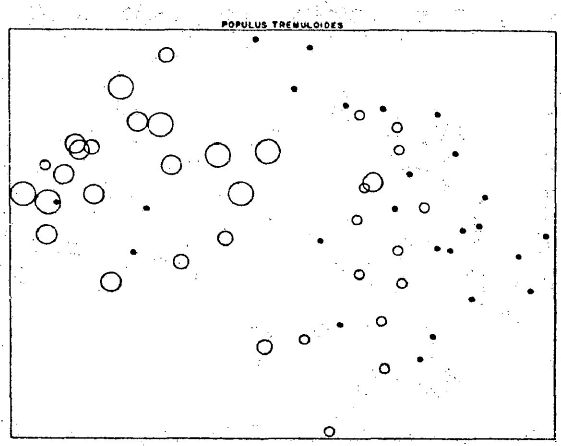
Figure 4.1.2.1.1. Polar ordination of all data. End-points (open circles) are the aggregate of seven stands. Wisconsin double standardization has been applied to the data. An internal association of 85% was used.

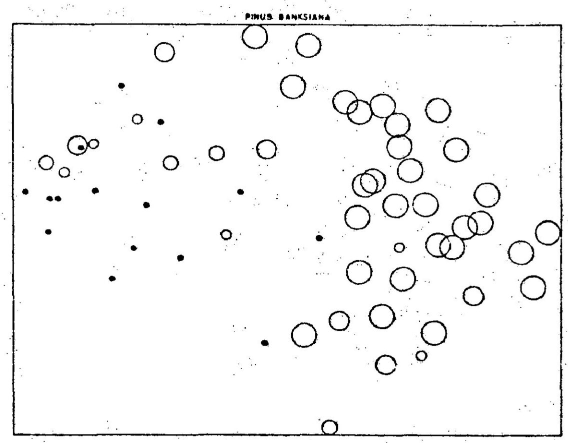
(Bray and Curtis, 1957; Gauch, 1977) was performed on the data set before ordination. An 85% internal association was used to determine index of dissimilarity. The x- and y-axis end points are aggregates of seven stands. The x-axis endpoints are the average of the computer-generated endpoints and the six stands most similar to each of these stands. Preliminary y-axis endpoints were chosen by criteria suggested by Mueller-Dombois and Ellenberg (1974). Both preliminary y-axis endpoints were averaged with six stands which were most similar and which would result in a final aggregate y-axis endpoint whose x-axis location was close to the location of the preliminary y-axis endpoint. The six stands weren't the six most similar to the preliminary y-axis endpoint. The most similar stands were chosen which had an average x-axis score close to that of the preliminary y-axis endpoint. These aggregate endpoints have the quality of being different from one another and being similar to several other stands.

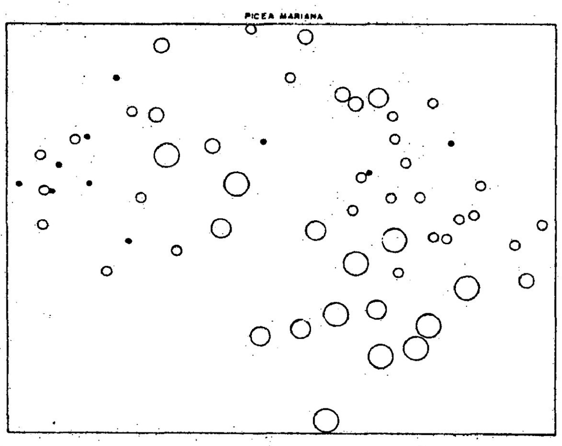
The ordination shows a fairly distinct break between mixedwood stands and jack pine - black spruce stands. The central portion of the ordination field is so sparse that meaningful endpoints for a third axis could not be found.

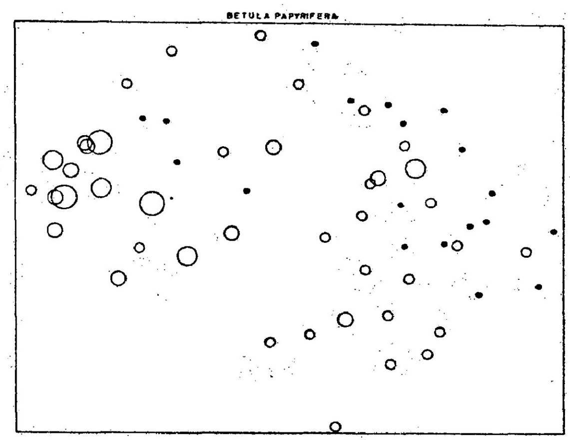
The importance values of individual tree species are shown for each stand in Figure 4.1.2.1.2. The relative importance value is indicated by the size of the circle.

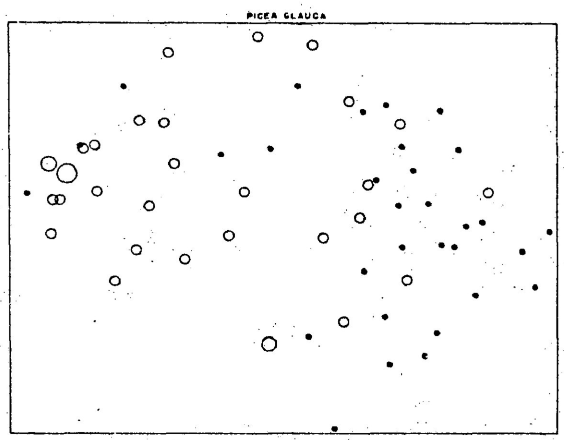
Most of the right half of the ordination field is dominated by jack pine. Jack pine shares dominance with

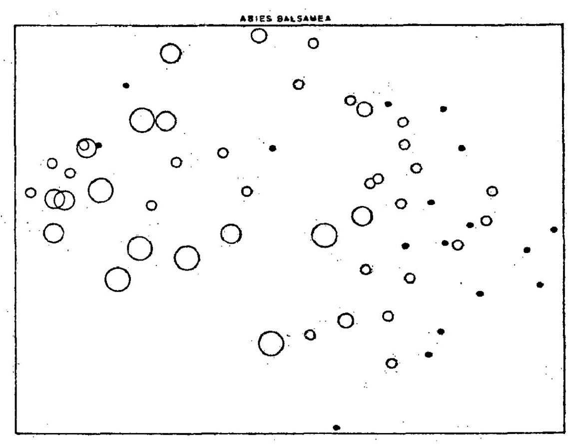












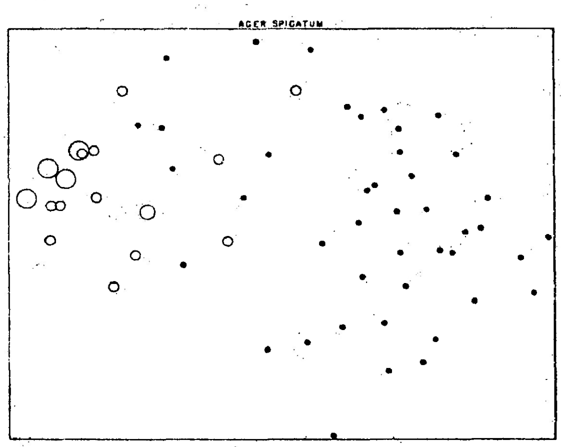
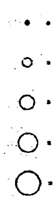


FIGURE 4.1.2.1.2. TREE SPECIES DISTRIBUTION ON POLAR ORDINATION

IMPORTANCE VALUE



black spruce in the lower right portion. Black spruce is also of moderate abundance in several of the uppermost jack pine stands. Aspen, birch, balsam fir and white spruce all appear sporadicly throughout the jack pine dominated stands. Only the stands on the farthest right are free of this mixedwood component.

Mixedwood stands appear on the left half of the ordination field. All of the species in Figure 4.1.2.1.2. have moderate abundance in at least a few of the mixedwood stands. Jack pine appears in some of the mixedwood stands in the upper portions of the left half of the ordination graph. Jack pine's appearance may represent drier sites or may represent a mesic site surrounded by jack pine dominated stands. Black spruce is present in many of the mixedwood stands. Black spruce is of moderate importance in either the drier mixedwood stands where jack pine is present, or in the moister mixedwood stands where jack pine is absent.

White spruce is present at a low importance value in most of the mixedwood stands. Part of this observation is a real ecological fact, but the observation is also caused by the impact of man. Timber harvesting has been carried out in or near all of the study area. White spruce had a high priority for harvesting. Several stands were rejected for sampling when white spruce stumps were found beneath old birch and aspen. White spruce never had an importance value of greater than twenty-five percent in the sampled stands. Although white spruce always had low density in upland stands in the study area, white spruce may dominate on other soils or along rivers.

Aspen, balsam fir and paper birch are all found in most mixedwood stands. These species had individual importance values greater than 80% in only two stands. Apparently, these species cannot exclude one another from any site, at least not at a scale of .1 ha. The only limitation on their distribution seems to be establishment of a seedling or sprout at a period favorable for growth. An individual species can only infrequently obtain sufficient precedence to utilize all "safe sites" (Harper, 1977) in any given area and thereby exclude all other species.

Mountain maple (Acer spicatum) is a large shrub which often attains a dbh greater than 2.5 cm. It is present in many of the mixedwood stands, sometimes possessing an importance value greater than 20%.

Succession does have a minor role in the composition of the mixedwood forest; succession will be considered in a later section.

The distribution of four understorey species is shown in Figure 4.1.2.1.3. These species were chosen because they are representative of many other species. Cornus canadensis shows no preference to any portion of the ordination; its broad ecological tolerance and high abundance assures Cornus 's presence in most stands.

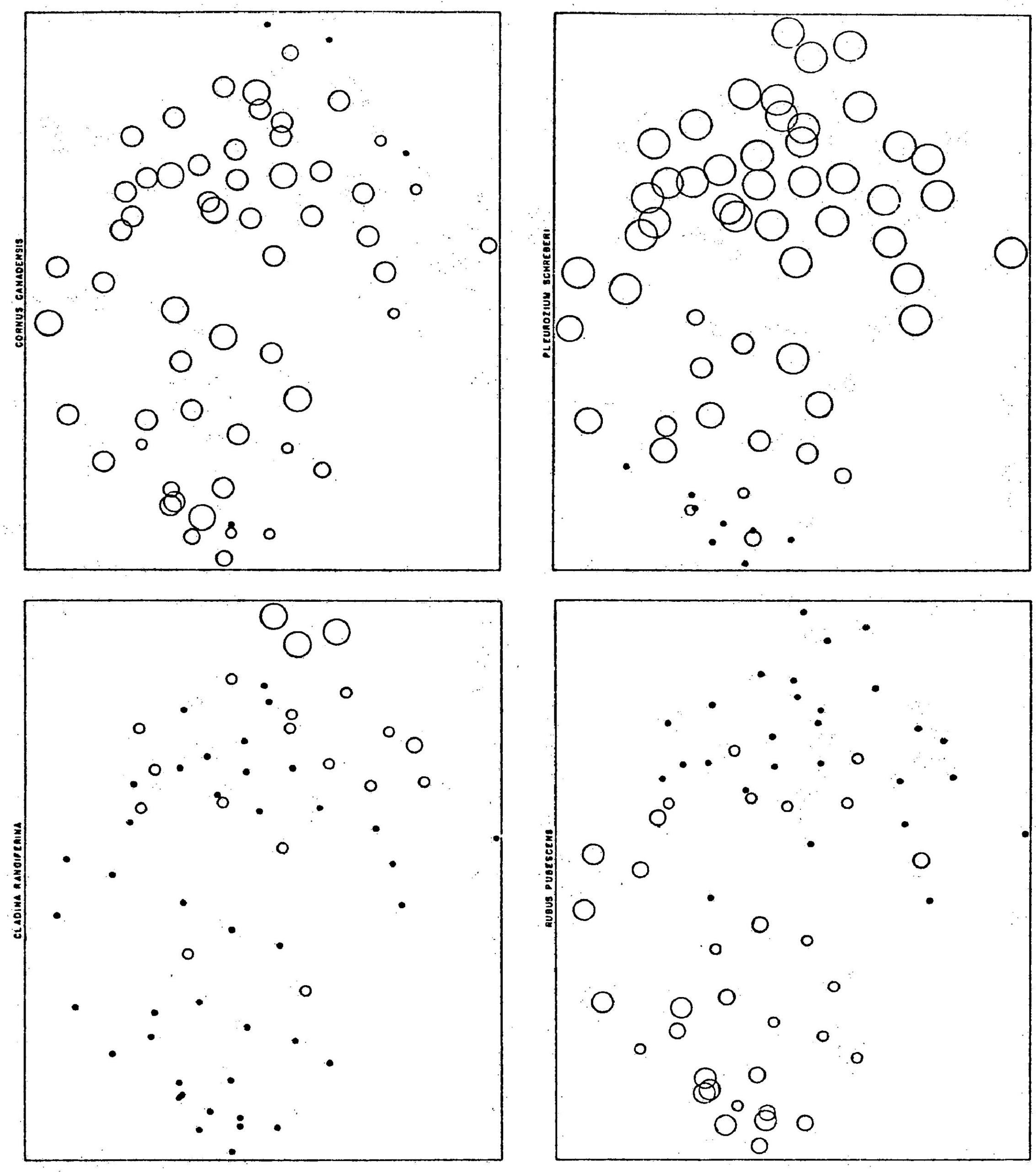


FIGURE 4.1.2.1.3. DISTRIBUTION OF FOUR REPRESENTATIVE UNDERSTOREY SPECIES ON POLAR ORDINATION.
IMPORTANCE VALUE
● = 0; ○ = 0.1 TO 2.0; ○ = 2.1 TO 5.0; ○ = 5.1 TO 10.0; ○ = 10.1 TO 20.0; ○ = >20.0

Maianthemum canadense, Diervilla Lonicera (in herb strata), Aralia nudicaulis, Trientalis borealis , Clintonia borealis, and Coptis trifolia have broad distributions similar to Cornus.

Pleurozium schreberi is a common and abundant species which does show some specificity. It dominates all of the conifer stands on the right portion of the ordination. It has moderate to high importance in several of the mixedwood stands, but only where a coniferous component (particularly jack pine and the spruces) is present. Pleurozium schreberi 's distribution appears to be limited more by the presence of conifers than by the physical environment. Pleurozium only grows well over a litter layer of coniferous needles. Broadleaved litter may smother Pleurozium and other mosses. The development of a Pleurozium carpet over the forest floor changes the seed bed from coniferous litter to an almost continuous moss mat.

Rubus pubescens is an example of a moderately common species which has some specificity. It is common in mixedwood stands, but only appears sporadicly in the coniferous stands. The coniferous stands where Rubus pubescens attains some importance tend to be fairly moist. Other fairly common species favoring mixedwood stands include: Acer spicatum, Carex, spp., Aster macrophyllus, Streptopus roseus, Corylus cornuta, Galium triflorum, Mitella nuda, and Lycopodium obscurum. Species primarily limited to coniferous stands include: Ledum groenlandicum, Vaccinium angustifolium, and Chiogenes hispidula.

Cladina rangiferina is the best example of a species with a high specificity. While Cladina rangiferina appears in several stands, including three mixedwood stands, it only has a high importance value in the three stands farthest to the right. These three jack pine, Vaccinium myrtilloides, Cladina stands have been discussed before. The distribution of Cladina alpestris differs only in the number of stands and in the magnitude of the importance values. Sphagnum, spp. and Peltigera apthosa show a high specificity to stands with a high component of black spruce. Athyrium Filix-femina and Gymnocarpium Dryopteris are restricted to moist, mixedwood stands with a high proportion of balsam fir. Other species show a scattered, broadly adapted distribution intermediate between the distributions characterized by Cornus canadensis and Rubus pubescens. More species will be treated individually in later sections.

Two independent polar ordinations using only the tree stratum and a combination of herb plus shrub strata are shown in Figure 4.1.2.1.4. Aggregate endpoints were used to make the ordinations comparable to the polar ordination of all data. The ordination of understorey vegetation retains much of the structure of the original ordination; the positions are changed only slightly. The polar ordination of only tree stratum data gives highly distorted

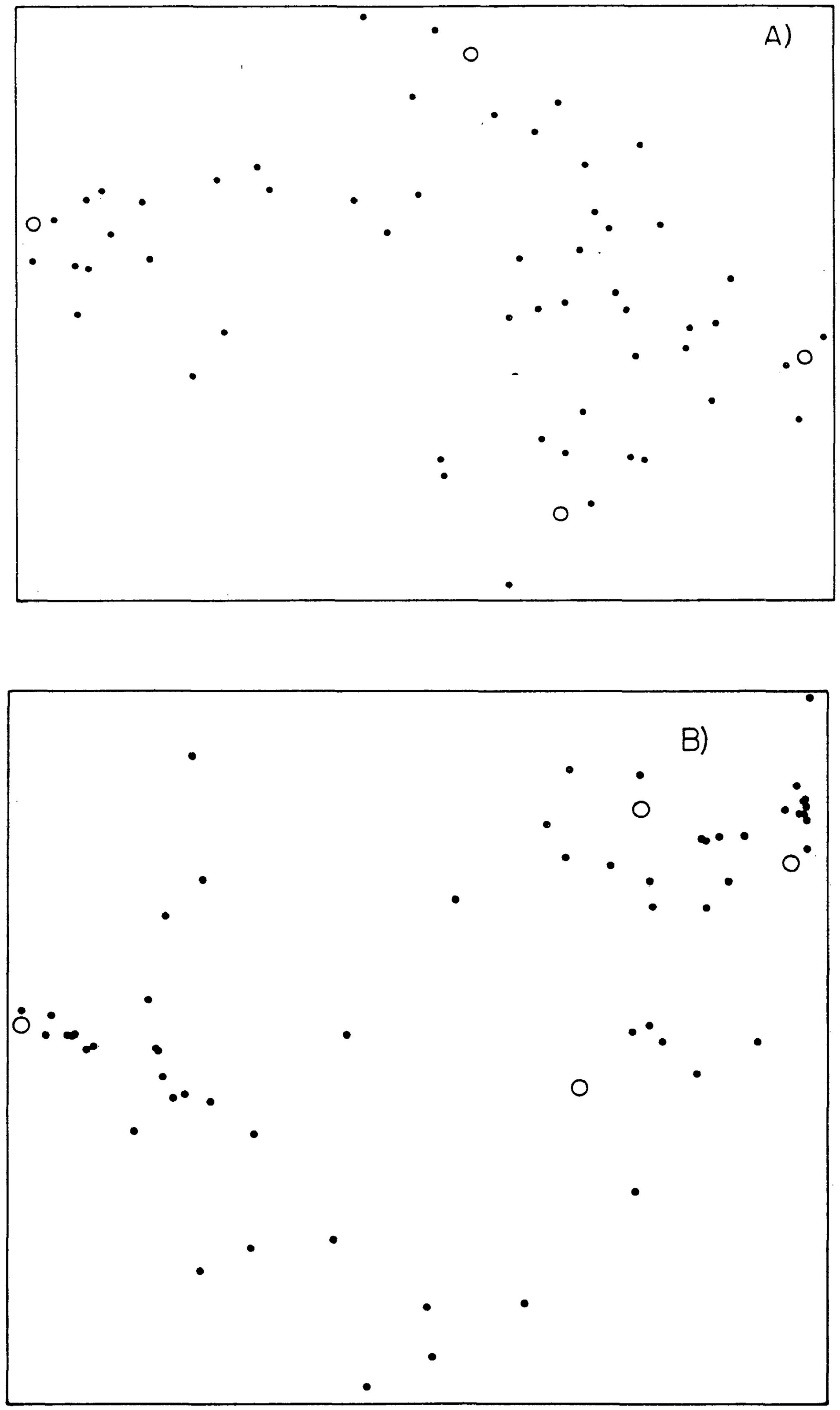


Figure 4.1.2.1.4. Polar ordination using aggregate endpoints (open circles) and: A) herb and shrub strata, only; B) tree stratum only.

results. Stands which were separated on the original polar ordination are clustered together, particularly within the jack pine dominated group. This is not merely a result of the aggregate endpoints. A polar ordination of the tree data with computer generated endpoints gave similar results. If one can assume that the all-data polar ordination represents real ecological differences among stands, then tree data alone do not clearly resolve these ecological differences. There may not be enough ecological information in the tree data to resolve the finer differences. There are few tree species and all have fairly broad ecological tolerances.

The ordination of tree data alone was improved somewhat by dividing each tree species into several diameter class X crown class X species combinations. If these combinations had fewer than four occurances they were combined with a crown class within the same diameter class. The six main tree species were thus divided into sixty-five "psuedo-species". The improvement is due to an increased number of variables, but the results were still not as interpretable as the ordination of all species.

4.1.2.2. Detrended Correspondence Analysis

A detrended correspondence analysis (DECORANA) applied to untransformed data is shown in Figure 4.1.2.2.1. The

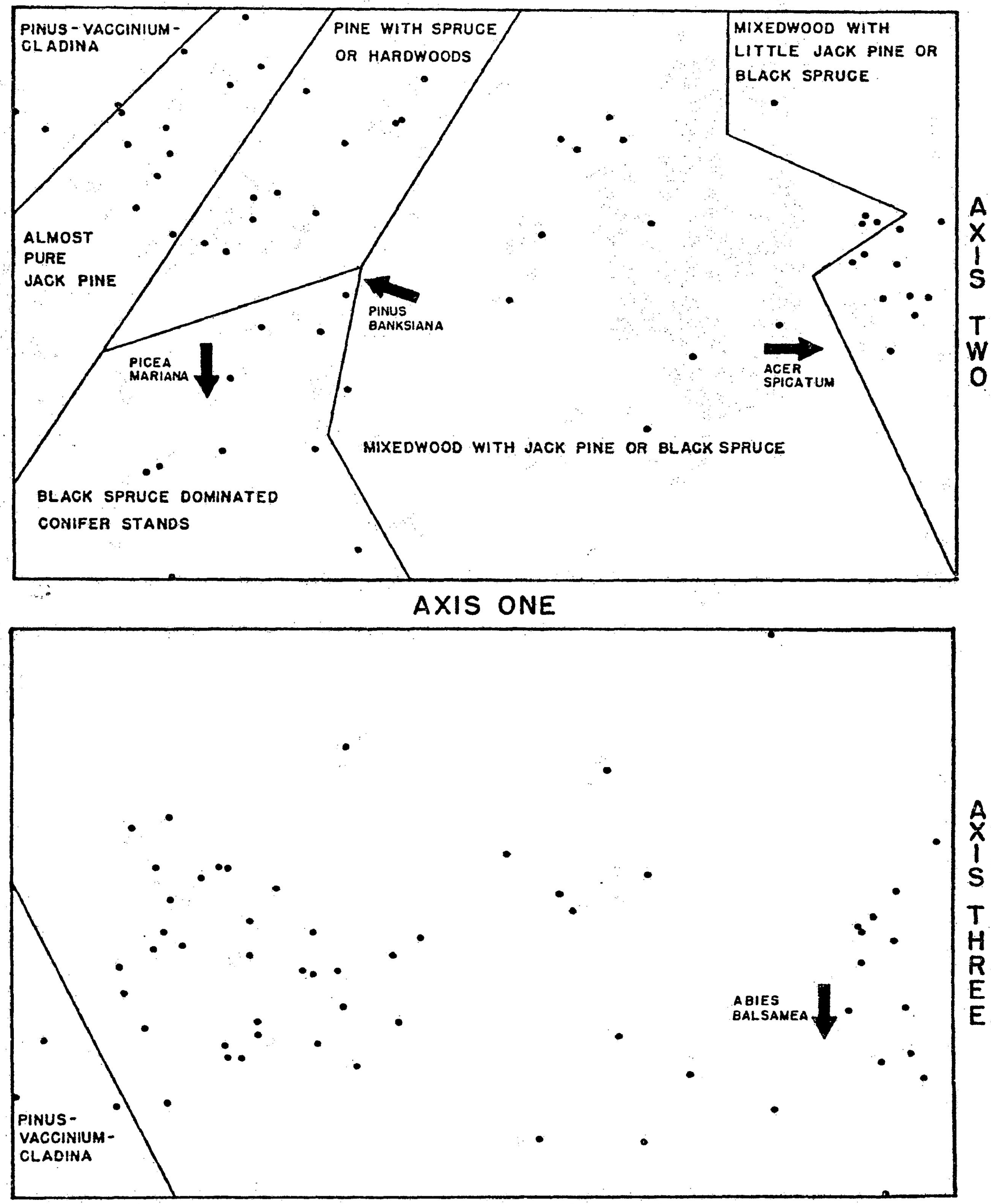


Figure 4.1.2.2.1. DECORANA ordination using untransformed data. Arrows point in the direction of increasing abundance for the indicated species.

first, second and third axes have eigenvalues of .645, .228 and .143 and lengths of 3.68, 2.36 and 1.43 "standard deviations", respectively. The eigenvalue and length of the first axis indicate a moderately high level of environmental heterogeneity. The relative magnitude of the eigenvalues show that the first axis accounts for almost three times the variation extracted by the second axis. In spite of their relatively lower eigenvalues, the second and third axes do express ecologically significant information.

General vegetational trends are indicated on the ordination graph. Arrows point in the direction of increased importance values for the indicated tree species. The lines do not represent distinct boundries. A few stands are misplaced by even this general delineation.

The first axis separates jack pine dominated stands from mixedwood stands. The mixedwood stands lacking pine and spruce are compressed into a narrow range on the first axis. This is a characteristic of the species distribution and is not a reflection on the homogeneity of the environments among these stands. There are more species restricted to these stands than there are species restricted to stands far to the left. There are twenty-three species (seventeen appearing in six or more stands) with their scores in the upper twenty percent of the first axis, but only seven species (four appearing in six or more stands) in the lower twenty percent of the first axis. The DECORANA program is supposed to compensate for situations as this, but apparently the difference was too great. Common species occur in both the conifer and mixedwood stands. There are more species restricted to mixedwood stands than species restricted to conifer stands. Species are most likely restricted from stands in the left portion of the ordination by their inability to endure the poorer growing conditions and are restricted from stands in the right portion of the ordination by their inability to endure competition. The environment is a greater factor in limiting species distributions than is competition. Random chance associated with establishment in any given stand would exist as unaccounted-for noise.

Species ranked among the thirty end-most for the first axis and which were present in six or more stands are listed in Table 4.1.2.2.1. High values are associated with the right end and low values with the left end. While the axis separates well the conifer dominated stands from the mixedwood stands, only two true tree species are listed. Betula papyrifera has a high score and Pinus banksiana has a low score. Both of these species are well down the list. All boreal tree species are broadly adapted. Only more specifically adapted herb and shrub species obtain the more terminal scores. There is a general moisture gradient from the dry left side to the moist right side. The species with terminal scores are indicative of these moisture conditions.

The second axis primarily separates the conifer stands

Table 4.1.2.2.1. Terminal species scores for the first DECORANA axis. Strata is indicated where it is ambiguous.

High Values

Species	Score
Mertensia paniculata	4.73
Mitella nuda	4.61
Acer spicatum (tree)	4.43
Osmunda cinnamomea	4.36
Acer spicatum (herb)	4.35
Acer spicatum (shrub)	4.35
Mnium, spp.	4.22
Carex, spp.	4.19
Galium triflorum	4.14
Aster macrophyllus	4.11
Athyrium Filix-femina	3.96
Rhytidiadelphus, spp.	3.84
Viola renifolia	3.77
Actaea, spp.	3.72
Gymnocarpium Dryopteris	3.71
Streptopus roseus	3.70
Lonicera hirsuta (herb)	3.60
Lycopodium obscurum	3.57
Populus tremuloides (herb)	3.51
Corylus cornuta (herb)	3.42
Abies balsamea (herb)	3.42
Betula papyrifera (tree)	3.36

Low Values

Species	Score
Cladina alpestris	-2.18
Cladina rangiferina	-1.85
Vaccinium myrtilloides (shrub)	-0.95
Epigaea repens	-0.90
Salix Bebbiana (shrub)	-0.65
Picea mariana (shrub)	-0.54
Cladina mitis	-0.35
Salix Bebbiana (herb)	-0.22
Cypripedium acaule	-0.19
Vaccinium angustifolium (herb)	-0.17
Ledum groenlandicum (shrub)	-0.15
Chiogenes hispidula	-0.10
Oryzopsis pungens	-0.08
Ledum groenlandicum (herb)	0.22
Pinus banksiana (tree)	0.49
Lycopodium complanatum	0.53
Chimaphila umbellata	0.62

with different proportions of black spruce. The stands where black spruce is most important, or shares importance with jack pine, are at the lower end of axis two. Axis two also separates some mixedwood stands along a similar jack pine - black spruce gradient. Uppermost mixedwood stands have jack pine with or without black spruce, while lower mixedwood stands have black spruce without jack pine. Table 4.1.2.2.2 gives species associated with the higher and lower ends of axis two. Most species are associated with the left end of axis one since axis two primarily extracted variance among conifer stands. Oryzopsis pungens, Prunus pennsylvanica and Salix Bebbiana have the highest scores on axis two. They, and other species with a high ranking, are indicative of a comparatively thin canopy since they require moderately high levels of light (Bakuzis and Hansen, 1959). Melampyrum lineare , which has a high second axis score, is a hemi-parasite on the roots of jack pine.

Tree, shrub and herb strata Picea mariana had low ranking on the second axis, as did the feather mosses Hylocomium splendens and Ptilium crista-castrensis and the lichen Peltigera apthosa. Stands with an almost pure jack pine canopy typically have Pleurozium schreberi as the solitary feather moss and have one of the Cladina , spp. as the only lichen. Ledum groenlandicum and Chiogenes hispidula are two species which are common in coniferous stands, but have higher importance in stands containing

Table 4.1.2.2.2. Terminal species scores for the second DECORANA axis. Strata is indicated where it is ambiguous.

High values

Species	Score
Oryzopsis pungens	4.42
Prunus pennsylvanica (shrub)	4.32
Salix Bebbiana (herb)	3.85
Prunus pennsylvanica (tree)	3.69
Salix Bebbiana (shrub)	3.64
Polygala paucifolia	3.21
Alnus viridis ssp. *crispa* (herb)	3.19
Amelanchier humilis (herb)	3.17
Alnus viridis ssp. *crispa* (shrub)	3.14
Amelanchier humilis (shrub)	3.00
Epigaea repens	2.97
Apocynum androsaemifolium	2.91
Cypripedium acaule	2.89
Melampyrum lineare	2.83
Corylus cornuta (herb)	2.81

Low values

Species	Score
Hylocomium splendens	-1.02
Picea mariana (tree)	-0.71
Ptilium crista-castrensis	-0.50
Picea mariana (shrub)	-0.41
Peltigera apthosa	-0.34
Betula papyrifera (shrub)	-0.31
Monotropa uniflora	-0.21
Populus tremuloides (shrub)	-0.10
Ledum groenlandicum (shrub)	0.15
Abies balsamea (shrub)	0.17
Chiogenes hispidula	0.31
Pyrola secunda	0.39
Goodyera repens	0.40
Rhytidiadelphus, spp.	0.41
Gymnocarpium Dryopteris	0.45
Polytrichum, spp.	0.48
Picea mariana (herb)	0.48
Sorbus decora (herb)	0.48
Sphagnum, spp.	0.50
Mnium, spp.	0.52
Ledum groenlandicum (herb)	0.53

black spruce. These species differences are due to either lower light conditions where black spruce is in the overstorey or differences between black spruce and jack pine litter, or differences in the habitat.

Axis three is similar to axis two. However, axis three mainly extracts variation among mixedwood stands and reverses, compresses and distorts the black spruce to jack pine trend among the conifer dominated stands. The balsam fir dominated mixedwood stands are in the lower portion of axis three while the aspen dominated stands are in the uppermost portion.

Species ranked high and low on axis three are listed in Table 4.1.2.2.3. Several of the species listed are not directly associated with the gradient of primary ecological interest. This would be expected given the rather low eigenvalue for axis three; the axis is affected by variation in the data set external to the variation across the gradient of interest.

The lower mixedwood stands have a high balsam fir component. The mosses Rhytidiadelphus, spp. and Mnium , spp. and oak fern, Gymnocarpium Dryopteris , are highly associated with these stands. The uppermost mixedwood stands have few balsam fir in the tree strata; aspen dominates with jack pine, black spruce and paper birch also important in some stands. Species associated with these upper stands include Corylus cornuta, Lonicera canadensis, Lonicera hirsuta, and Streptopus roseus. Petasites

Table 4.1.2.2.3. Terminal species scores for the third Decorana axis. Strata is indicated where it is ambiguous.

High Values

Species	Score
Corylus cornuta (herb)	3.76
Petasites frigidus	3.39
Corylus cornuta (shrub)	3.22
Pteridium aquilinum	3.18
Actaea, spp.	2.93
Frageria virginiana	2.91
Populus tremuloides (tree)	2.67
Ledum groenlandicum (herb)	2.66
Lonicera canadensis (herb)	2.57
Ledum groenlandicum (shrub)	2.55
Lonicera hirsuta (herb)	2.46
Galium triflorum	2.43
Lonicera canadensis (shrub)	2.33
Epilobium angustifolium	2.32
Oryzopsis asperifolia	2.29
Lycopodium complanatum	2.08
Streptopus roseus	2.01
Alnus viridis ssp. *crispa* (tree)	1.98
Rubus strigosus (shrub)	1.97
Anemone quinquifolia	1.95
Acer spicatum (tree)	1.93
Rosa acicularis (herb)	1.92

Low Values

Species	Score
Rhytidiadelphus, spp.	-2.83
Mnium, spp.	-1.71
Peltigera apthosa	-1.47
Betula papyrifera (shrub)	-1.29
Abies balsamea (tree)	-1.04
Gymnocarpium Dryopteris	-1.01
Cladina mitis	-0.96
Abies balsamea (shrub)	-0.78
Sorbus decora (herb)	-0.54
Lycopodium annotinum	-0.31
Vaccinium myrtilloides (shrub)	-0.28
Sorbus decora (shrub)	-0.23
Abies balsamea (herb)	-0.12
Sphagnum, spp.	-0.10

fridgidus and *Galium triflorum* have high third axis scores, but appear in moist stands with or without balsam fir. The gradient observed in axis three has three likely causes: 1) moisture gradient; 2) disturbance gradient; 3) successional gradient. The stands with more balsam fir tend to be: 1) moister; 2) initiated without fire or with a low intensity patchy fire; 3) older. Most stands with balsam fir do not possess all these characteristics. Some moist sites do not contain balsam fir and balsam fir appears on some fairly dry sites. Some young, even-aged stands possess a large balsam fir component. Characteristics of stand initiation are difficult to determine when sampling forty to one hundred years later. Considering the silvics of balsam fir, it appears that stand initiation characteristics are important. Some balsam fir must remain after the stand-initiating disturbance. Advance regeneration after blowdown, budworm, or harvesting, or residual fir after a patchy fire must be present in the area for the development of a large balsam fir component in the resulting stand. These characteristics are most common in moister areas. Balsam fir will increase as a stand ages, but some balsam fir must be present soon after stand initiation or its invasion will be slow. Many old stands can be found with few or no balsam fir. Succession, as such, seems to be of little significance; characteristics of stand initiation apparently override successional trends. Succession will be considered more fully in a later section. The three factors, moisture, disturbance characteristics and succession interact strongly.

4.1.3. Species Diversity

The Shannon function (Pielou, 1977) was used to calculate species diversity for separate strata and for all strata combined. Figure 4.1.3.1. superimposes total species diversity on the polar ordination considered in section 4.1.2.1. The mixed hardwood and conifer stands possess the greatest species diversity. Stands with low species diversity are characterized by either a pure jack pine canopy or a mixed jack pine - black spruce canopy lacking deciduous trees.

The diversity of the individual strata are highly correlated. The Spearman rank correlation between herb stratum diversity and tree stratum diversity is .63; $p < .01$. This correlation can be explained by two mechanisms: 1) a diverse tree stratum will contribute to a diverse herb stratum because of a heterogeneous light regime in the understorey; 2) diversity of the herb and tree strata are both controlled by the environment. Diversity indices were also calculated for tree stratum "psuedo-species". Psuedo-species were defined by diameter classes and by diameter X crown class combinations. The rank correlation

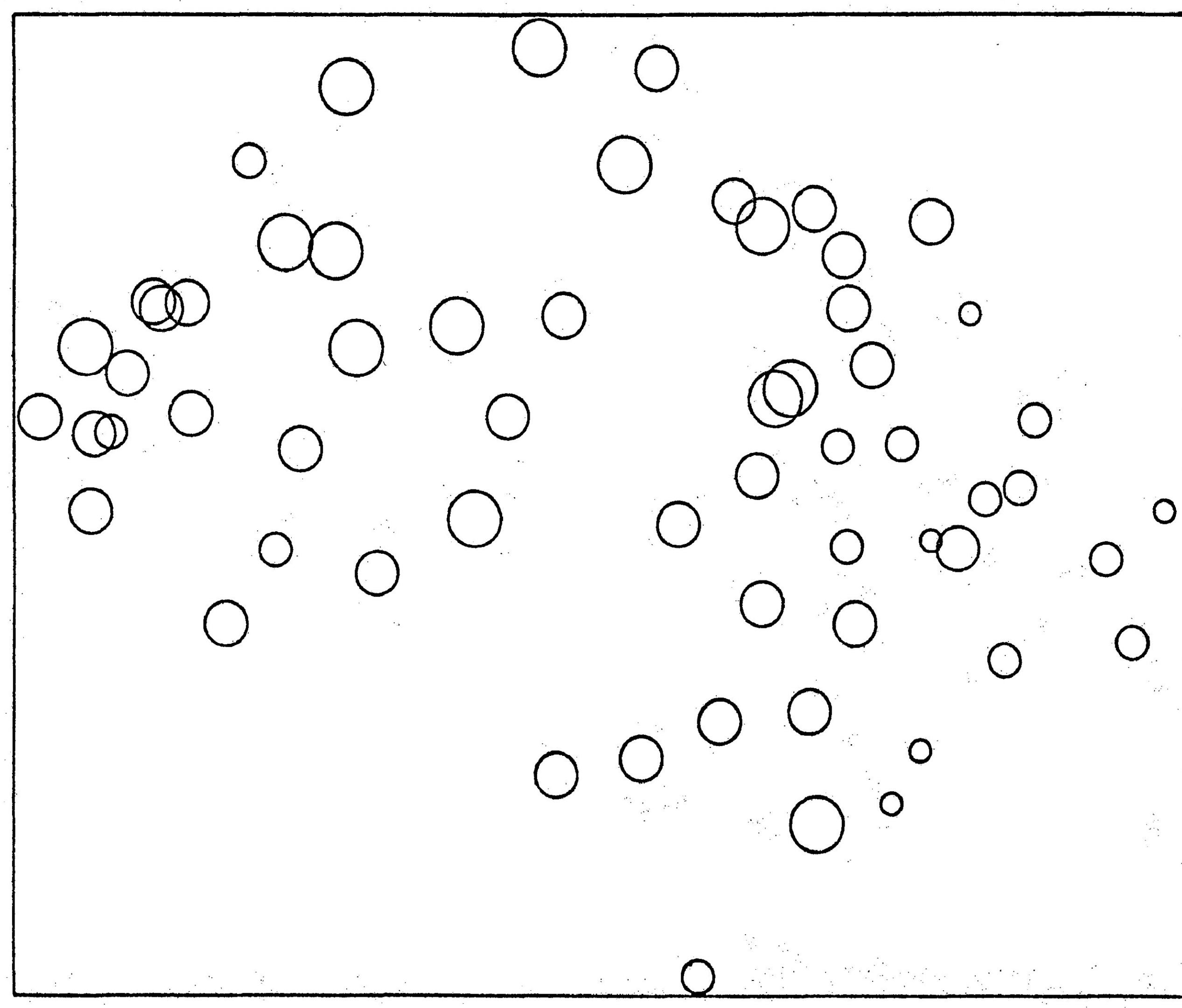


FIGURE 4.1.3.1. TOTAL SHANNON FUNCTION DIVERSITY SUPERIMPOSED ON THE POLAR ORDINATION OF FIGURE 4.1.2.1.1. KEY:
○ =< 0.9; ○ = 0.9 TO 1.04; ○ = 1.05 TO 1.20; ○ => 1.20.

between diversity indices of the herb stratum and of the tree diameter class data was .60; $p < .01$. The rank correlation between diversity indices of the herb stratum and of the tree diameter X crown class data was .49; $p < .01$. Breaking the tree data into psuedo-species should give a more precise description of the canopy heterogeneity. However, the correlation coefficient decreased as the tree data were broken into finer groups. Therefore, the environment, rather than the canopy heterogeneity, is the main determinant of understorey diversity. Simply, there are more species present on more favorable sites or heterogeneous habitats.

4.1.4. Summary of Community Composition

The upland boreal forest communities in the study area do not form discrete associations. Most species have wide environmental tolerances. Instead of discrete associations, the vegetation can be characterized by the population patterns of the individual species. These population patterns are largely independent. Community composition is primarily determined by the environment and species precedence on a site.

4.2. SUCCESSION

Scatter-plots of shrub stratum vs. tree stratum importance values for four tree species are shown in Figure 4.2.1. These scatter-plots relate overstorey composition to the presence of reproduction. Jack pine and white spruce are not shown; both species had few occurances in the shrub stratum. Jack pine is intolerant and infrequently exists beneath a canopy. The white spruce seed source seems to be limiting in the study area. Balsam fir, aspen and black spruce have similar scatter-plots. Shrub stratum importance values are insensitive to tree stratum importance values. Balsam fir seedlings and saplings become established in stands where few fir are in the overstorey. Aspen reproduction is due to root suckers in mixedwood stands and root suckers and seedlings in conifer dominated stands. Four stands which had no aspen in the tree stratum had aspen in the shrub stratum. These seedlings of the intolerant aspen will probably not survive unless the stand is soon regenerated without fire. The scatter-plot for black spruce may indicate that shrub stratum importance values decreased at high tree stratum importance values. The dense shade beneath canopies dominated by black spruce may eliminate the establishment of seedlings and saplings. Black spruce seedlings are common in mixed conifer stands; a jack pine canopy allows more light to reach the understorey.

Gregory (1979) and Carleton and Maycock (1978) found

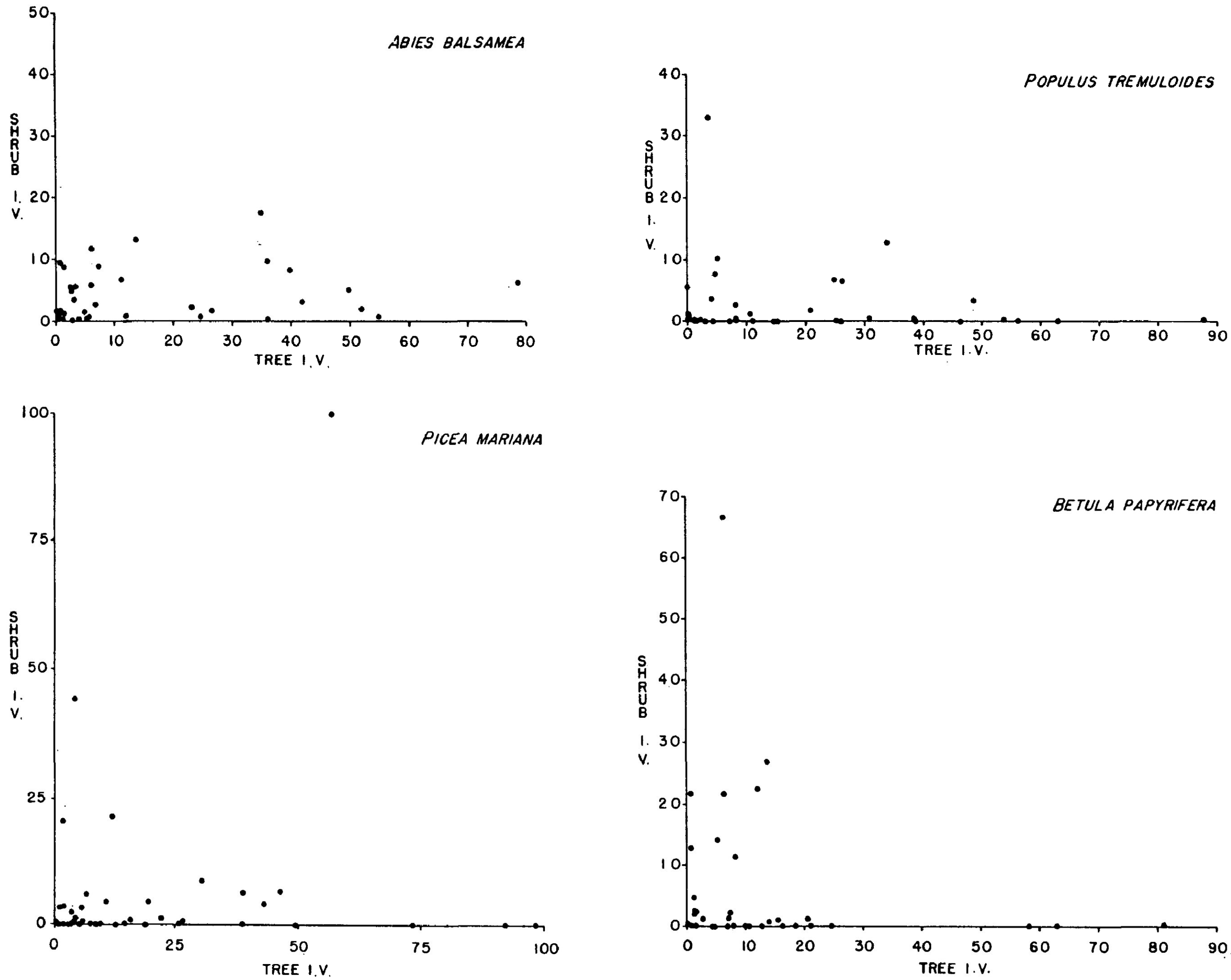


Figure 4.2.1. Scatter-plots of shrub stratum vs. tree stratum importance values for Abies balsamea, Populus tremuloides, Picea mariana, and Betula papyrifera.

different results with the same species. They found sapling importance value increasing with an increase in tree strata importance for black spruce and aspen. Those studies are not directly comparable with the present study. Both studies considered uplands and lowlands while this study is restricted to uplands. They included stems up to 10 cm dbh in their sapling data while I included all stems greater than 2.5 cm dbh in the tree strata. Suppressed trees are included in their sapling data. My data give a better estimate of reproduction while their data may give a better representation of short-term stand dynamics.

The paper birch scatter-plot shows higher shrub stratum importance values associated with low tree stratum importance values. This result is similar to Gregory's (1979) but is the opposite of Carleton and Maycock (1978). Stands with a shrub stratum importance value of paper birch exceeding 10% are indicated on the polar ordination of all data (Figure 4.2.2.). These stands are conifer-dominated, or mixedwood stands with a black spruce component. Apparently, sufficient light passes through the conifer canopies to allow paper birch to survive; reproduction was primarily by stump sprouting in the mixedwood stands. Gregory (1979) also found paper birch saplings to be most abundant on moderately dry sites. Although birch may become established, most grow slowly and would not reach the canopy unless an opening occurs. Paper birch may act as a "gap phase" species (Bray, 1956; Watt, 1947) to a

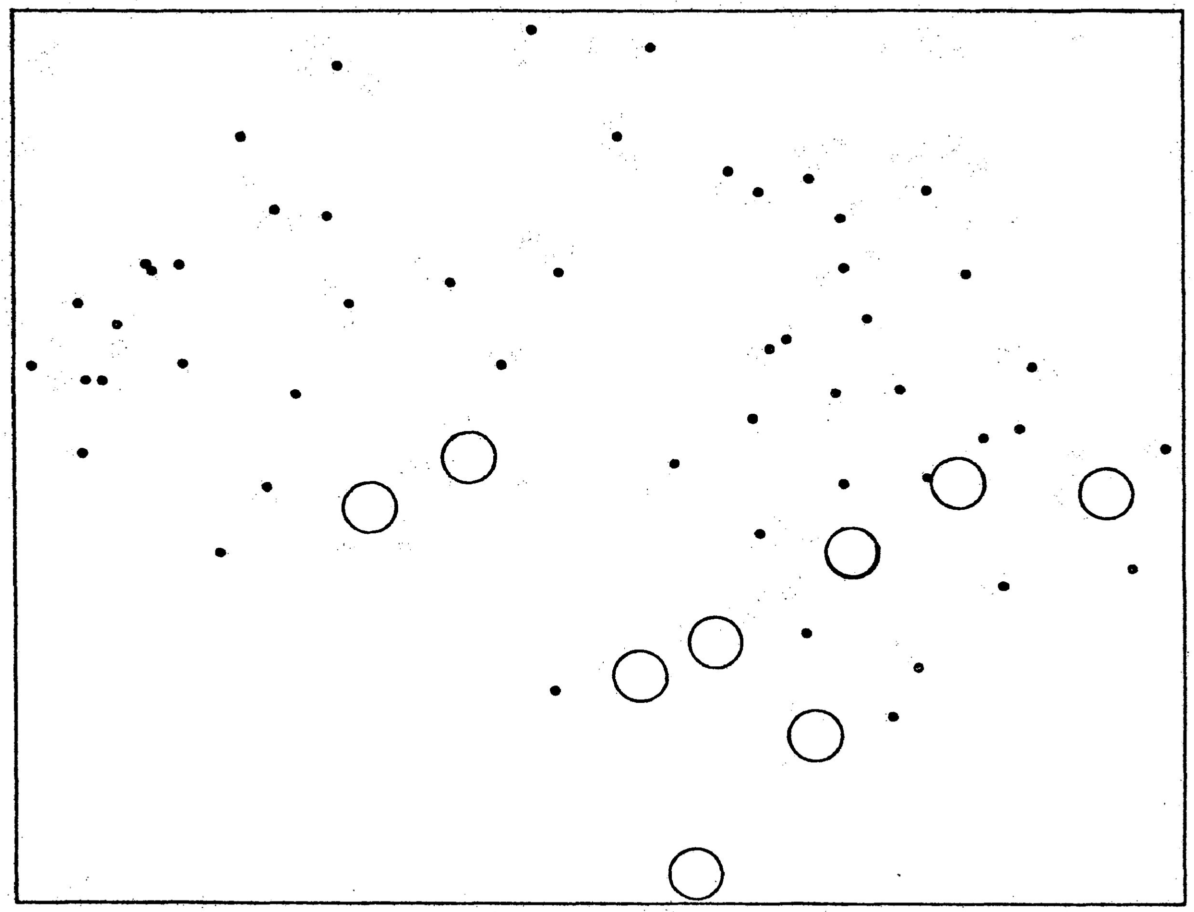


Figure 4.2.2. Stands with a shrub stratum importance value for paper birch exceeding ten percent (open circles) displayed on the polar ordination of Figure 4.1.2.1.1.

limited extent in these conifer stands. The behavior of paper birch in these stands is similar to Prunus serotina in southwest Wisconsin oak stands (Auclair and Cottam, 1971). If the stand is regenerated without fire this birch reproduction would probably survive, perhaps after resprouting.

These scatter diagrams show that all tree species have limited representation in the shrub stratum. Establishment is greater in mixed conifer stands where more light reaches the understorey. However, no tree species is able to dominate the shrub stratum. Individuals established after the stand initiation phase (Oliver, 1981) probably require some disturbance to reach the canopy. Sprugel (1976) has shown that even balsam fir, the most tolerant boreal tree species, requires disturbance to reach the canopy.

Goff and Zedler (1972) developed the method of succession vectors to study succession. They derived succession vectors from a principal components analysis of psuedo-species composed of tree species diameter classes. The vectors are formed by joining the diameter classes of an individual species with a line from the smallest to the largest diameter class. Carleton and Maycock (1978) have applied this method to boreal forest data. Carleton and Taylor (1983) used detrended correspondence analysis, rather than PCA to construct succession vectors.

I used both PCA and DECORANA to construct succession vectors. The size classes used were: 5 cm dbh; 10 cm dbh; 15 cm dbh; 20 cm dbh; 25 and 30 cm dbh; $\geq$ 35cm dbh class. Several different PCA runs were attempted. Centered and non-centered PCA were used. Raw data, standardized data and presence-absence data were used with PCA. All PCA runs gave highly distorted results. The best PCA run had succession vectors of long, narrow ellipses for aspen and jack pine. The primary PCA axis did not show a gradient of jack pine dominated stands to deciduous dominated stands, although every other method showed this was the major source of variability. The PCA succession vectors will not be considered further.

Figure 4.2.3. gives succession vectors on the first, second and third DECORANA axes. Generally, all species vectors point to the right, mixedwood, side of the ordination.

Jack pine shows increasing association with the mixedwood section as diameter class increases. This is caused by two factors: 1) jack pine grows faster on the finer textured soils occupied by mixedwood stands; 2) the period between fires is longer on the moister habitats occupied by mixedwood stands and therefore jack pine lives to a greater age. Both of these factors are environmental rather than successional. The black spruce vector indicates a similar, although less pronounced, pattern on the first and second axes. On the first and third axes, the smaller and intermediate size classes of black spruce show a strong association with the larger size classes of

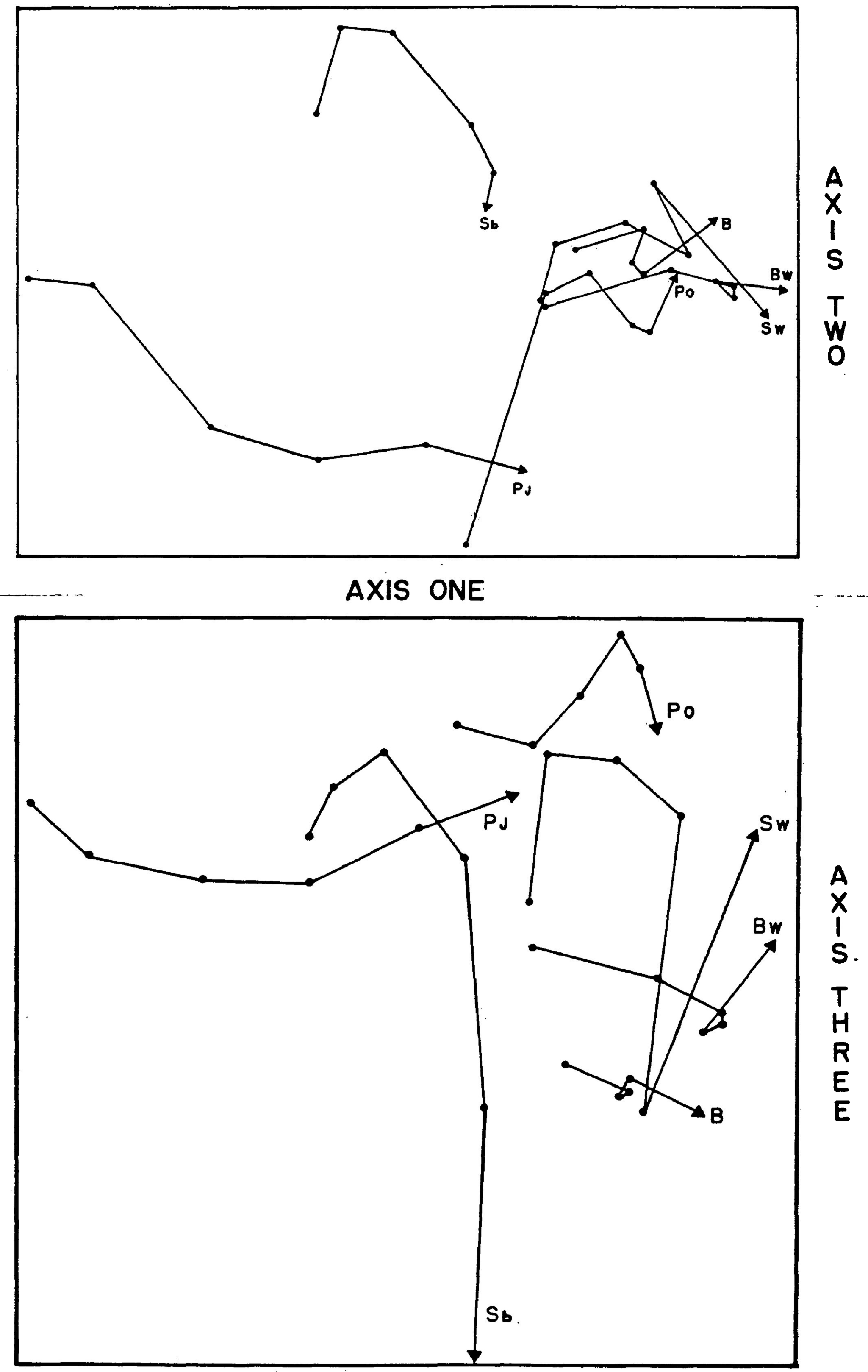


Figure 4.2.3. Succession vectors on the first, second, and third DECORANA axes. Species abbreviations are the same as Table 4.1.

jack pine, while the larger size classes of black spruce do not. This substantiates the observation of smaller black spruce growing beneath jack pine.

The smallest size class of aspen shows an association with jack pine. Again, this observation is environmental rather than successional. Aspen grows poorly on the dryer sites dominated by jack pine. The aspen vector proceeds into a tight cluster of species which dominate the mixedwood stands.

No strong successional trends are evident within the mixedwood cluster. On the first and second axes, balsam fir seems to be associated with white spruce; the larger size classes of aspen are associated with the smaller size classes of paper birch. The larger size classes of paper birch are associated with the larger size classes of white spruce. Paper birch and white spruce may live to a greater age than other boreal species common in mixedwood stands. This may indicate an aspen and birch to birch, spruce and fir successional path. A few stands of widely scattered large, old birch and spruce with smaller fir and scattered clumps of aspen suckers or birch sprouts were observed. Fallen stems of aspen, birch or fir were common and a distinct tall shrub layer was present. Such stands were not sampled because they did not meet the criterion of being closed-crown forests. Such stands are infrequent and typically only occur in fire-protected areas. The physiognomy of the stand would facilitate crowning of any fire. Such irregular-crowned stands could not be regarded as an endpoint of succession. The dominant trees are remnants of the original stand; tree reproduction is not sufficient to close the large canopy gaps. The overwhelming importance of fire may have precluded the evolution of late successional species (Loucks, 1970; Shafi and Yarranton, 1973).

The vectors on the first and third axes do not show the same associations within the mixedwood section that the first and second axes did. The third axis separates aspen from balsam fir. This might represent a successional relationship. However, if balsam fir was the late successional dominant in mixedwood stands, then the vectors of other common mixedwood species would point towards balsam fir. This is not evident. The separation is probably due to disturbance intensity. Balsam fir occurs where the stand is initiated without fire or where fire intensity is low and residual balsam occurs in the area.

Instead of strong successional trends, only environmental effects are noted. Succession is apparently of little consequence where the time between fires is less than the maximum age of the component species. Disturbance intensity may affect stand composition only by affecting the composition of the regenerating stand. The concept of succession would need to be greatly broadened to include disturbance intensity as a successional trend rather than the starting point for succession.

The succession vectors derived here differ considerably from Carleton and Maycock (1978). The only similarity is found in the association of aspen with paper birch. Carleton and Maycock's vectors appear to be determined more by the environment than those derived here. Carleton and Maycock's data set included uplands as well as lowlands. Black spruce was isolated from jack pine even though black spruce was common in jack pine stands in their study area (Carleton, 1982a; b). If the succession vectors technique is used, it is mandatory that most of the variability in the data set be caused by succession rather than environmental gradients. While Goff and Zedler (1972) found some strong successional trends, some of their species separated on the basis of environmental requirements. For example, jack pine and Hill's oak, which occur on dry outwash plains in Wisconsin, were adjacent to each other and did not exhibit any successional trends. Whenever succession is studied by arranging different stands into a time sequence, homogeneity of the site conditions must be established (Laven, 1982). Either some sort of covariance analysis must remove the effect of the environment or the data set must be restricted to a specific environment.

Succession vectors were derived (Figure 4.2.4.) using only stands which had a sum total importance value for aspen, paper birch, white spruce, and balsam fir exceeding twenty percent. These vectors are similar to Figure 4.2.3.

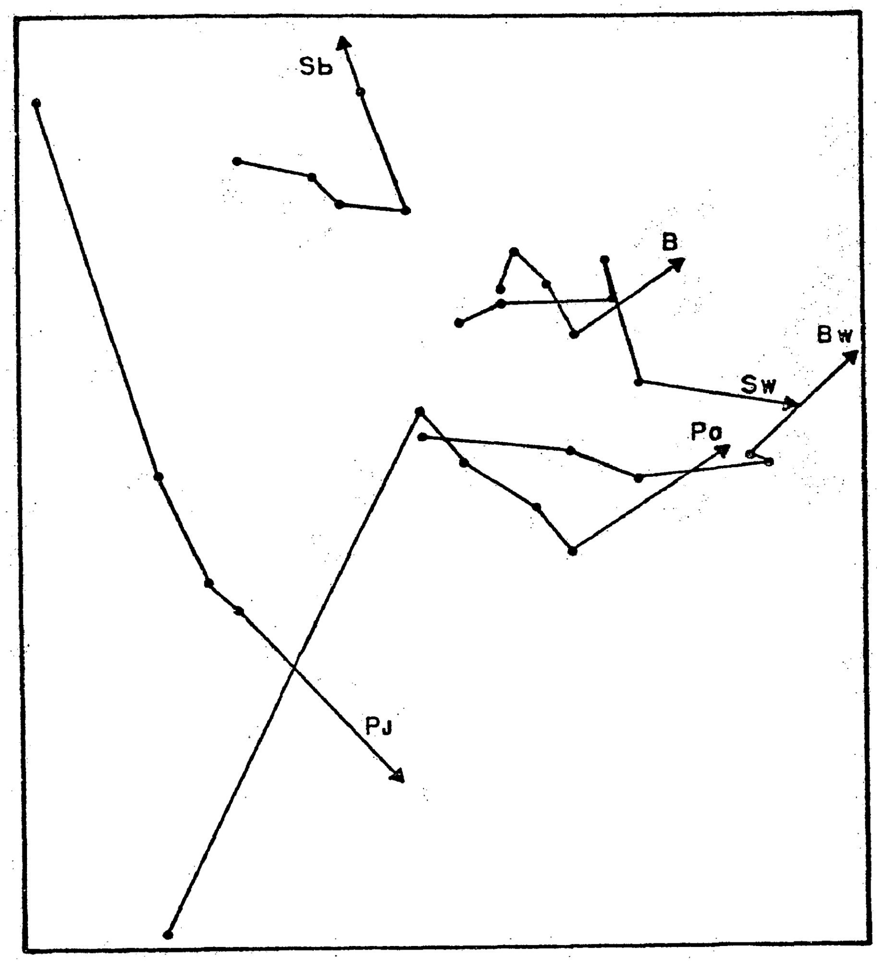


Figure 4.2.4. Succession vectors on the first and second axes of a DECORANA ordination of mixedwood stands. Only stands with an importance value exceeding twenty percent for the sum of aspen, white spruce, balsam fir and paper birch were used. Species abbreviations are the same as Table 4.1.

Only the black spruce and jack pine vectors differ. The black spruce succession vector points away from the mixedwood section. The jack pine vector is not directed as strongly to the right. Black spruce and jack pine are apparently only fortuitous occupants of mixedwood stands.

Succession was also investigated by calculation of 2X2 chi-square contingency tables for all possible tree species combinations. The two states of the chi-square compared average basal area per tree of a species in a given stand to average basal area per tree of a species in the entire data set. The positive state indicates that the quadratic mean diameter in a stand is greater than or equal to the total average. The negative state indicates that the quadratic mean diameter within a stand is less than the total average. Only stands where both species were present were included in the contingency tables. This technique resembles the intraspecific diameter distribution technique of Auclair and Goff (1974), although computationally simpler. There are fifteen possible combinations of the six tree species. Four of these combinations were significant at alpha=0.05.

The jack pine X black spruce combination was significant. Smaller jack pine were almost exclusively associated with smaller black spruce. This is caused by faster growth of jack pine on all upland sites. The aspen X black spruce combination was significant because larger aspen were always associated with larger black spruce;

black spruce grows better on mixedwood sites. The aspen X paper birch combination was significant because larger aspen were associated with larger than average paper birch and smaller aspen were associated with smaller than average birch. This occurred even though the aspen were almost always larger than the paper birch. Aspen and paper birch become established on a site about the same time, but aspen maintains a superior crown position for at least as long as the typical interval between fires. The birch X black spruce combination was also significant. This relationship was significant since smaller black spruce were associated with smaller birch. This situation was common where intermediate and suppressed birch and black spruce were present beneath a jack pine overstorey. There is no indication that the birch will replace the jack pine without a disturbance. The birch is primarily in the 5 cm dbh class with fewer taller stems reaching the canopy.

Most of these results are due to differing growth rates rather than a replacement of species. Few individuals become established after the stand initiation phase. The development of a stand is determined by the initial cohort which establishes before crown closure. Precedence on a site and recurring fire overshadows any successional trends. Smaller intermediate or suppressed trees may reach the canopy, but these individuals were established around the same time as the canopy trees.

There is no indication of the classical relay floristics succession (Egler, 1954). Rather, crown stratification may occur due to differing growth rates. For example, aspen may gain early dominance over white spruce. Later, white spruce may overtop aspen as the canopy starts to thin. This observation is based on differing growth rates. Inferior crown position can be equated with later successional position only when the species lives longer, is capable of reaching the canopy and reproducing itself in the absence of disturbance. None of the boreal tree species fulfill this requirement.

4.3. Environment

Moisture regime values are displayed on the first and second DECORANA axes in Figure 4.3.1. The Ontario Ministry of Natural Resources soil moisture regime (Belisle, 1980), is determined by soil texture, depth to mottling and gleying and, to a limited extent, percent slope. Generally, moister soils are associated with mixedwood stands and dryer soils are associated with jack pine and black spruce stands. The pure jack pine stands tend to be dryer than jack pine stands with a black spruce or deciduous component. These trends are general, there are several exceptions.

In Figure 4.3.2., landform types are delineated on the DECORANA ordination. Deltaic sands and valley trains are

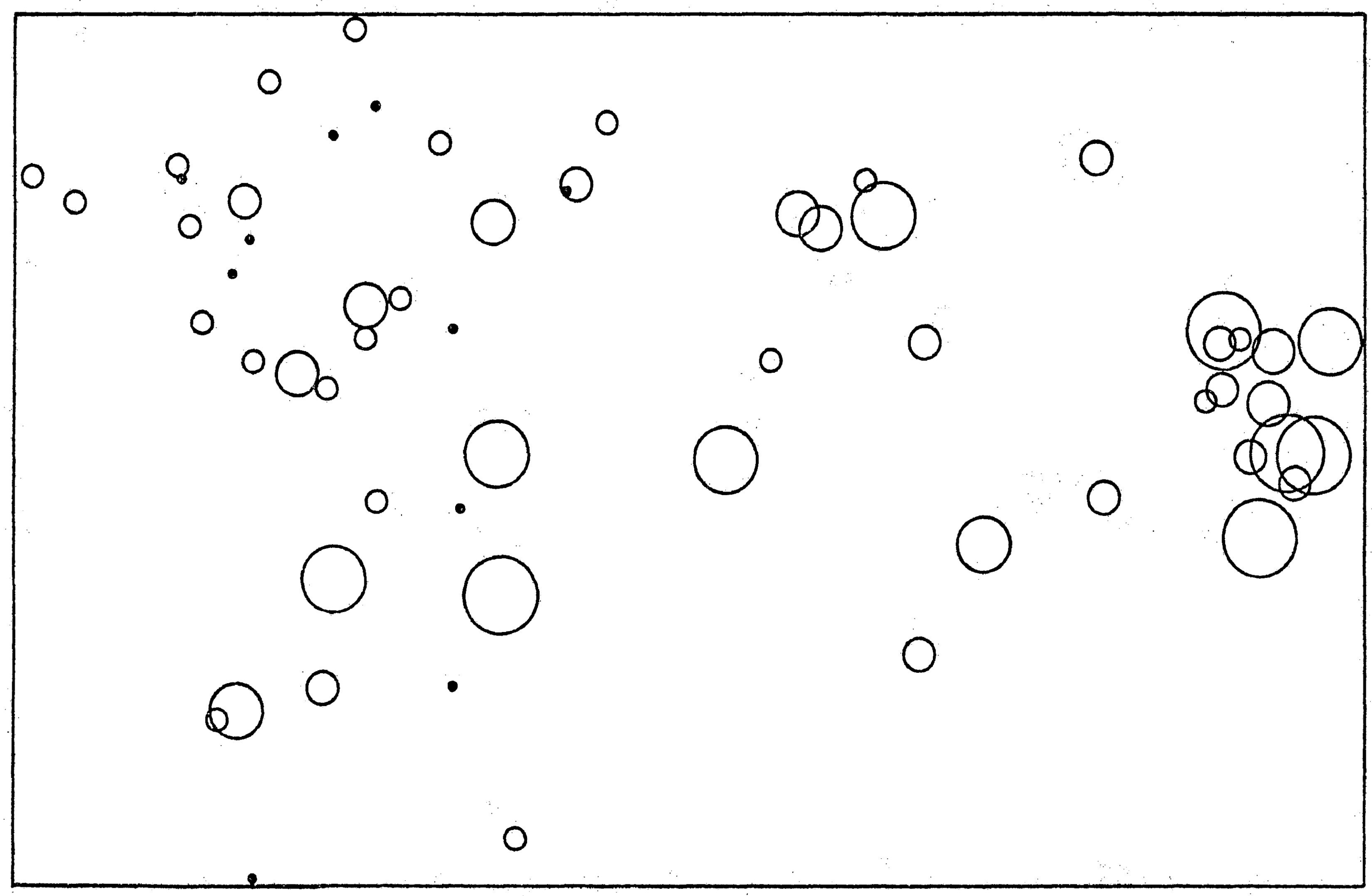


FIGURE 4.3.1. OMNR MOISTURE REGIME SUPERIMPOSED ON THE DECORANA ORDINATION OF FIGURE 4.1.2.2.1. KEY: ● = 0 ; ○ = 1; ○ = 2; ○ = 3; ○ = 4; ○ = 5; ○ = 6.

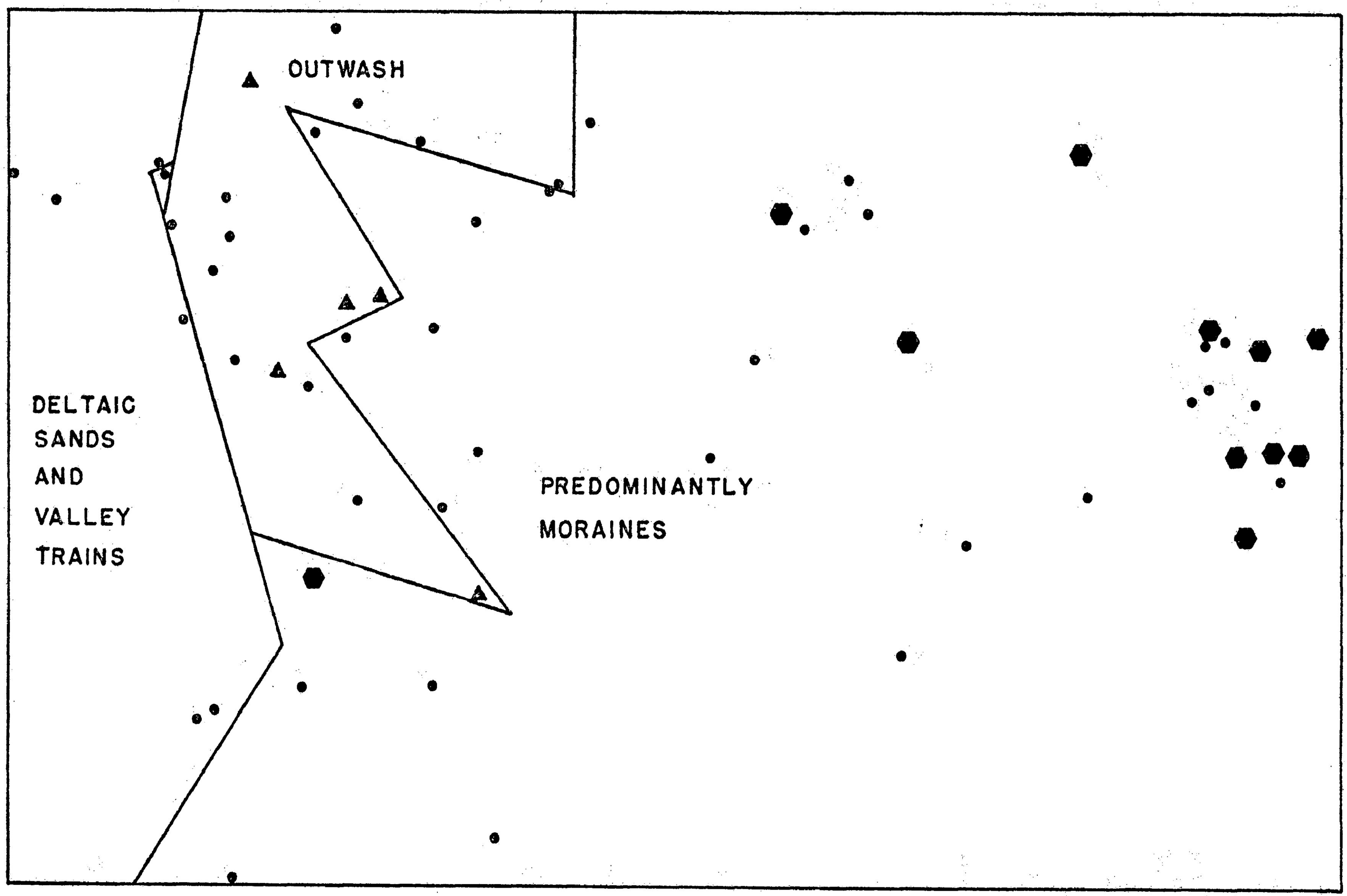


Figure 4.3.2. Landforms superimposed on the DECORANA ordination of Figure 4.1.2.2.1. Hexagons indicate moraines with a loess cap. Triangles indicate outwash with a sandy loam horizon.

found to the left of the ordination. Jack pine stands predominate on these sites; black spruce is more abundant where the site is moister or where an abundant black spruce seed source was present. Outwash plains are dominated by jack pine. Black spruce is more abundant on moister loamy outwash. One mixedwood stand occurred on very moist, loess covered outwash.

Moraines may be covered by an almost pure stand of either jack pine, black spruce, aspen, or paper birch. Ground moraines cannot be separated from terminal moraines on the ordination graph. The soil texture of the different moraines may vary from sands to clay loams. Stoneyness, soil depth and topography may override texture in determining the moisture status of a site, thus the OMNR moisture regime may be misleading in some cases. Loess-capped moraines tend to be moister, but this is moderated by topography. Within moraines, there is no strict relationship between vegetation and characteristics of the site. Loess covered moraines which receive some water from lateral seepage tend to be moistest; jack pine is infrequent on these sites while moisture-preferring herbs are more common. Black spruce is more common on shallow ground moraine. Jack pine importance value increases as soils become coarser.

The vegetation on moraines may be characterized as a random assemblage. While environmental factors have an effect, stand composition is determined by precedence and seed source availability rather than exact relationships between the vegetation and environment or time. The various vegetational trends noted in section 4.1 are weak. Several factors contribute to the characteristics of the vegetation, but none dominate. These factors interact, making the effect of any one factor indistinct. Overriding all factors are the stochastic effects of seed or sprout availability. The soils of moraines may be more variable, thus the soils may also contribute to the variability of the vegetation.

pH of the upper soil horizon varies with the vegetation (Figure 4.3.3). The lowest pH is found in stands with a moderate to large black spruce component. Black spruce produces nutrient poor litter (Damman, 1971; Gordon, 1983) which may acidify the soil. Jack pine dominated stands also have low pH; pH is higher in jack pine and black spruce stands which have a broadleaved component. pH is also high in mixedwood stands, although stands with a black spruce component on ground moraine may have a very low pH. The cause-effect relationships between pH and the vegetation are unclear. pH may be low because of an acidic substrate or because of nutrient cycling patterns within the ecosystem. Species may be associated with low pH because of a preference for acidic soils or because the species promote acidification. There is little variation in the substrate acidity within the study area; all deposits are slightly to strongly acidic (Zoltai,

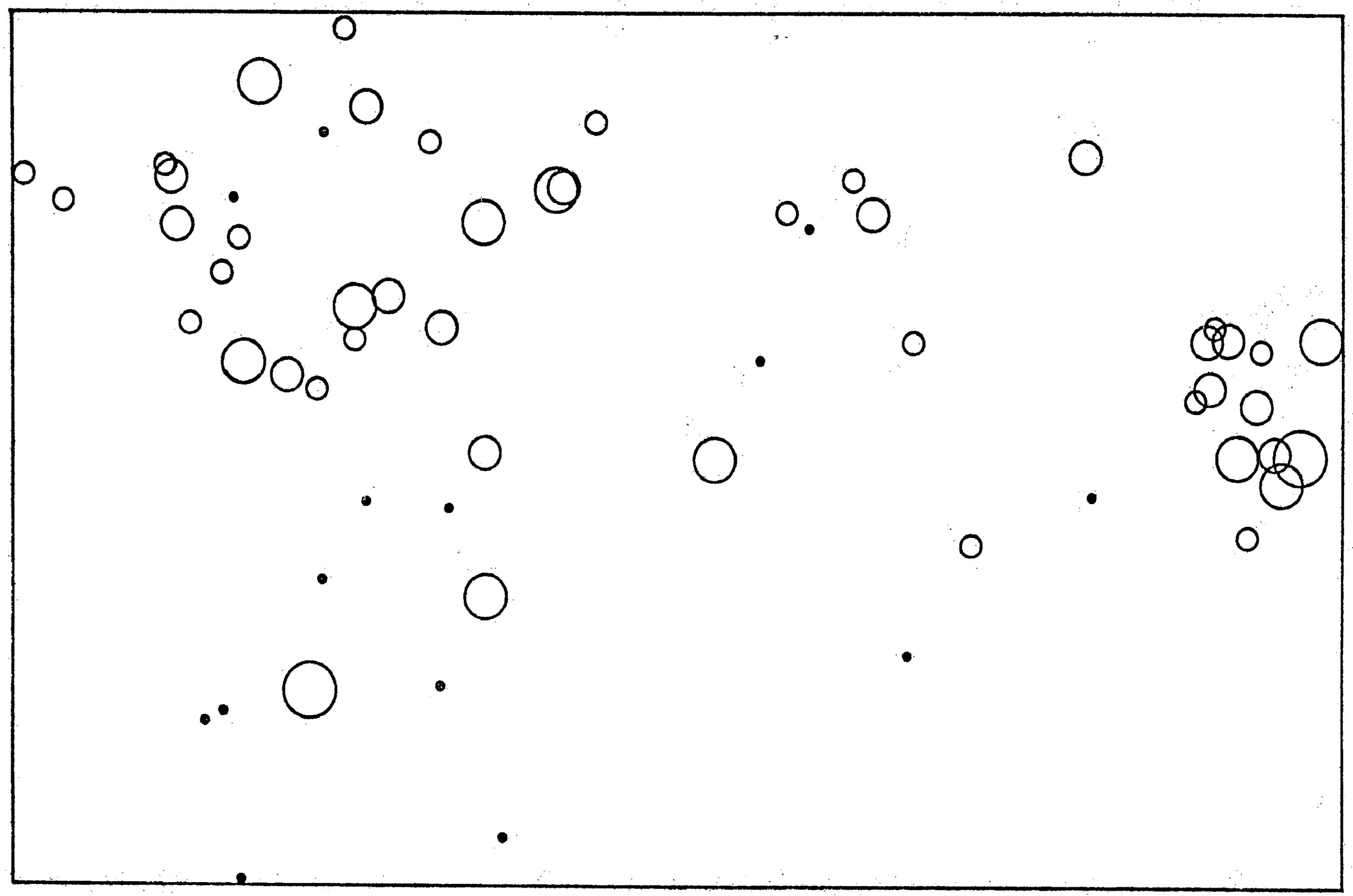


FIGURE 4.3.3. pH SUPERIMPOSED ON THE FIRST AND SECOND DECORANA AXES OF FIGURE 4.1.2.2.1. KEY: • $<$ 4.0; ○ = 4.0 TO 4.5; ◯ = 4.51 TO 5.0; ◯ = 5.01 TO 5.5; ◯ $>$ 5.5.

pH DETERMINED FOR SURFACE SOIL HORIZON.

1965). This may indicate that the vegetation may cause part of the small differences (3.7 to 5.6) in pH. pH may be reduced where conservative nutrient cycling patterns exist, such as black spruce stands (Gordon, 1983) and, to a lesser extent, jack pine stands. More rapid nutrient cycling by broadleaf trees may increase pH.

There is little variation in organic layer thickness (Figure 4.3.4.). Thickness is slightly greater where black spruce is an overstorey component. Hardwood dominated stands may tend to have a slightly thinner organic layer. There is no clear relationship between organic layer thickness and either pH or moisture regime.

The effect of moisture regime on individual species was investigated by weighted averages (Gauch, 1977). A species score equals the weighted (by importance value) average of moisture regime values of all stands in which it occurs. Only species present in greater than ten percent of the stands were included in this analysis. Table 4.3.1. gives species scores across the moisture gradient. Low scores indicate species common to dry sites; high scores indicate species common to wet sites. One was added to the moisture regime values, giving a range of 1 to 7. A species restricted to moderately dry sites would have a score of 1.0; a species restricted to very moist stands would have a score of 7.0. The actual range of species scores was from 1.824 for Vaccinium myrtilloides to 5.563 for Rhytidiadelphus, spp. Since each moisture regime was

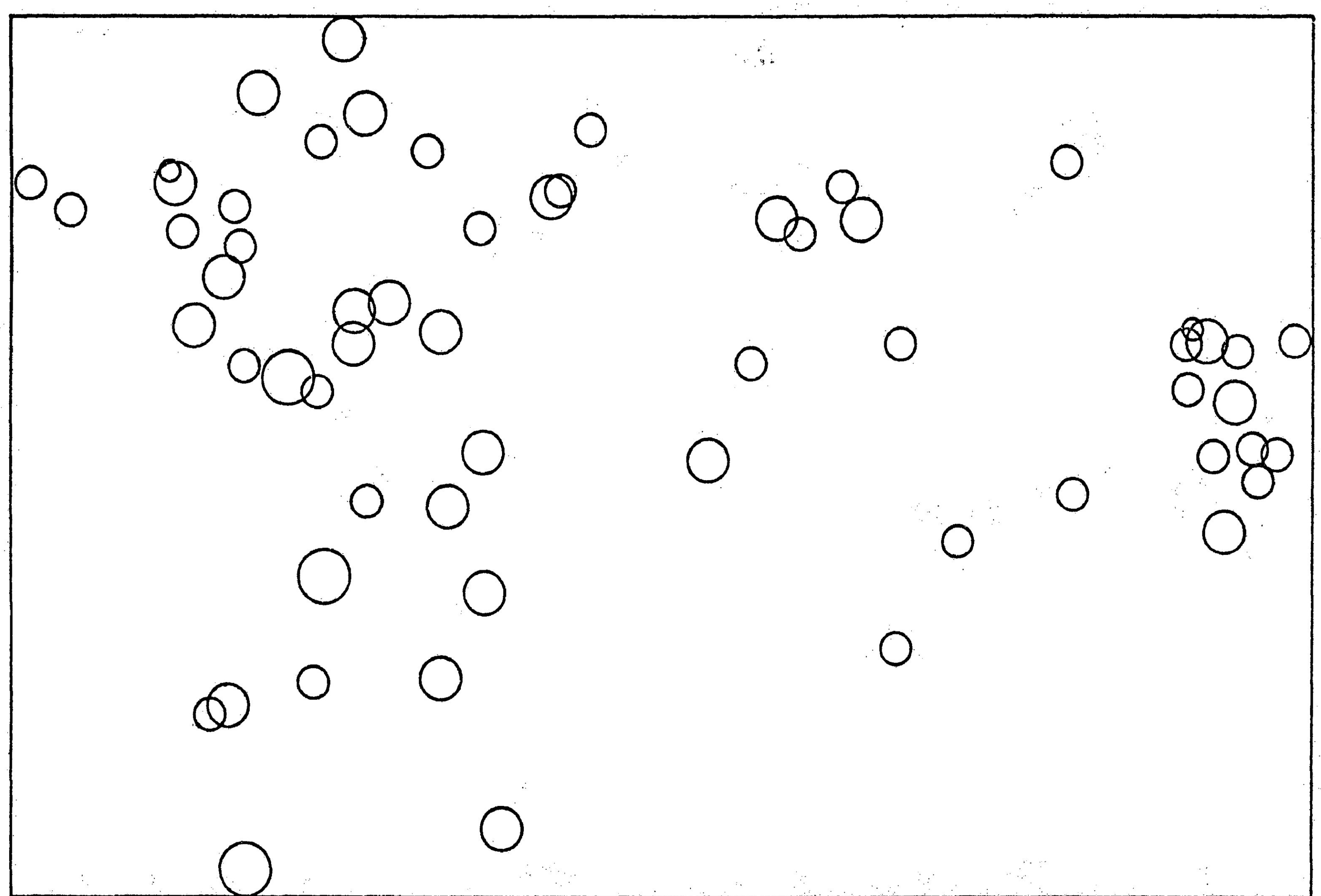


FIGURE 4.3.4. O-HORIZON THICKNESS SUPERIMPOSED ON THE FIRST AND SECOND AXES OF THE DECORANA ORDINATION OF FIGURE 4.1.2.2.1. KEY:

○ =0 TO 5.0CM; ○ =5.1 TO 10.0CM; ○ =10.1 TO 15.0CM; ○ >15.0CM.

Table 4.3.1. Species weighted average of OMNR moisture regime values. Averages are weighted by importance values. Low values indicate species restricted to dry sites; high values indicate species restricted to moist sites.

Species	No. Stands	Score
Vaccinium myrtilloides (shrub)	29	1.824
Prunus pennsylvanica (tree)	9	1.841
Prunus pennsylvanica (shrub)	12	1.936
Melampyrum lineare	20	1.938
Peltigera apthosa	8	1.976
Oryzopsis pungens	7	2.002
Cladina rangiferina	19	2.025
Cladina alpestris	9	2.028
Cypripedium acaule	15	2.033
Cladina mitis	17	2.130
Chiogenes hispidula	31	2.151
Salix Bebbiana (herb)	7	2.185
Dicranum, spp.	49	2.219
Vaccinium myrtilloides (herb)	47	2.265
Vaccinium angustifolium (herb)	39	2.284
Amelanchier humilis (herb)	12	2.311
Pinus banksiana (tree)	45	2.327
Picea mariana (shrub)	29	2.381
Amelanchier humilis (shrub)	21	2.414
Pteridium aquilinum	8	2.426
Betula papyrifera (shrub)	24	2.434
Rosa acicularis (herb)	23	2.440
Monotropa uniflora	8	2.446
Hylocomium splendens	23	2.477
Pleurozium schreberi	52	2.497
Epigaea repens	9	2.539
Picea mariana (herb)	24	2.611
Alnus viridis ssp. *crispa* (shrub)	23	2.622
Rosa acicularis (shrub)	19	2.636
Chimaphila umbellata	12	2.694
Alnus viridis ssp. *crispa* (tree)	9	2.706
Apocynum androsaemifolium	7	2.769
Ptilium crista-castrensis	42	2.819
Betula papyrifera (herb)	12	2.837
Linnaea borealis	50	2.888
Ledum groenlandicum (shrub)	20	2.918
Diervilla Lonicera (herb)	39	2.931
Populus tremuloides (shrub)	26	2.962
Cornus canadensis	56	2.983
Goodyera repens	23	2.989
Maianthemum canadense	57	3.031
Lycopodium clavatum	25	3.050
Corylus cornuta (shrub)	21	3.076
Corylus cornuta (herb)	17	3.077
Picea glauca (shrub)	8	3.101
Picea mariana (tree)	49	3.131
Oryzopsis asperifolia	26	3.216

Table 4.3.1. (Continued)

Species	No. Stands	Score
Ledum groenlandicum (herb)	31	3.223
Lycopodium annotinum	23	3.225
Sorbus decora (tree)	10	3.264
Pyrola secunda	7	3.279
Abies balsamea (shrub)	39	3.296
Diervilla Lonicera (shrub)	32	3.323
Betula papyrifera (tree)	41	3.352
Polygala paucifolia	9	3.384
Epilobium angustifolium	15	3.386
Pyrola virens	16	3.447
Coptis trifolia	38	3.453
Rubus strigosus (herb)	10	3.566
Lycopodium obscurum	36	3.569
Alnus viridis ssp. *crispa* (herb)	17	3.574
Lonicera hirsuta (herb)	8	3.589
Aralia nudicaulis	46	3.618
Sorbus decora (herb)	19	3.623
Tientalis borealis	39	3.670
Clintonia borealis	44	3.690
Dryopteris austriaca	16	3.691
Lycopodium complanatum	14	3.763
Anemone quinquifolia	17	3.771
Galium triflorum	15	3.810
Lonicera canadensis (herb)	7	3.860
Osmunda cinnamomea	11	3.906
Abies balsamea (herb)	27	3.920
Rubus pubescens	33	3.986
Picea glauca (tree)	29	3.993
Abies balsamea (tree)	43	4.029
Populus tremuloides (tree)	35	4.068
Acer spicatum (herb)	24	4.076
Moneses uniflora	8	4.101
Streptopus roseus	30	4.105
Sorbus decora (shrub)	13	4.272
Polytrichum, spp.	23	4.387
Acer spicatum (shrub)	24	4.440
Populus tremuloides (herb)	23	4.559
Acer spicatum (tree)	17	4.635
Viola renifolia	30	4.737
Athyrium Filix-femina	11	4.759
Gymnocarpium Dryopteris	11	4.903
Frageria virginiana	9	4.985
Aster macrophyllus	23	5.145
Carex, spp.	17	5.147
Petasites frigidus	14	5.259
Mitella nuda	13	5.373
Mnium, spp.	10	5.397
Mertensia paniculata	8	5.538
Rhytidiadelphus, spp.	11	5.563

not equally represented in the data set, a species which had the same importance value in all stands would have a score of 3.1. Species with scores from 2.8 to 3.8 have little tendency for either dry or moist sites. Species with scores in this range are either most abundant in the middle of the moisture gradient, or are present throughout the moisture gradient. Species with scores less than 2.8 are characteristic of dryer sites; species with scores greater than 3.8 are characteristic of moister sites. Rarer species scores may be less reliable than common species. Although the scores are based on moisture regime, the gradient is confounded by other factors covarying with moisture regime. Light reaching the forest floor and soil fertility are associated with moisture status. A complex moisture-fertility-light gradient is realized rather than a simple moisture gradient. These factors are not independent; while light or nutrient levels may directly control a species' distribution, the species distribution will also be indicative of the moisture status of a site.

Species with a high ranking on the first DECORANA axis have high moisture gradient weighted averages and species with low ranking have low weighted averages. This substantiates the hypothesis of a moisture gradient across the first DECORANA axis.

Bakuzis and Hansen (1959) determined the moisture requirements of Minnesota forest species using a weighted average of subjective appraisals of the moisture availability in a given stand. Maycock and Curtis (1960) subjectively identified species common to specific portions of the moisture gradient. These studies are in general agreement with the results in Table 4.3.1. Several discrepancies are noted for individual species. Bakuzis and Hansen rated Chiogenes hispidula, Picea mariana, Lycopodium annotinum and Ledum groenlandicum as having high moisture requirements. Apparently, they must be common on lowland sites which Bakuzis and Hansen sampled. Table 4.3.1. shows these species to have no distinct moisture preference, or to be indicative of dry sites. These species have somewhat bimodal distributions, occurring on both dry and very moist sites. Maycock and Curtis (1960) found bimodal distributions for Chiogenes hispidula, Ledum groenlandicum and Picea mariana. Maianthemum canadense and Pyrola secunda were rated dry-site species by Bakuzis and Hansen, while these species indicated no moisture preference in the present study. Maianthemum occurred in 57 stands in the present study, more than any other species. It obviously exhibits no clear moisture preference in upland stands. Maycock and Curtis (1960) agreed that Maianthemum was a ubiquitous species. Aster macrophyllus exhibited a strong preference for moister sites while Bakuzis and Hansen (1959) rated Aster as having intermediate moisture requirements. Maycock and Curtis (1960) differed from the present study by assigning Corylus cornuta to the dry species group and by assigning Rubus pubescens to the group of species that grew everywhere. Corylus cornuta showed no strong moisture preference in the present study, rather, Corylus was excluded from both the driest and moistest sites. Rubus pubescens was restricted from the drier sites in the present study. Some of these differences are due to differences in the portion of the moisture gradient which was sampled. Only upland stands were sampled in the present study. Bakuzis and Hansen studied uplands and lowlands, but sampling was not done evenly across the entire moisture gradient. Minnesota has a slightly different climate and a largely different flora than the present study area. None of Minnesota is in the true boreal zone (Rowe, 1972). The realized niche of a species is affected by the vegetation in which it exists. Species may have evolved slightly differently in the different areas in reaction to other species present in each area. Maycock and Curtis (1960) sampled uplands and lowlands across the boreal forest border throughout the Great Lakes region. The differences in results can be attributed to different study areas.

The species scores in Table 4.3.1. were used to predict moisture regime of each stand. Instead of using moisture regime of each stand to derive a weighted average for each species, the species scores were used to derive a weighted average for each stand. Christensen and Peet (1984) used this technique to derive a predicted pH. A Spearman's rank correlation was performed between observed and predicted moisture regime. Rs equalled .64 ($p < .01$). Christensen and Peet (1984) found observed and predicted pH to also be highly correlated. However, these statistical results are virtually meaningless. The method is tautological. Moisture regime (or pH) is used to derive species moisture (or pH) preferences; then these species scores are used to predict the original value. While original moisture regime scores vary from 0 to 6, the predicted moisture regime scores vary from 2.197 to 4.222. Obviously the predicted moisture regime scores are on a different scale and do not accurately predict the original moisture regime.

4.3.1. <u>Site Index</u>

Although the predicted moisture regime, based on species values, is not an accurate predictor of the original moisture regime, no statement can yet be made on how the two values relate to plant response. One of the values may be a better predictor of plant performance. A Spearman rank correlation was used to compare the two moisture indices with jack pine site index values. The Rs for the soil based moisture regime was .43. The Rs for the vegetation based moisture regime was .46. Both correlation coefficients were significant at $p < .01$. Assuming that jack pine site index is related to available water, then the vegetation and the soil are equally good predictors of the site's moisture status, as it is perceived by the plants.

The rank correlations are highly significant; however neither soil-based nor vegetation-based moisture regimes are adequate predictors of site index. The trends are evident, but the precision is low.

Soil data has been extensively used to predict site index (Carmean, 1975); quantitative vegetation data has been very infrequently used to predict site index (MacLean and Bolsinger, 1973). Soil data consists of many discrete variables which can be used as independent variables in a multiple regression. Vegetation data cannot be used since it doesn't satisfy most of the assumptions of ordinary least squares estimation. The weighted averages technique could be used to derive a predicted site index from vegetation data, but this does not seem profitable. The correlation coefficient would be similar to the correlation coefficient between predicted and observed moisture regimes. This correlation coefficient is lower than typical of successful soil-site studies (Carmean, 1975). The result of the weighted average of species scores would have to be rescaled to recover the original range in site index. The rescaling function would be empirical, non-linear, arbitrary and have no theoretical basis.

The potential use of vegetation to derive a precise value for site index seems poor. This is not a limitation of the vegetation, as such; the vegetation can be used to derive information about the site. Rather, the limitation is on the statistical methods which can be appropriately used with the vegetation data. The vegetation data cannot be used to derive a continuous function to determine site index. Discrete classes of vegetation have been used to predict site quality. However, these classes usually have a large range of site index and a large overlap with other classes (Carmean, 1975). Soil types have a similar, poor relation to site index (Carmean, 1975; Grigal, 1984). It is asking too much to expect discrete vegetation classes to accurately predict a continuous variable such as site index when discrete soil classes fail at the same task.

Figure 4.3.5. shows jack pine site index values superimposed on a DECORANA analysis of all stands with a jack pine importance value exceeding 4.0. The landforms are clearly delineated on the ordination. Site index is lowest on the washed sands of deltas and valley trains. Intermediate site index is found on outwash sands. Outwash sands with a sandy loam A or B horizon tend to have slightly higher site indices. Jack pine height growth is best in mixedwood stands on fine to medium textured soils, although typically jack pine is a small component of such stands. While jack pine growth tends to be better on moraines, there are exceptions. Several very low site indices are found where rooting is restricted by shallow, bouldery or gravelly soils. Hansen (1946) found that jack

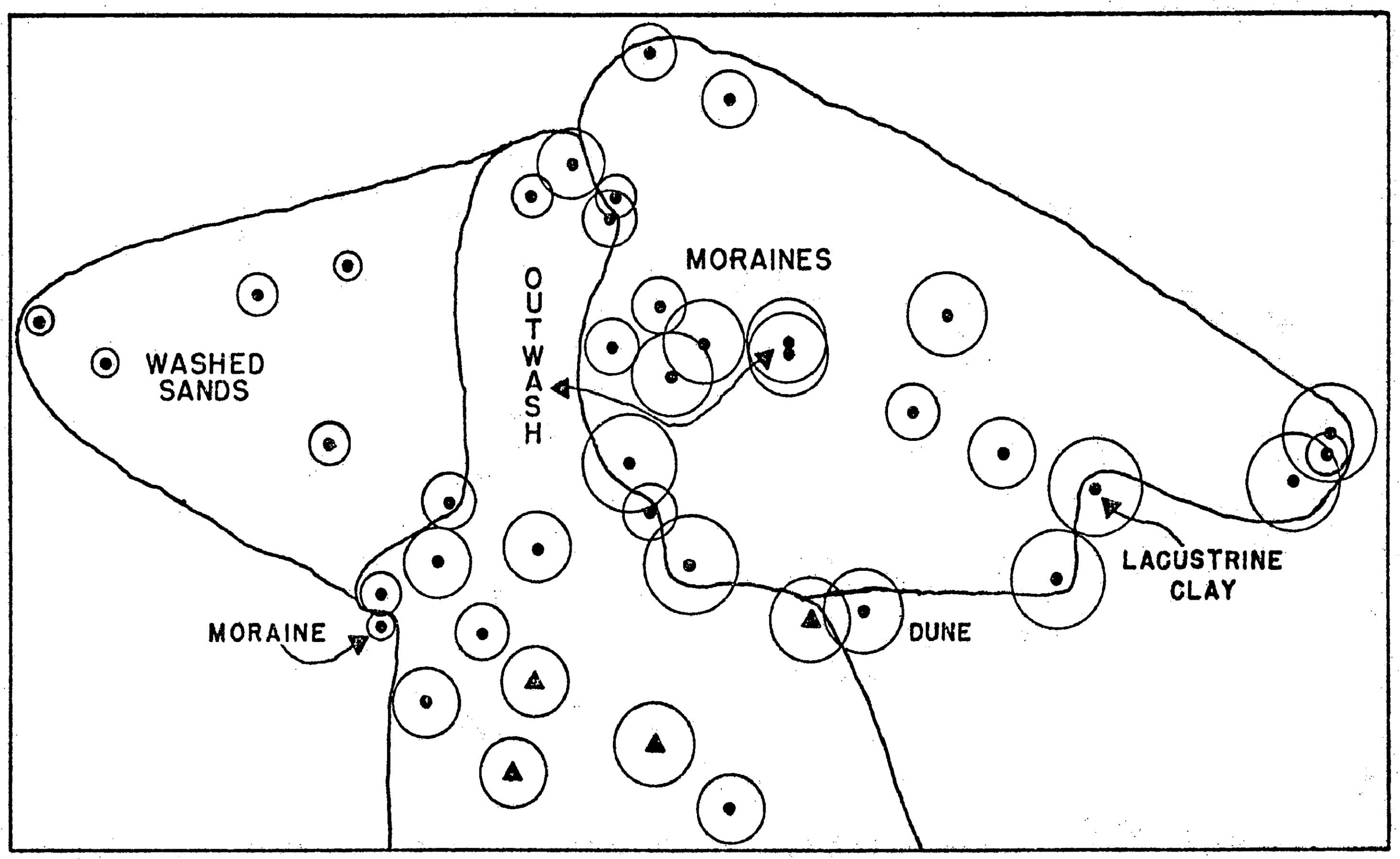


FIGURE 4.3.5. JACK PINE SITE INDEX SUPERIMPOSED ON A DECORANA ORDINATION OF ONLY STANDS WHICH HAVE JACK PINE IMPORTANCE VALUE EXCEEDING FOUR PERCENT. "▲" INDICATES OUTWASH WITH SANDY LOAM HORIZON. KEY:
○ < 15M; ○ = 15 TO 16.9M; ○ = 17 TO 17.9;
○ = 18 TO 18.9M ○ = 19 TO 19.9M; ○ > 20M.

pine height growth was best in mixedwood stands, but that soil factors and site index were poorly correlated. However, since jack pine site indices show a strong relationship with geomorphology, the potential for soil-site work is great. Hansen was severely limited by a lack of modern computers. The general findings of the present study agree with the equally general findings of Ritchie (1961), Rowe (1957) cited in Cayford, Chrosciewicz and Sims (1967), Cayford, Chrosciewicz and Sims (1967), Bedell and MacLean (1952).

Aspen site index is superimposed on the DECORANA ordination in Figure 4.3.6. Aspen generally grows poorly in jack pine dominated stands. Aspen does achieve moderate growth on fresh to moist loess-covered outwash. Loess-capped moraines have good to excellent site indices for aspen. The best aspen sites encountered were loess soils which were enriched with lateral water seepage. Site index is low on shallow or coarse moraines. Kittredge (1938) found poorest aspen growth on outwash; apparently there were no loess-covered outwash in his area. According to Kittredge, fine to medium textured moraines were best and sandy moraines were intermediate for aspen growth. This is in general agreement with the present findings. Kittredge did not use topographic position as a factor. However, sites enriched from lateral seepage were found to be the best aspen sites in the present study.

All other tree species were infrequent in the dominant

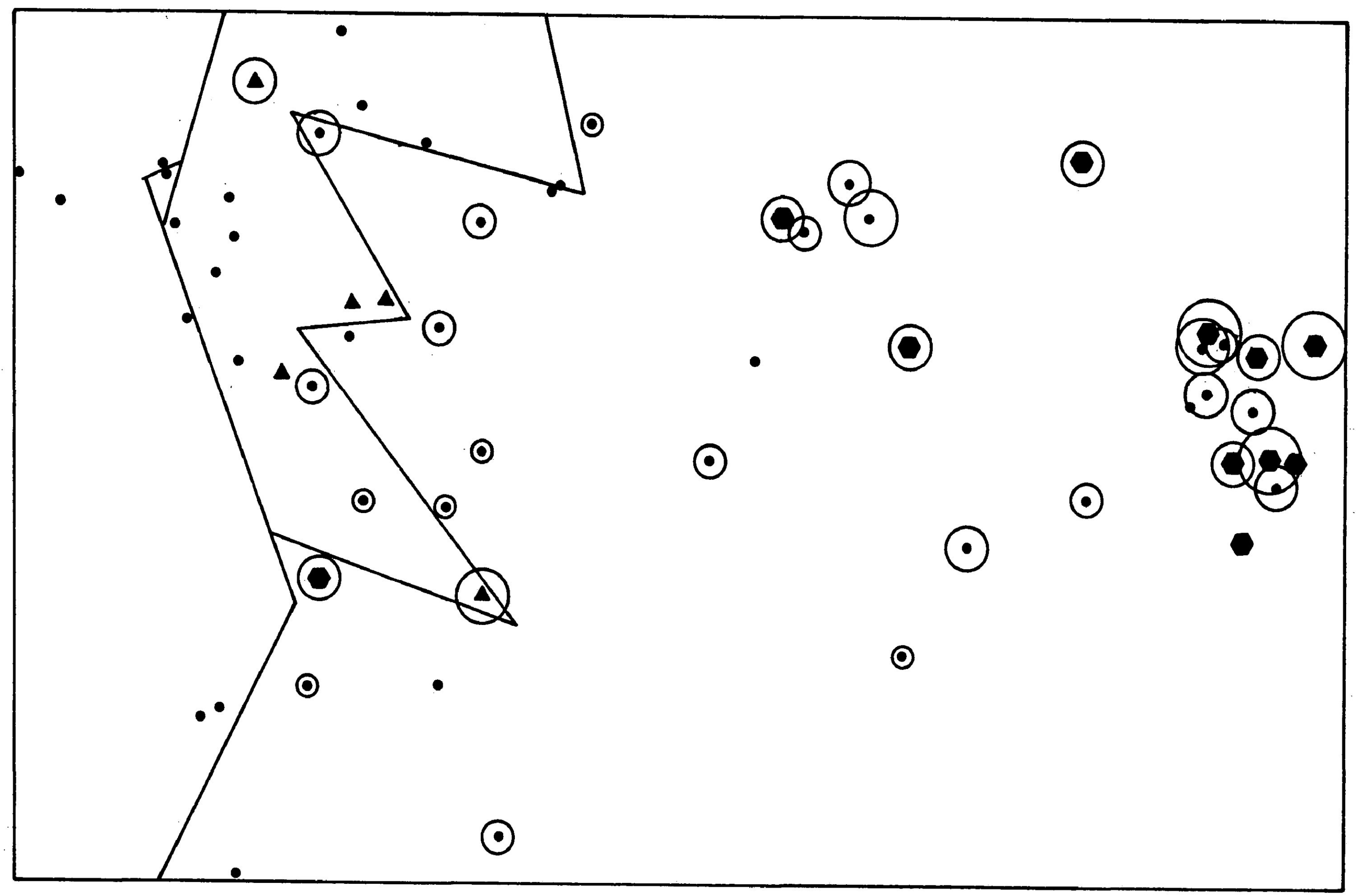


FIGURE 4.3.6. ASPEN SITE INDEX SUPERIMPOSED ON THE FIRST AND SECOND DECORANA AXES OF FIGURE 4.1.2.2.1. LANDFORM TYPES ARE DELINEATED AS ON FIGURE 4.3.2. KEY FOR ASPEN SITE INDEX: ○ ≤ 13.8M ○ = 13.9 TO 16.9M; ○ = 17.0 TO 19.9M; ○ = 20.0 TO 23.1M; ○ ≥ 23.2 M.

or codominant crown class. Therefore, site index cannot be demonstrated across a wide range of site conditions.

4.4. APPLICATIONS TO SILVICULTURE

The previous sections of this thesis have covered the basic ecology of upland stands in the study area. However, much of this basic ecology is directly applicable to silviculture. The implications of the results may not be clear to a practicing forester who has had little exposure to the methods and terminology of ecology. In this section I state more explicitly the silvicultural implications of my results. Admittedly, others could give different interpretations. These applications are not independent of the basic information. They are largely objective; they are based on information derived from the preceeding analyses. Information on community composition, structure, dynamics and productivity were utilized. Recommendations were derived by relating this information to silvicultural reviews and common silvicultural knowledge. Silvicultural reviews which were, more or less, helpful include: Eyre and LeBarron, 1944; Jarvis, et al., 1966; Cayford, Chrosciewicz and Sims, 1967; Sutton, 1969; Benzie, 1977; Johnston, 1977; Perala, 1977; Hacker, Marshall and Erickson, 1983; Safford, 1983; Rudolph, 1984. The recommendations are simplistic; they were meant to be.

There is considerable latitude in their interpretation. The recommendations are intended only as a method to transfer information to a forester who makes silvicultural prescriptions.

4.4.1. Assumptions and Limitations

Silvicultural practices cannot be carried out in a vacuum. Site conditions and the economic environment will determine how appropriate a given practice may be.

4.4.1.1. Study Area

The results of this study are only applicable to the study area or to an area with similar soils, climate and vegetation. The surficial geology and climate were covered in the description of the study area. The vegetation has been described throughout much of this thesis. Only upland stands have been studied.

4.4.1.2. Management Intensity

Management implies action. All actions have associated costs. Increased levels of management imply increased costs. These costs must be weighed against the benefits which the actions obtain. No particular level of management is best. The level of management must be in accord with the economic environment. Bananas could be grown at the North Pole. This would be an acceptable level of management if it ever becomes economically practical to build a controlled environment suitable for banana production at the North Pole.

Stone (1975) divided forests managed at different intensities into wildlands, exploited forests, regulated forests, and domesticated forests. Wildlands are not managed. Exploited forests are dominated by extraction. Regulated forests are regenerated to native species to provide yields similar to the original forest. Stone called this "Ecological Forestry". Domesticated forests use exotic species or intensive cultural practices, or both, to increase yields. A seed orchard would be an extreme example of a domesticated forest. Stone termed the management required to produce domesticated forests, "Technological Forestry".

Since I am assuming some form of management is appropriate, wildlands can be eliminated as a suitable management intensity. Exploited forests should be eliminated as irresponsible management.

The boreal forest in northwestern Ontario has long been an exploited forest. Attempts have been made to intensify management. This intensification is based on the assumption that more intensive forestry is, somehow, better forestry. The intensification may be too great.

The first crop of trees came cheaply. No one had to pay to regenerate and grow the original forests. Forestry was primarily extraction. Thus, by definition, the boreal forest was an exploited forest. This level of forestry is appropriate as long as there is a frontier where extraction can be extended. When the frontier diminishes and second growth must be harvested, then the consequences of exploitation are felt. Then someone must start paying to regenerate and grow the next crop. A regulated forest must be developed.

In my study area, a regulated forest is superior to the domesticated forest because, currently, most intensive practices will not pay for themselves. Baskerville (1983) stated, "At current interest rates, standard discounting practices would prohibit all activities except exploitation [of the boreal forest]." The boreal forest cannot compete on a hectare per hectare basis with the southern pines or the Pacific Coast conifers. The economics combined with the slow growth rate of the boreal forest force us to minimize costs. Given the current stumpage prices and alternate rate of return, very little, if any, of the boreal forest in the area is suited for intensive forestry (technological forestry in the terminology of Stone, 1975). Ecological forestry is most suited to the characteristics of the boreal forest of northwest Ontario. Ecological characteristics of the boreal forest must be used to the advantage of forest management. The decision is ultimately economic. Ecological forestry is less expensive.

My silvicultural recommendations are based on the following assumptions: 1) costs must be minimized; 2) the conifer, particularly spruce and secondarily pine, component of the forest must be maximized. These two assumptions are often at odds. I have had to balance them to make recommendations.

4.4.2. Delineation of Land Types

The classification of plant communities failed to show discrete associations. My results show that a classification of plant communities for management purposes would be arbitrary. The classification would be based on numerical characteristics of the data set which do not have a strong ecological basis. The units would be indicative of characteristics of the data set which would not truly represent distinct differences in the field.

In my literature review I stated that there is considerable theoretical and empirical evidence to assume that discrete associations only occur as an artifact of subjective sampling methods and of subjective analytical methods. The most distinct, the most real, plant associations are often more easily identified by environmental conditions (for example, Whittaker, 1956; Mueller-Dombois, 1964; Peet, 1980). An a priori decision to base a classification on any single factor seems fatuous. A clear model of the landscape can only be developed by considering several alternatives.

Instead of plant communities, silvicultural alternatives will be considered for different land types. Land types are not absolutely discrete; however, they are more discrete than plant communities. The land types are based on simple geomorphological features. These geomorphological features have been combined or divided based on differences which imply different silvicultural practices. The land types I will describe are conceptually similar to the landtypes of Hills(1952; 1960; 1961), although they were derived very differently. Within a land type, silvicultural practices are discussed for various cover types which may be present. By combining land types with the silvics of the individual species, an ecosystematic approach is taken; both abiotic and biotic elements are considered.

Landforms were displayed on the DECORANA ordination in Figure 4.3.2. The glaciofluvial deposits appear distinct from the moraines. Therefore, my first dichotomy separates glaciofluvial deposits from moraines.

Three land types are distinguished on level to slightly rolling glaciofluvial deposits: 1) medium sands of deltaic or valley train origin which have been affected by lake action. This land type is quite distinct on Figure 4.3.2. 2) outwash which is sand or loamy sand throughout. 3) outwash with a sandy loam horizon. The finer horizon may be in the A or B horizon. The sandy loam horizon may be due to a thin layer of loess, or to a slowing of the outwash flow during deposition. These finer soils indicate a moister habitat. Outwash which is moister due to topographic position could also be included in this land type. This land type is not absolutely distinct on Figure 4.3.2.; it differentiates better on Figure 4.3.5. More black spruce is present on this land type than on coarser outwash. Also, jack pine site index tends to be higher than on coarser outwash (Table 4.4.2.1.). These characteristics were deemed important enough to separate this landtype from the more general, coarser outwash land type.

Four land types are distinguished on moraines: 1) shallow ground moraines; 2) sandy to loamy sand ground or end moraines; 3) ground or end moraines with sandy loam to clay loam soils; 4) ground or end moraines with a loess cap. The shallow ground moraines are arbitrarily given the maximum average depth of 50 cm. A bouldery or cobbly C horizon which excludes all roots may effectively reduce soil depth and thus be considered a shallow moraine. None of my sampled stands are rock outcrops. Typically, rock outcrops were too small and too poorly stocked to meet the sampling criteria. Black spruce is abundant with jack

Table 4.4.2.1. Average and range (in parentheses) of jack pine and aspen site index for the seven land types. Site index equals height in meters at a base age of fifty years.

Land Type	Plots	Aspen	Plots	Jack Pine
1) Outwash with sands or loamy sands throughout			10	17.8(15.3-19.8)
2) Outwash with a sandy loam horizon			4	18.8(18.1-19.7)
3) Deltaic sands affected by lake action			6	15.1(13.0-17.9)
4) Shallow ground moraine	3	12.5(10.7-13.7)	3	13.7(11.5-15.5)
5) Sand or loamy sand moraines	10	16.1(13.1-18.9)	11	18.4(15.1-21.0)
6) Moraines with sandy loam or finer loam soils	6	17.5(14.9-20.1)	3	19.2(17.9-21.0)
7) Moraines with a loess cap	9	20.4(17.7-23.8)	4	19.5(18.1-20.8)
7a) Loess receiving seepage water	3	23.5(23.2-23.8)		

pine, balsam fir, paper birch and aspen common on the shallow ground moraines.

None of the land types on moraines are truly distinct. They grade into one another. They are based on two trends indicated in the previous analyses. As moraines get deeper and finer-textured, site index increases and the hardwood and balsam fir component increases. Site index values are shown in Table 4.4.2.1. Although there is some overlap, there is a clear relationship of site index to the land types.

The cover type trend is less distinct. These land types are not delineated on Figure 4.3.2. The shallow moraines are on the lower edge of the moraine group. The sandy moraines tend toward the upper left portion of the moraines, although some aspen dominated sandy moraines are towards the right portion of the ordination. The loess-capped moraines appear on the moister, right portion of the ordination graph. A few of these loess-capped moraines are in the middle of the moraine group; these stands are on the top of end moraines and have somewhat better drainage. Jack pine and the spruces are more abundant here than on other loess-covered moraines. The loamy moraines appear between and within these groups. Actually, all groups overlap with each other. There is too much intermingling of these groups to actually portray them on a figure. However, these groups do have utility. The groups are related to potential productivity, as indicated by site index. The variability of cover types within a land type is not a drawback. When silvicultural practices are considered for these land types, cover type and the silvics of the component species will be integrated into the discussion.

4.4.3. Silvicultural Considerations for Each Land Type

4.4.3.1. Outwash with Sands or Loamy Sands Throughout

This land type is typically dominated by almost pure stands of jack pine. Competition from other species is slight. Average jack pine site index is 17.8m (range 15.3 to 19.8m). Jack pine can be easily and satisfactorily regenerated on these sites by scarifying and lopping and scattering cone bearing slash (Cayford, Chrosciewicz and Sims, 1967; Ball, 1975; Hacker, Marshall and Erickson, 1983). This method simulates the natural regeneration of jack pine after fires. Scarification is used to prepare the seed bed rather than a hot natural fire. Serotinous jack pine cones will open when exposed to the heat of a fire or when exposed to the heat at the ground surface. Breaking and scattering slash can be performed during scarification. Rolling drum choppers, sharkfin barrels or disc plows may adequately modify and distribute cone-bearing slash. This will eliminate an additional operation of hand lopping and scattering. Harvesting methods which leave slash on site should be used. Mechanical harvesters which strip branches will produce slash which is more easily modified by scarification procedures. Harvesting methods which leave whole tops may require hand lopping and scattering. Planting jack pine is an unnecessary expense on these sites when an abundance of cones exist in the canopy. Seeding should be considered when cones are insufficient to achieve adequate regeneration (Benzie, 1977; Clark, 1984; Rudolph, 1984; Smith, 1984). Stands older than sixty-five years may have opened up, particularly after a light fire (Carleton, 1982a;b). Competition from balsam fir and hardwood trees and shrubs will be more severe in such stands. A seed tree cut followed by burning and scarification will reduce brush competition (Moore, 1984). Aerial or direct seeding can be performed during or after scarification in lieu of the seed tree cut (Chrosciewicz, 1983; Clark, 1984; Smith, 1984). Herbicide release treatment may be required if a prescribed burn is low intensity.

4.4.3.2. Outwash With a Sandy Loam Horizon.

The sandy loam horizon is due to either a thin loess layer or a slowing of water currents during the deposition of the outwash. Jack pine is the most abundant species; there is typically more black spruce than in the previous land type. Deciduous species and balsam fir are sometimes present. Competition is greater than on dryer sands (Eyre and LeBarron, 1944, and this thesis). Jack pine site index is slightly higher than on coarser outwash (18.8m average, 18.1 to 19.7m range). Regeneration can be obtained as on the previous land type. A seed tree, burn and scarify method, or seeding after site preparation, may be best due to increased competition on these sites.

Management for black spruce is a viable alternative on these sites. Planting would be required to regenerate black spruce. Black spruce is naturally more abundant than in the previous land type; survival may be greater on these sites. Productivity is higher than on the other outwash, making planting more economically viable. Flat outwash is easier to treat and plant than moraines. Regeneration to black spruce may be the best alternative, since black spruce is preferred by industry. Black spruce is desired and this land type is more suitable for black spruce production than other, dryer outwash.

4.4.3.3. Deltaic or Valley Train Sands Affected by Lake Action

This land type differs slightly from outwash. Productivity is lower (15.1m average jack pine site index, 13.0 to 17.9m range), but regeneration may be obtained by the same methods.

4.4.3.4. Shallow Ground Moraines

Average soil depth of shallow moraines may vary from 10 to 50 cm; a bouldery C horizon will effectively reduce soil depth. Rock outcrops are not included in this land type. Black spruce and jack pine dominate with paper birch, aspen and balsam fir commonly present. These stands invariably regenerated after a hot fire. The stands are broadly even-aged and may extend over large areas. Productivity of these stands is low. Average jack pine site index is 13.7m (11.5 to 15.5m range); average aspen site index is 12.5m (10.7 to 13.7m range).

Strip cutting was initiated to limit erosion on fragile sites (Jeglum, 1980). However, strip cutting used on shallow soil upland black spruce has led to fair to poor stocking of desirable species and an increase in the undesirable balsam fir and hardwoods (Fraser, et al., 1976; Jeglum, 1982; 1983). Furthermore, strip cutting costs more than harvesting larger areas (Ketcheson, 1979).

The original stands were initiated after hot fires. Such fires covered large areas of the landscape and these areas regenerated naturally to desirable species. These sites have low productivity. However, low productivity is not equivalent to fragility. Fragility is a term that exists in the minds of men. It is not a quantifiable characteristic of the ecosystem. Ecologists use the term stability. One component of stability is resilience - whether a similar stand will occur after a disturbance (Leps, Osbornova-Kosinova and Rejmanek, 1982). By definition, the upland shallow-soil black spruce ecosystem is highly stable since, after natural fires, a new black spruce stand regenerates. Black spruce is adapted to fire; while a recently burned stand may appear devastated, spruce regeneration will soon occur (Larsen, 1980).

Silvicultural practice would do well to emulate natural processes when these natural processes provide adequate quality stands. The following silvicultural alternative is derived from this viewpoint. An appropriate regeneration system would be a seed tree cut followed by a prescribed burn. This method has been applied to jack pine (Hacker, Marshall and Erickson, 1983) but not to black spruce, to my knowledge. Feather mosses, the dominant ground vegetation on this land type, produce a poor seedbed for black spruce (Johnston, 1977). Burning will improve the seedbed and reduce competition (Johnston, 1977).

Research would be required to derive recommendations on the number of seed trees required to regenerate the stand. Seed trees should be chosen which have a large number of serotinous cones and which have naturally pruned the lower branches. Such trees are fairly common in closed-crown upland black spruce. Some scorching of the crowns can be expected; slash should not be piled beneath seed trees. The seed tree method is highly dependent on seeding periodicity. However, serotinous cones (or semi-serotinous for black spruce) assure an adequate seed source. This tremendous silvical advantage should not be forsaken. Some light mechanical site preparation may be necessary after the prescribed burn, particularly if the fire is low intensity. The best situation would be a hot prescribed burn during suitable weather periods. If logistical problems do not allow burning during such weather, a prescribed burn followed by some scarification should be sufficient. If the soil is very shallow, (less than 15cm, say) and the organic mat is the main rooting medium, then the prescribed burn should be fairly light. The moss layer should be killed to prepare a seed bed, but most of the organic mat should remain.

It is mandatory that site preparation be carried out shortly after logging. Exposed black spruce trees on shallow soil are susceptible to windthrow (Fleming and Crossfield, 1983). The seed bed must be prepared while the seed trees are still standing. Winter logging followed by summer burning and scarification would probably be best.

The seed trees will eventually be windthrown. Salvage operations probably aren't feasible.

This recommendation is innovative and controversial. Research is required to derive specific, practical guidelines. It is possible that unforeseen factors could limit the use of this method. For example, it might be impossible to keep the seed trees standing long enough to adequately seed the area, no matter how many seed trees are left. However, I believe the method has potential.

These black spruce sites have low productivity and long rotations will be required. As long as they are adequately regenerated, they can provide considerable quantities of black spruce pulp.

4.4.3.5. Sand or Loamy Sand Ground or End Moraines

Stands on this land type may be dominated by aspen, birch, jack pine, balsam fir or black spruce; white spruce may also occur in some stands. Appropriate silviculture is determined by the species present in the stand and the species which are desired in the subsequent stand. The variability within this land type is tremendous. A forester needs to determine the characteristics of the stand and prescribe individual treatment for each stand. I will give very general guidelines based on the dominant species.

Jack pine dominated stands may contain considerable to insignificant amounts of other species. Jack pine tends to grow best on sites where balsam fir, white spruce or the hardwoods are present and jack pine grows poorly in stands of almost pure jack pine or where jack pine is mixed with black spruce. Black spruce may indicate moister outwashes, but it indicates coarser or shallower tills. Average jack pine site index is 18.4m (15.1 to 21m range). Potential hardwood competition is greater on tills than outwash, although tills don't necessarily have a greater water holding capacity. Sandy tills may be as coarse as outwash and have additional gravel and boulders. The heterogeneity of tills, compared to the homogeneity of outwash, may produce moister microsites in a matrix of dryer soil. Individuals may utilize these moister microsites to survive. Lopping and scattering slash may not succeed due to greater competition (Hacker, Marshall and Erickson, 1983). A seed-tree followed by a prescribed burn and scarification is more suitable for these sites. Scarification must be carried out shortly after burning. Heat from the prescribed burn will open cones of the seed trees and seed will begin to be released. Some of the intricacies of the seed tree and burn method for jack pine are reviewed by Hacker, Marshall and Erickson (1983). Seeding could also be used as an alternative to a seed-tree system (Clark, 1984; Smith, 1984).

Sandy moraines tend to be poor aspen sites (16.1m average site index; 13.1 to 18.9m range), but aspen frequently dominates such sites. Conversion to another species may slightly increase productivity. This may not be economically advantageous. Aspen eradication would require considerable effort including herbicides, severe site preparation, or both. Precedence was found to be important in determining subsequent vegetation. Aspen root suckers can quickly gain precedence over much of the site. Eradicating aspen may not be worthwhile since the treatment is difficult and this land type is not exceptionally productive. Unless conversion is necessary, regeneration by aspen suckers should be preferred where aspen dominates. Balsam fir or paper birch stands can be more easily converted to other species.

Balsam fir can be easily regenerated by advance regeneration present after clearcutting. If balsam fir is not desired, either a prescribed burn or severe scarification can eliminate the fir. The scarification must cover the entire area rather than patches or furrows. Jack pine or black spruce should be planted.

Paper birch can be regenerated by the seed tree system. Scarification must follow the seed tree cut (Bjorkbom, 1967; Marquis, 1969; Safford, 1983). If elimination of birch is desired, stump sprouting must be eliminated by exposing or uprooting stumps during scarification, or by herbicide. Paper birch residuals that remain after logging inadvertantly produce a paper birch seed tree cut. All paper birch stems must be cut during logging if a paper birch stand is not desired. Planting jack pine or black spruce should follow scarification.

Black spruce dominated stands can be regenerated similarly to shallow soil black spruce stands. Competition from aspen and birch will be more abundant on these deeper soils, so release treatments may be necessary to shorten rotations.

Most stands on this land type are not monospecific. A forester must determine which species are present in what quantity and which species are desirable in the subsequent stand. The forester must integrate the considerations presented above to come to a final decision. It will be difficult to obtain an absolute monospecific stand. The treatments favor individual species, but no species will be absolutely excluded. Treatments can be combined to favor two or more species at the expense of another.

4.4.3.6. Moraines with Sandy Loam or Finer Loam Soils

Mixedwood stands of various species composition are common on this land type. Jack pine height growth is superior to previous land types. Average jack pine site index is 19.2m (17.9 to 21m range). However, greater competition on these sites precludes management for jack pine until more intensive management becomes feasible.

This land type has average to above average site indices for aspen (17.5m average; 14.9 to 20.1m range).

The elimination or regeneration of the various species should be carried out similarly to the previous land type. Although aspen grows better on this land type, other species do also. Despite greater competition from aspen, conversion may be a more economically viable alternative. Black spruce and white spruce are species most suited for plantation establishment on this land type.

Black spruce typically doesn't form a large enough percentage of the stand to use natural regeneration. If black spruce is well distributed throughout the stand, a seed tree, burn and scarify treatment could be prescribed. This would require additional treatment to eliminate hardwood species. A large percentage of the possible black spruce harvest would have to be invested in seed trees. Black spruce tends to be in intermediate or suppressed crown positions in these stands. Haavisto (1975) has shown that inferior crown class black spruce have few seed. Natural regeneration of black spruce would only be likely to succeed in very exceptional stands. Artificial seeding of spruces has had poor results (Jarvis, 1966; Jarvis, et al., 1966; Fraser, 1981; Cayford, 1983). Natural seeding of small blocks increases the balsam fir component (Hughes, 1967). Therefore, if conversion is required, black spruce or white spruce (or an exotic species) must be planted after thorough site preparation. Subsequent release treatments of the plantations will probably be required to ensure adequate stocking.

4.4.3.7. Moraines with a Loess Cap

This land type may be the most productive in the study area. Average aspen site index is 20.4m (range 17.7 to 23.8m); Average jack pine site index is 19.5m (range 18.1 to 20.8m). All boreal tree species may occur in these stands. Aspen usually has a large component in all stands.

The most productive situation occurs when the site receives seepage water. Average aspen site index is 23.5m (23.2 to 23.8m range). Aspen usually dominates these sites, but other species are often present. Aspen should be regenerated on these seepage sites because these sites are well-suited for production of veneer grade aspen logs. Root suckering will be sufficient to restock the stand. Scarification or a light prescribed burn may be used to eliminate balsam fir, when present. Thinning can shorten the rotation. See Perala (1977; 1978) or Steneker and Jarvis (1966) for appropriate thinning schedules.

White spruce sawlog production should be considered on the tops and upper slopes of loess covered end moraines and on relatively flat, well drained loess covered ground moraines. On low-lying ground moraine a hardwood cover may be required to reduce frost damage to planted white spruce seedlings (Sutton, 1969). Herbicide would be needed to release the spruce after they have become established. A second release may be necessary due to potentially severe competition on these sites.

Aspen should be regenerated on all steep slopes. Aspen quickly revegetates a site and can reduce loss of the easily eroded loess.

Natural regeneration of hardwoods or planting of black spruce should be carried out on other sites within this land type. Considerations mentioned in the other moraines must be followed. Regeneration should be achieved promptly after scarification. It would be unfortunate if the best upland soils in the study area were eroded away.

4.4.3.8. Getting Out of the Ivory Tower

I have not attempted to give prescriptions, as such. The only one capable of prescribing silvicultural treatments is a forester in the field. I have given no hard-and-fast rules to follow. The only hard-and-fast rule in forestry is that there are no hard-and-fast rules. Instead, I have tried to give some general information and some general guidelines. It is much better to give a forester information and allow him to make a decision rather than giving him a key and telling him, "You will regenerate operation group X by method Y." There is too much variation in the real world to be included in any classification. A forester must interpret. For example, a loamy moraine dominated by black spruce would probably best be treated by my recommendations for sandy moraine black spruce rather than my recommendations for deeper loamy moraines. I just didn't happen to find any deep loamy moraines where black spruce was the most abundant species. A greater yield and more competition would be expected. If a broad esker happened to have a thick layer of loess on the slope, this site could be best treated as a loess covered moraine. Everything is open to interpretation. A classification may condense information, but judgement is required to determine how the information should be applied to a particular case. A classification goes from the specific to the general. The decision maker must go from the general to the specific case at hand. I have attempted to pass along some of the information I've obtained. I hope that someone may make use of it.

5. Literature Cited

Alexander, M.E. and D.L. Euler. 1981. Ecological role of fire in the uncut boreal mixedwood forest. In Boreal Mixedwood Symposium. R.D. Whitney and K.M. McClain, eds. Can. For. Serv. Great Lakes For. Res. Centre. COJFRC Symposium Proceedings O-P-9. p.42-64.

Auclair, A.N. and G. Cottam. 1971. Dynamics of black cherry (Prunus serotina erhr.) in southern Wisconsin oak forests. Ecol. Monogr. 41, 153-177.

Auclair, A.N. and F.G. Goff. 1974. Interspecific diameter differentiation as a measure of species replacement potential. Can. J. For. Res. 4, 424-434.

Bakuzis, E.V. and H.L. Hansen. 1959. A provisional assessment of species synecological requirements in Minnesota forests. Minn. For. Note No. 84. 2pp.

Ball, W.J. 1975. An appraisal of natural regeneration on scarified jack pine cutovers, Saskatchewan. Env. Can. Can. For. Serv. North. For. Res. Cen. Inf. Rept. NOR-X-136. 20pp.

Barnes, B.V. 1983. Ecosystem Classification -- Number 1 Priority. In Proceedings: Artificial Regeneration of Conifers in the Upper Great Lakes Region. G.D. Mroz, J.F. Berner, eds. Mich. Techn. Univ., Houghton, MI. p 8-30.

Barnes, B.V., K.S. Pregitzer, T.A. Spies, and V.H. Spooner. 1982. Ecological Forest Site Classification. J. For. 80, 493-498.

Baskerville, G. 1983. A resource management viewpoint of boreal forest ecosystems. In Resources and Dynamics of the Boreal Zone. R.W. Wein, R. R. Riewe, I.R. Methven, eds. ACUNS, Ottawa. p. 534-544.

Beals, E.W. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bull. 72, 156-181.

Beals, E.W. 1965. Species patterns in a Lebanese Poterietum. Vegetatio 13, 69-87.

Beals, E.W. 1973. Ordination: mathematical elegance and ecological naivete. J. Ecol. 61, 23-35.

Bedell, G.H.D. and D.W. MacLean. 1952. Nipigon growth and yield survey. Canada Dept. Res. Dev. For. Branch. Silv. Res. Note 101. 51pp.

Belisle, J.(ed.) 1980. Field Manual for Describing Soils. Ontario Inst. Ped. University of Guelph. Guelph, Ontario.

Bellefleur, P. and A.N. Auclair. 1972. Comparative ecology of Quebec boreal forests: a numerical approach to modelling. Can. J. Bot. 50, 2357-2379.

Benzie, J.W. 1977. Manager's handbook for jack pine in the north central States. U.S.D.A. For. Serv. North Central For. Expt. Stn. Gen. Tech. Rept. NC-32. 18pp.

Bicknell, S.H. 1982. Development of canopy stratification during early succession in northern hardwoods. Forest Ecology Manage. 4, 41-51.

Bitterlich, W. 1948. Die Winkelzahlprobe. Allgem. Forest-u, Holzw. Ztg. 59(1/2), 4-5.

Bjorkbom, J.C. 1967. Seedbed preparation methods for paper birch. U.S.D.A. For. Serv. Northeastern For. Expt. Stn. Res. Pap. NE-79. 15pp.

Black, R.A. and L.C. Bliss. 1978. Recovery sequence of Picea mariana - Vaccinium uliginosum forests after burning near Inuvik, Northwest Territories, Canada. Can. J. Bot. 56, 2020-2030.

Braun-Blanquet, J. 1932. Plant Sociology; The Study of Plant Communities. (Transl. by G.D. Fuller and H.S. Conard) McGraw-Hill, New York. 438 pp.

Bray, J.R. 1956. Gap phase replacement in a maple-basswood forest. Ecology 37, 598-600.

Bray, J.R. and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27, 325-349.

Buell, M.F. and W.A. Niering. 1957. Fir-spruce-birch forest in northern Minnesota. Ecology 38, 602-610.

Cajander, A.K. 1926. The theory of forest types. ACTA For. Fenn. 29, 1-108.

Carleton, T.J. 1982a. The composition, diversity, and heterogeneity of some jack pine (Pinus banksiana) stands in northeastern Ontario. Can. J. Bot. 60, 2629-2636.

Carleton, T.J. 1982b. The pattern of invasion and establishment of Picea mariana (Mill.) B.S.P. into the subcanopy layers of Pinus banksiana Lamb. dominated stands. Can. J. For. Res. 12, 973-984.

Carleton, T.J. and P.F. Maycock. 1978. Dynamics of the boreal forest south of James Bay. Can. J. Bot. 56, 1157-1173.

Carleton, T.J. and P.F. Maycock. 1980. Vegetation of the boreal forests south of James Bay: non-centered component analysis of the vascular flora. Ecology 61, 1199-1212.

Carleton, T.J. and P.F. Maycock. 1981. Understorey-canopy affinities in boreal forest vegetation. Can. J. Bot. 59, 1709-1716.

Carleton, T.J. and S.J. Taylor. 1983. The structure and composition of a wooded urban ravine system. Can. J. Bot. 61, 1392-1401.

Carmean, W.H. 1975. Forest site quality evaluation in the United States. Advances in Agronomy 27, 209-268.

Carmean, W.H. 1978. Site index curves for northern hardwoods in northern Wisconsin and upper Michigan. North Central Forest Experiment Station Research Paper NC-160. U.S.D.A. Forest Service. 16pp.

Carmean, W.H. and J.T. Hahn. 1981. Revised site index curves for balsam fir and white spruce in the lake states. North Central Forest Experiment Station. Research Note NC-269. U.S.D.A. Forest Service. 4pp.

Cayford, J.H. 1966. Operational trials of regeneration methods for jack pine in southeastern Manitoba. Can. Dept. For. Dept. For. Pub. No. 1165.

Cayford, J.H. (ed.) 1973. Direct Seeding Symposium. Dept. Env. Can. For. Serv. Publ. No. 1339. 178pp.

Cayford, J.H. and D.J. McRae. 1983. The ecological role of fire in jack pine forests. <u>In</u> The Role of Fire in Northern Circumpolar Ecosystems. R.W. Wein, D.A. MacLean, eds. Wiley and Sons, New York. p. 183-199.

Cayford, J.H., Z. Chrosciewicz and H.P. Sims. 1967. A review of silvicultural research in jack pine. Canada Dept. For. Rural Dev. For. Branch. Dept. Publ. No. 1173. 255pp.

Chapman, L.J. and M.K. Thomas. 1968. The climate of northern Ontario. Can. Dept. Trans. Clim. Study No. 6. 58pp.

Christensen, N.L. and R.K. Peet. 1984. Convergence during secondary forest succession. J. Ecology 72, 25-36.

Chrosciewicz, Z. 1983. Jack pine regeneration following postcut burning and seeding in central Saskatchewan. Dept. Env. Can. For. Serv. North. For. Res. Cen. Info. Rept. NOR-X-253. 11pp.

Clark, A. 1984. Ground seeding requirements for jack pine regeneration. In Jack Pine Symposium. C.R. Smith and G. Brown, co-chairmen. Can. For. Serv. Great Lakes For. Res. Cen. COJFRC Symposium Proceedings O-P-12. p.87-92.

Clements, F.E. 1936. Nature and structure of the climax. J. Ecology 24, 252-284.

Coffman, M.S., E.A. Alynak and R. Resovsky. 1980. Field Guide: Habitat Classification System. Cooperative Res. For. Soils, Mich. Techn. Univ., Houghton, Mich.

Coffman, M.S. and N.J. Hall. 1976. The use of plant indicator species to predict productivity in Red Pine plantations. Mich. Acad. 9, 157-172.

Coffman, M.S. and G.L. Willis. 1977. The use of indicator species to classify climax sugar maple and eastern hemlock forests in upper Michigan. Forest Ecology Manage. 1, 149-168.

Cogbill, C.V. 1982. Analysis of vegetation, environment and dynamics in the boreal forests of the Laurentian Highlands, Quebec. Ph.D. thesis. University of Toronto. 244pp.

Corns, I.G.W. 1983. Forest community types of west-central Alberta in relation to selected environmental factors. Can. J. For. Res. 13, 995-1010.

Cottam, G. 1955. Correction for various exclusion angles in the random pairs method. Ecology 36, 271-287.

Cottam, G. and J.T. Curtis. 1949. A method for making rapid surveys of woodlands by means of pairs of randomly selected trees. Ecology 30, 101-104.

Cottam, G. and J.T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37, 451-460.

Cottam, G., J.T. Curtis and B.W. Hale. 1953. Some sampling characteristics of a population of randomly dispersed individuals. Ecology 34, 741-757.

Cottam, G., F.G. Goff and R.H. Whittaker. 1978. Wisconsin comparative ordination. In Ordination of Plant Communities. R.H. Whittaker, ed. Junk, The Hague. p. 185-214.

Crum, H.A., W.C. Steere and L.E. Anderson. 1973. A new list of mosses of North America north of Mexico. Bryologist 76, 85-130.

Curtis, J.T. and R.P. McIntosh. 1951. An upland forest continuum in the prarie-forest border region of Wisconsin. Ecology 32, 476-496.

Damman, A.W.H. 1964. Some forest types of central Newfoundland and their relation to environmental factors. For. Sci. Monogr. 8. 62pp.

Damman, A.W.H. 1971. Effect of vegetation changes on the fertility of a Newfoundland forest site. Ecol. Monogr. 41, 253-270.

Daniel, T.W., J.A. Helms and F.S. Baker. 1979. Principles of Silviculture. Second ed. McGraw-Hill, New York. 500pp.

Daubenmire, R.F. 1976. The use of vegetation in assessing the productivity of forest lands. Bot. Rev. 42, 115-143.

Daubenmire, R. and J.B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Exp. Stn. Techn. Bull. 60. 104pp.

Davis, R.B. 1966. Spruce-fir forests of the coast of Maine. Ecol. Monogr. 36, 79-94.

Day, R.J. 1972. Stand structure, succession and use of southern Alberta's Rocky Mountain forest. Ecology 53, 472-478.

Day, R.J. and G.T. Woods. 1977. The role of wildfire in the ecology of jack and red pine forests in Quetico Provincial Park. Ont. Min. Nat. Resour., Quetico Prov. Park Fire Ecol. Std. Rept. 5. 79pp.

Day, R.J. and E.M. Harvey. 1981. Forest dynamics in the boreal mixedwood. In Boreal Mixedwood Symposium. R.D. Whitney and K.M. McClain, eds. Can. For. Serv. Great Lakes For. Res. Centre. COJFRC Symposium Proceedings O-P-9. p. 29-41.

Delaney, B.B. and M.J. Cahill. 1978. A pattern of forest types on ribbed moraines in eastern Newfoundland. Can. J. For. Res. 8, 116-120.

Dix, R.L. and J.M.A. Swan. 1971. The roles of disturbance and succesion in upland forest at Candle Lake, Saskatchewan. Can. J. Bot. 49, 657-676.

Drury, W.H. and I.C.T. Nisbet. 1973. Succession. J. Arnold Arbor. 54, 331-368.

Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition - a factor in old-field vegetation development. Vegetatio 4, 412-417.

Eyre, F.H. and R.K. LeBarron. 1944. Management of jack pine stands in the Lake States. U.S.D.A. For. Serv. Lake States For. Expt. Stn., Tech. Bull. 863. 66pp.

Farmer, R.E., P. Knowles and W.H. Parker. 1983. Genetic resources of the North American Boreal Forest. In Resources and Dynamics of the Boreal Zone. R.W. Wein, R.R. Riewe and I.R. Methven, eds. ACUNS, Ottawa. p.40-51.

Fleming, R.L. and R.M. Crossfield. 1983. Strip cutting in shallow-soil upland black spruce near Nipigon, Ontario. III Windfall and mortality in the leave strips: Preliminary results. Can. For. Serv. Env. Can. Great Lakes For. Res. Centre. Info. Rept. O-X-354. 27pp.

Foster, D.R. 1983. The history and pattern of fire in the boreal forest of southeastern Labrador. Can. J. Bot. 61, 2459-2471.

Foster, D.R. 1984. Phytosociological description of the forest vegetation of southeastern Labrador. Can. J. Bot. 62, 899-906.

Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S.D.A. For. Serv. Pacific Northwest Forest and Range Expt. Stn. Gen. Techn. Rept. PNW-8. 417pp.

Fraser, J.W. 1981. Operational direct seeding trials with black spruce on upland cutovers. Dept. Env. Can. For. Serv. Great Lakes For. Res. Cen. Rept. O-X-321. 34pp.

Fraser, J.W., V.F. Haavisto, J.K. Jeglum, T.S. Dai and D.W. Smith. 1976. Black spruce regeneration on strip cuts and clearcuts in the Nipigon and Cochrane areas of Ontario. Can. For. Serv. Dept. Env. Great Lakes For. Res. Centre. Rept. O-X-246. 33pp.

Frayer, W.E., L.S. Davis and P.G. Risser. 1978. Uses of land classification. J. For. 76, 647-649.

Gauch, H.G. 1977. ORDIFLEX. Release B. Ecology and Systematics, Cornell University, Ithaca, New York.

Gauch, H.G. 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, New York. 298 pp.

Gauch, H.G. and R.H. Whittaker. 1972. Comparison of ordination techniques. Ecology 53, 868-875.

Gauch, H.G., R.H. Whittaker and T.R. Wentworth. 1977. A comparative study of reciprocal averaging and other ordination techniques. J. Ecol. 65, 157-174.

Gehrels, J. 1982. Field Manual for the Forest Land Productivity Survey. Phase III (1:15,840 Forest Soil Mapping Program). Northeast Region, Ont. Min. Nat. Resour. 125pp.

Gleason, H.A. 1926. The individualistic concept of the plant association. Bull. Torr. Bot. Club 53, 7-26.

Gleason, H.A. and A. Cronquist. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Van Nostrand, New York. 810 pp.

Goff, F.G. and P.H. Zedler. 1972. Derivation of species succession vectors. Am. Midl. Nat. 87, 397-412.

Goodall, D.W. 1954. Objective methods for the classification of vegetation. III An essay in the use of factor analysis. Aust. J. Bot. 2, 304-324.

Gordon, A.G. 1983. Nutrient cycling dynamics in differing spruce and mixedwood ecosystems in Ontario and the effects of nutrient removals through harvesting. <u>In</u> Resources and Dynamics of the Boreal Zone. R.W. Wein, R.R. Riewe and I.R. Methven, eds. ACUNS, Ottawa. p. 97-118.

Grant, T.C. 1984. Preliminary Polymorphic Site Index Curves for Black Spruce in Northwestern Ontario. B.Sc.F. thesis. Lakehead University, Thunder Bay, Ontario. 42 pp.

Gregory, D.R. 1979. A Phytosociological Analysis of the Forests of the Southern Part of Northwestern Ontario. M.S. Thesis. Dept. Bot. Univ. Toronto, Toronto, Ontario. 177pp.

Grigal, D.F. 1984. Shortcomings of soil surveys for forest management. In Forest Land Classification: Experiences, Problems, Perspectives. North Central Forest Soils Committee. In Press.

Groenewoud, H. van. 1965. An analysis and classification of white spruce communities in relation to certain habitat features. Can. J. Bot. 43, 1025-1036.

Grosenbaugh, L.R. 1952. Plotless timber estimates - new, fast, easy. J. For. 50, 32-37.

Haavisto, V.F. 1975. Peatland black spruce seed production and dispersal in northeastern Ontario. In Black Spruce Symposium. Great Lakes For. Res. Centre. Can. For. Serv. Dept. Env. Symposium proceedings 0-P-4. p. 250-264.

Hacker, J.J., P.E. Marshall and A.W. Erickson. 1983. A review of jack pine regeneration in the Lake States. Mich. State Univ. Agric. Expt. Stn. Res. Rept. 443. 31pp.

Hale, M.E. and W.L. Culberson. 1970. A fourth checklist of the lichens of the continental United States and Canada. Bryologist 73, 499-543.

Hansen, H.L. 1946. An Analysis of Jack Pine Sites in Minnesota with Special Reference to Site Index, Plant Indicators, and Certain Soil Features. Ph. D. Thesis. University of Minnesota. 115 pp.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, London. 892pp.

Havel, J.J. 1980a. Application of fundamental synecological knowledge to practical problems in forest management. I. Theory and Methods. Forest Ecology Manage. 3, 1-29.

Havel, J.J. 1980b. Application of fundamental synecological knowledge to practical problems in forest management. II. Application. Forest Ecology Manage. 3, 81-111.

Heimburger, C.C. 1934. Forest-type studies in the Adirondack region. Cornell Univ. Agr. Expt. Stn. Memoir 165. 122 pp.

Hill, M.O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol. 61, 237-244.

Hill, M.O. 1974. Correspondence analysis: a neglected multivariate method. J.R. Statist. Soc. Ser. C. 23, 340-354.

Hill, M.O. 1979a. DECORANA, a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ecology and Systematics, Cornell Univ. Ithaca, New York. 52pp.

Hill, M.O. 1979b. TWINSPAN, a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systematics, Cornell Univ. Ithaca, New York. 90pp.

Hill, M.O., R.G.H. Bunce and M.W. Shaw. 1975. Indicator species analysis: a divisive polythetic method of classification and its application to a survey of native pinewoods in Scotland. J. Ecol. 63, 597-613.

Hill, M.O. and H.G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42, 47-58.

Hills, G.A. 1952. The classification and evaluation of site for forestry. Ont. Dep. Lands For. Res. Rept. No. 24. 41pp.

Hills, G.A. 1960. Regional site research. For. Chron. 36, 401-423.

Hills, G.A. 1961. The ecological basis for land-use planning. Ont. Dep. Lands For. Res. Rept. No. 46. 204pp.

Horn, H.S. 1974. The ecology of secondary succession. Ann. Rev. Ecol. Syst. 5, 25-37.

Hughes, E.L. 1967. Studies in stand and seedbed treatment to obtain spruce and fir reproduction on the mixed mixedwood slope type of northwestern Ontario. Can. Dept. For. Rur. Dev., For. Br. Dept. Publ. No. 1189. 138pp.

Hurley, R.T. and R.P. McIntosh. 1964. The spruce-fir forests of the Catskill Mountains. Ecology 45, 314-326.

Jarvis, J.M. 1966. Seeding white spruce, black spruce and jack pine on burned seedbeds in Manitoba. Can. Dept. For. Publ. No. 1166. 8pp.

Jarvis, J.M., G.A. Steneker, R.M. Waldron, J.C. Lees. 1966. Review of silvicultural research. White spruce and trembling aspen cover types Mixedwood Forest Section, Boreal Forest Region Alberta-Saskatchewan-Manitoba. Can. Dept. For. Rur. Dev. For. Br. Dept. Publ. No. 1156. 189pp.

Jeglum, J.K. 1980. Stripcutting in upland black spruce near Nipigon, Ontario. I. Study establishment and site conditions. Can. For. Serv., Dept. Env. Great Lakes For. Res. Centre. Rept. 0-X-315.

Jeglum, J.K. 1982. Strip cutting in shallow soil upland black spruce near Nipigon, Ontario. II. Regeneration in the first study area. Can. For. Serv. Dept. Env. Great Lakes For. Res. Centre. Info. Rept. 0-X-337.

Jeglum, J.K. 1983. Changes in tree species composition in naturally regenerating strip clearcuts in shallow-soil upland black spruce. In Resources and Dynamics of the Boreal Zone. R.W. Wein, R.R. Riewe, I.R. Methven, eds. ACUNS, Ottawa. p. 180-193.

Jeglum, J.K., R. Arnup, R.K. Jones, G. Pierpoint and G.M. Wickware. 1982. Forest Ecosystem Classification. In Symposium on Artificial Regeneration of Conifers in the Upper Great Lakes Region. Mich. Techn. Univ., Houghton, Mich. p. 111-128.

Johnston, W.F. 1977. Manager's handbook for black spruce in the North Central States. U.S.D.A. For. Serv. North Cent. For. Expt. Stn. Gen. Tech. Rept. NC-34. 18pp.

Jones, R.K., G. Pierpoint, G.M. Wickware and J.K. Jeglum. 1983. A classification and ordination of forest ecosystems in the great clay belt of northeastern Ontario. In Resources and Dynamics of the Boreal Zone. R.W. Wein, R.R. Riewe and I.R. Methven, eds. ACUNS, Ottawa. p.83-96.

Kayll, A.J. 1968. The role of fire in the boreal forest of Canada. Can. Dept. For. Rural Develop., For. Branch. Info. Rept. PS-X-7. 15pp.

Ketcheson, D.E. 1979. A study of the cost of strip cutting black spruce stands in northern Ontario. Dept. Env. Can. For. Serv. Great Lakes For. Res. Cen. Rept. O-X-301. 23pp.

Kittredge, J. 1938. The interrelations of habitat, growth rate and associated vegetation in the aspen community of Minnesota and Wisconsin. Ecol. Monogr. 8, 151-246.

Klinka, K., M.C. Feller and L.E. Lowe. 1981. Characterization of the most productive ecosystems for growth of Psuedotsuga menziesii var. menziesii in southwestern British Columbia. Supplement to Land Manage. Rept. No. 6. Province of British Columbia, Ministry of Forests.

Klinka, K., W.D. Van der Horst, F.C. Nuszdorfer and R.G. Harding. 1980a. An ecosystematic approach to a subunit plan. Land Management Rept. No. 5. Province of British Columbia, Ministry of Forests.

Klinka, K., W.D. Van der Horst, F.C. Nuszdorfer and R.G. Harding. 1980b. An ecosystematic approach to forest planning. For. Chron. 56, 97-103.

Kotar, J. and M.S. Coffman. 1982. Application of habitat type concept to regeneration of conifers in the upper Great Lakes region. In Proceedings: Artificial Regeneration of Conifers in the Upper Great Lakes Region. G.D. Mroz, J.F. Berner, eds. Mich. Techn. Univ. Houghton, Mich. p. 53-64.

Kotar, J. and M. Coffman. 1984. Habitat type classification system in Michigan and Wisconsin. In Forest Land Classification: Experiences, Problems, Perspectives. North Central Forest Soils Committee. In press.

La Roi, G.H. 1967. Ecological studies in the boreal spruce-fir forests of the North American taiga. I. Analysis of the vascular flora. Ecol. Monogr. 37, 229-253.

La Roi, G.H. and M.H. Stringer. 1976. Ecological studies in the boreal spruce-fir forests of the North American taiga. II. Analysis of the bryophyte flora. Can. J. Bot. 54, 619-643.

Larsen, J.A. 1980. The Boreal Ecosystem. Academic Press, New York. 500pp.

Laven, R.D. 1982. Establishing homogeneity in studies of forest succession. Forest Ecology Manage. 4, 161-177.

Leak, W.B. 1978. Relationship of species and site index to habitat in the White Mountains of New Hampshire. U.S.D.A. For. Serv. Res. Pap. NE-397. 9pp.

Leak, W.B. 1980. Influence of habitat on silvicultural prescriptions in New England. J. For. 78, 329-333.

Leps, J., J. Osbornova-Kosinova and M. Rejmanek. 1982. Community stability, complexity and species life history strategies. Vegetatio 50, 53-63.

Linteau, A. 1953. Site Classification. Pulp and Paper Mag. Canada 54(7), 147-155.

Linteau, A. 1955. Forest site classification of the northeastern coniferous section, boreal forest region, Quebec. Canada Dept. N. Aff. Nat. Resour. For. Branch For. Res. Div. Bull. 118. 85pp.

Losee, S. 1965. Sites on Abitibi woodlands laboratory. unpublished ms. 18pp.

Loucks, O.L. 1962. A Forest Classification for the maritime provinces. Proc. Nova Scotia Inst. Sci. 25, 85-167.

Loucks, O.L. 1970. Evolution of diversity, efficiency and community stabilty. Am. Zool. 10, 17-25.

Lutz, H.F. 1960. Fire as an ecological factor in the boreal forest of Alaska. J. For. 58, 454-460.

MacLean, C.D. and C.L. Bolsinger. 1973. Estimating Dunning's site index from plant indicators. Pacific Northwest Forest and Range Expt. Stn. U.S.D.A. For. Serv. Res. Note PNW-197. 11pp.

MacLean, D.W. 1960. Some aspects of the aspen-birch-spruce-fir type in Ontario. Can. Dept. For. For. Res. Div. Techn. Note No. 94. 24pp.

MacLean, D.W. and G.H.D. Bedell. 1955. Northern clay belt growth and yield survey. Can. Dept. N. Aff. and Nat. Resour., For. Br., For. Res. Div., Techn. Note 20. 31pp.

Marquis, D.A. 1969. Silvical requirements for natural regeneration. In Birch Symposium Proceedings. Northeastern For. Expt. Stn. U.S.D.A. For. Serv. p. 40-49.

Maycock, P.F. and J.T. Curtis. 1960. The phytosociology of boreal-conifer hardwood forests of the Great Lakes region. Ecol. Monogr. 30, 1-35.

McClain, K.M. 1981. Definition and distribution of the boreal mixedwood forest in Ontario. In Boreal Mixedwood Symposium. R.D. Whitney and K.M. McClain, eds. Can. For. Serv. Great Lakes For. Res. Centre. COJFRC Symposium Proceedings O-P-9. p. 5-9.

Moon, D.E. 1984. Forest land resources inventory in British Columbia. In Forest Land Classification: Experiences, Problems, Perspectives. North Central Forest Soils Committee. In press.

Moore, W.S. 1984. Status and potential of jack pine in Ontario. In Jack Pine Symposium. C.R. Smith and G. Brown, co-chairmen. Can. For. Serv. Great Lakes For. Res. Cen. COJFRC Symposium Proceedings O-P-12. p.1-8.

Moss, E.H. 1953. Forest communities in northwestern Alberta. Can. J. Bot. 31, 212-252.

Mueller-Dombois, D. 1964. The forest habitat types in southeastern Manitoba and their application to forest management. Can. J. Bot. 42, 1417-1444.

Mueller-Dombois, D. 1965. Eco-geographic criteria for mapping forest habitats in southeastern Manitoba. For. Chron. 41, 188-206.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York. 547 pp.

Nelson, D., G.A. Harris and T.E. Hamilton. 1978. Land and resource classification - who cares? J. For. 76, 644-646.

Oliver, C.D. 1978. The development of northern red oak in mixed species stands in central New England. Yale Univ. Sch. For. Env. Std. Bull. No. 91. 63pp.

Oliver, C.D. 1981. Forest development in North America following major disturbances. Forest Ecology Manage. 3, 153-168.

Orloci, L. 1978a. Multivariate Analysis in Vegetation Research. Junk, The Hague. 451pp.

Orloci, L. 1978b. Ordination by resemblance matrices. In Ordination of Plant Communities. R.H. Whittaker, ed. Junk, The Hague. p. 241-275.

Peet, R.K. 1980. Ordination as a tool for analyzing complex data sets. Vegetatio 42, 171-174.

Peet, R.K. and N.L. Christensen. 1980. Hardwood forest vegetation of the North Carolina piedmont. Veroff. Geobot. Inst. ETH, Stiftung Rubel, Zurich 69, Heft, 14-39.

Perala, D.A. 1977. Aspen in the north-central states. North Central For. Expt. Stn. U.S.D.A. For. Serv. Gen. Techn. Rept. NC-36. 30pp.

Perala, D.A. 1978. Thinning strategies for aspen: a prediction model. U.S.D.A. For. Serv. North Central For. Expt. Stn. Res. Pap. NC-161. 19pp.

Pfister, R.D., B.L. Kovalchik, S. Arno and R.C. Presby. 1977. Forest habitat types of Montana. Intermountain For. Range Expt. Stn. U.S.D.A. For. Serv. Gen. Techn. Rept. INT-34. 174pp.

Pielou, E.C. 1977. Mathematical Ecology. John Wiley and Sons, Inc., New York. 385pp.

Pierpoint, G. 1981. Site types in the boreal mixedwood forest. In Boreal Mixedwood Symposium. R.D. Whitney, K.M. McClain, eds. Can. For. Serv., Dept. Env. Great Lakes For. Res. Centre. COJFRC Symposium Proceedings 0-P-9. p. 10-16.

Purchase, J.E. and G.H. La Roi. 1983. Pinus banksiana forests of the Fort Vermillion area, northern Alberta. Can. J. Bot. 61, 804-824.

Rice, B. and M. Westoby. 1983. Plant species richness at the 0.1 hectare scale in Australian vegetation compared to other continents. Vegetatio 52, 129-140.

Ritchie, J.C. 1956. The vegetation of northern Manitoba. I. Studies in the southern spruce forest zone. Can. J. Bot. 34, 528-561.

Ritchie, J.C. 1961. Soil and minor vegetation of pine forests in southeast Manitoba. Can. Dept. For., For. Res. Div. Techn. Note 96. 21pp.

Rowe, J.S. 1956. Uses of undergrowth plant species in forestry. Ecology 37, 461-473.

Rowe, J.S. 1957. Forest Site Classification. Canada Dept. N. Affairs and Nat. Resour. For. Branch, For. Res. Div. Unpubl. Ms. cited in Cayford, Chrosciewicz and Sims, 1967.

Rowe, J.S. 1961. Critique of some vegetational concepts as applied to forests of northwestern Alberta. Can. J. Bot. 39, 1007-1017.

Rowe, J.S. 1962. Soil, site and land classification. For. Chron. 38, 420-432.

Rowe, J.S. 1971. Why classify forest land? For. Chron. 47, 144-148.

Rowe, J.S. 1972. Forest regions of Canada. Can. For. Serv. Dept. Env. Publication 1300.

Rowe, J.S. 1980. Review of: Biogeoclimatic units of central and southern Vancouver Island. For. Chron. 56, 143-144.

Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. In The Role of Fire in Northern Circumpolar Ecosystems. R.W. Wein, D.A. MacLean, eds. John Wiley and Sons, New York. p. 135-154.

Rowe, J.S. and G.W. Scotter. 1973. Fire in the boreal forest. Quart. Res. 3, 444-464.

Rudolph, T.D. 1984. Status report on the management of jack pine in the Lake States. In Jack Pine Symposium. C.R. Smith and G. Brown, co-chairmen. Can. For. Serv. Great Lakes For. Res. Cen. COJFRC Symposium Proceedings O-P-12. p.38-55.

Safford, L.O. 1983. Silvicultural guide for paper birch in the Northeast. U.S.D.A. For. Serv. Northeast For. Expt. Stn. Res. Pap. NE-535. 29pp.

Shafi, M.I. and G.A. Yarranton. 1973. Vegetational heterogeneity during a secondary (postfire) succession. Can. J. Bot. 51, 73-90.

Smith, B.W. 1984. Aerial seeding requirements for jack pine regeneration. In Jack Pine Symposium. C.R. Smith and G. Brown, co-chairmen. Can. For. Serv. Great Lakes For. Res. Cen. COJFRC Symposium Proceedings O-P-12. p.78-86.

Soil Survey Staff. 1960. Soil Classification: A Comprehensive System, Seventh Approximation. U.S.D.A. Soil Conservation Service, Washington.

Soil Survey Staff. 1975. Soil Taxonomy. Handbook No. 436. U.S.D.A. Soil Conservation Service, Washington.

Soper, J.H. and M.L. Heimburger. 1982. Shrubs of Ontario. Royal Ontario Museum, Toronto. 495pp.

Sorensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. Det. Kong. Danske Vidensk. Selsk. Biol. Skr. 5, 1-34.

Spatz, G. and J. Siegmund. 1973. Eine Methode zur tabellarischen Ordination, Klassification und okologischen Auswerfung von pflanzensoziologischen Bestandsaufnahmen. Vegetatio. 28, 1-17.

Spilsbury, R.H. and D.S. Smith. 1947. Forest site types of the Pacific Northwest. A preliminary report. Dept. Lands. For. British Columbia For. Serv. Economics Div. 46pp.

Sprugel, D.G. 1976. Dynamic structure of wave-regenerated <u>Abies balsamea</u> forests in the north eastern United States. J. Ecol. 64, 889-911.

Steele, R., R.D. Pfister, R.A. Ryker, J.A. Kittams. 1981. Forest habitat types of central Idaho. Intermountain For. Range Expt. Stn. U.S.D.A. For. Serv. Gen. Techn. Rept. INT-114.

Steneker, G.A. and J.M. Jarvis. 1966. Thinning in trembling aspen stands, Manitoba and Saskatchewan. Can. Dept. For. Publ. No. 1140. 28pp.

Stone, E.L. 1975. Soil and man's use of forest land. <u>In</u> Forest Soils and Forest Land Management. B. Bernier, C. Winget, eds. Laval Univ. Press, Quebec. p. 1-9.

Sutton, R.F. 1969. Silvics of white spruce. Dept. Fish. For. Can. For. Br. Publ. No. 1250. 57pp.

Swan, J.M.A. and R.L. Dix. 1966. The phytosociological structure of upland forest at Candle Lake Saskatchewan. J. Ecol. 54, 13-40.

Viereck, L.A., C.T. Dyrness, K. Van Cleve and M.J. Foote. 1983. Vegetation, soils and forest productivity in selected forest types in interior Alaska. Can. J. For. Res. 13, 703-720.

Watt, A.S. 1947. Pattern and process in the plant community. J. Ecol. 35, 1-22.

Westman, W.E. and R.K. Peet. 1982. Robert Whittaker (1920-1980): The man and his work. Vegetatio 48, 97-122.

Westveld, M. 1954. Use of plant indicators as an index to site quality. Northeastern For. Expt. Stn. U.S.D.A. For. Serv. Sta. Pap. No. 69. 5pp.

Whittaker, R.H. 1953. A consideration of climax theory: the climax as a population and pattern. Ecol. Monogr. 23, 41-78.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26, 1-80.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30, 279-338.

Whittaker, R.H. 1962. Classification of natural communities. Bot. Rev. 28, 1-239.

Whittaker, R.H. (ed.) 1978a. Ordination of Plant Communities. Junk, The Hague. 388pp.

Whittaker, R.H. 1978b. Direct gradient analysis. In Ordination of Plant Communities. R.H. Whittaker, ed. Junk, The Hague. p. 7-50.

Whittaker, R.H. and H.G. Gauch. 1978. Evaluation of ordination techniques. In Ordination of Plant Communities. R.H. Whittaker, ed. Junk, The Hague. p. 277-336.

Whittaker, R.H. and W.A. Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona. II. A gradient analysis of the south slope. Ecology 46, 429-452.

Wierman, C.A. and C.D. Oliver. 1979. Crown stratification by species in even-aged mixed stands of Douglas-fir - western hemlock. Can. J. For. Res. 9, 1-9.

Woods, G.T. and R.J. Day. 1977a. Ecological effects of forest fire in poplar communities in Quetico Provincial Park. Ont. Min. Nat. Resour. Quetico Prov. Park Fire Ecol. Std. Rpt. No. 6. 35pp.

Woods, G.T. and R.J. Day. 1977b. Ecological effects of forest fire in black spruce communities in Quetico Provincial Park. Ont. Min. Nat. Resour. Quetico Prov. Park Fire Ecol. Std. Rpt. No. 7. 34pp.

Woods, G.T. and R.J. Day. 1977c. A summary of the fire ecology study of Quetico Provincial Park. Ont. Min. Nat. Resour. Quetico Prov. Park. Fire Ecol. Std. Rept. 8. 39pp.

Yarie, J. 1983. Environmental and successional relationships of the forest communities of the Porcupine River drainage, interior Alaska. Can. J. For. Res. 13, 721-728.

Zoltai, S.C. 1965. Glacial features of the Quetico-Nipigon area, Ontario. Can. J. Earth Sci. 2, 247-269.

APPENDIX

APPENDIX

ABBREVIATIONS AND FULL SCIENTIFIC NAMES

ABBREVIATION	FULL SCIENTIFIC NAME
ABIEBALS	*Abies balsamea*
ACERSPIC	*Acer spicatum*
ALNUVIRI	*Alnus viridis* ssp. *crispa*
AMELHUMI	*Amelanchier humilis*
ARALNUDI	*Aralia nudicaulis*
ASTEMACR	*Aster macrophyllus*
BETUPAPY	*Betula papyrifera*
CHIOHISP	*Chiogenes hispidula*
CLADRANG	*Cladina rangiferina*
CLINBORE	*Clintonia borealis*
CORNCANA	*Cornus canadensis*
CORNSTOL	*Cornus stolonifera*
CORYCORN	*Corylus cornuta*
DICRSPP.	*Dicranum*, spp.
DIERLONI	*Diervilla Lonicera*
LEDUGROE	*Ledum groenlandicum*
LYCOCOMP	*Lycopodium complanatum*
LYCOOBSC	*Lycopodium obscurum*
MAIACANA	*Maianthemum canadense*
MITENUDA	*Mitella nuda*
PICEMARI	*Picea mariana*
PLEUSCHR	*Pleurozium schreberi*
POLYSPP.	*Polytrichum*, spp.
POPUTREM	*Populus tremuloides*
PRUNPENN	*Prunus pennsylvanica*
PTERAQUI	*Pteridium aquilinum*
PTILCRIS	*Ptilium crista-castrensis*
ROSAACIC	*Rosa acicularis*
RUBUSTRI	*Rubus strigosus*
SALIBEBB	*Salix Bebbiana*
SORBDECO	*Sorbus decora*
SPHASPP.	*Sphagnum*, spp.
STREROSE	*Streptopus roseus*
TAXUCANA	*Taxus canadensis*
VACCMYRT	*Vaccinium myrtilloides*

LAKEHEAD UNIVERSITY
EXAMINER'S REPORT ON MASTER'S THESIS

NAME OF CANDIDATE: Jeffery C. Goelz

DEPARTMENT: Forestry

TITLE OF THESIS: A synecological Study of Upland Boreal Forest Vegetation in Northwest Ontario with Applications to Silviculture.

The examiner should indicate his or her assessment of the thesis by checking one of the boxes below.

- [X] Accepted with Commendation
- [ ] Accepted
- [ ] Accepted Subject to Revisions Specified
- [ ] Appreciable Revisions Required
- [ ] Thesis Rejected

Please comment below upon the reasons for your choice (continue overleaf)

This is a most interesting and significant thesis, and it represents--in terms of initial sampling of many (60) stands, the statistical analyses, and interpretation and thesis preparation--virtually, I should think, a work possibly minimally adequate for a doctoral thesis, and for this reason I am recommending a "With Commendation" appellation to the final version.

I have no recommendations for major revisions in respect to scientific content, which I believe is of some quite considerable importance and, so far as I am qualified to judge, the accuracy of the statistical analyses is without major apparent fault. I will

Signature:

Date: August 11, 1984

- [ ] Internal Examiner
- [X] External Examiner

discuss the scientific significance of the thesis below, and will first indicate that, in regard to some points of style, I would suggest a minor change at the beginning of the last section (4.4).

In introducing the last section, the statement is made that, "This thesis could have omitted any applications," and this seems a somewhat perfunctory introduction and detracts somewhat from the force of the presentation that follows, for, actually, the significance of the work lies to a considerable extent on the fact that it throws serious doubt on the validity and usefulness of much of the older, earlier work by foresters and ecologists, as well as forest soil scientists, to devise methods for judging the characteristics of the environment of various kinds of sites on the basis of the vegetational communities found there, particul the understorey communities.

To summarize the value of the thesis in terms of understanding of the structure and nature of vegetational communities, at least those of the boreal forest, let me reiterate the major points of the thesis that bear on community characteristics:

(1) Communities of the boreal forest are not discrete and consistently identifiable entities or units; they, rather, are continuously variable and non-discrete;

(2) What might be called "classical" studies that are intended to identify different discrete communities are, thus, not realistic portrayals of the "real" situation in the boreal forest;

(3) The work clearly demonstrates that different statistical techniques give different results with the data, particularly in the case of the shrub and herb strata, in which larger numbers of species are present than are present in the tree stratum;

(4) Analyses of the stand data reveal some consistencies in community composition (i.e., black spruce, Ledum, and Chiogenes), but these are not associated with the dominant tree species per se but with landform, moisture, disturbanc and other habitat characteristics to which the species are responding individualistically;

(5) Boreal species, in general, are broadly adapted, with preferences for specific moisture conditions in the somewhat more narrowly adapted species;

(6) Replacement over time of one tree species by another as dominants in the tree stratum, when and if it occurs, is the result of environmental conditions induced by habitat rather than successional trends that would be induced by the innate environmental responses of the trees. Fire is a major disturbance, other than human disturbance, and obscures successional trends because of its frequency;

(7) There is little consistency between site descriptions used variously in the past in forestry management practices and vegetational and/or soils data. Landform data, however, show better correlations with soils and vegetation of all strata; landforms, thus, are more discrete than the plant communities and variations in the latter do not necessarily conform to variations in the former.

I will not attempt to list or mention any of the publications based on the early unrealistic concepts that vegetational communities can be used to designate site characteristics, or the other works in which some attempt is made to use, verify, modify, or refute the concept; they are many, some have been mentioned, others not, by the author in his introductory section, and those that are omitted are so treated largely I presume because they are mostly now of historical interest.

I would, then, for these reasons, stress the practical significance of the work, and this aspect is, I would say, as important as the theoretical implications in regard to vegetational community structure and composition. The work clearly invalidates older, perhaps one might say classical concepts, which hold that plant communities are discrete units that can be employed to enviromentally characterize site conditions and habitat parameters. Perhaps the author is making an effort to go easy on the older workers in the field, who, of course, were doing the best they could with the methods available. In any case, I feel some perhaps greater emphasis should be placed in the last section on the fact that the work does throw some doubt on the validity of the old methods and concepts; the author does this, but not as forcefully or directly as he might. On the other hand, perhaps he feels that he would be beating a dead horse, and, if so, this recommendation could well be disregarded.

In summary, the work clearly has both theoretical and practical implications, and is important in both respects. The implications of the research are of quite considerable significance and for this reason I believe the thesis is a most worthy one. The results are certainly publishable, although I suspect there should be some effort to condense and summarize the work into a somewhat shorter version, or versions if more than one paper can be derived, perhaps in a series. It would be interesting if the author would carry on his investigations along the lines of some of the possibilities he mentions for future research. These would be important continuations of the research presented here.