

A FLORISTIC STUDY OF FORESTS AND BOG VEGETATION, NORTHWESTERN MINNESOTA¹

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Abstract. Single vegetation plots in forests and bogs in the deciduous and coniferous-hardwood formation in northwestern Minnesota were studied according to the field methods of the Zürich-Montpellier system. Plots and species were arranged so that the greatest coincidence of occurrences was obtained. Species that show approximately similar amplitudes were united in sociological groups. Plant communities typified by these groups were placed in a hierarchy. The plant communities appear to intergrade but are not completely continuous. Definite concentrations of occurrences remain present in the ordination. Fourteen main types of vegetation are recognized. Their relations to the environment are discussed, and their relations to vegetation in other regions are indicated.

Thirteen main types of vegetation (alliances) are recognized in the Itasca State Park region. Lowland vegetation has been divided into five alliances. In three of them the pathway of lake filling, starting in a eutrophic sedge mat and proceeding towards a mesotrophic *Picea mariana* bog forest, is depicted. The two remaining lowland types represent eutrophic swamp forest of *Fraxinus nigra* and *Ulmus americana* on shallow peat or young alluvial soils. Upland forests have been divided into three "rich" deciduous types and five "poor" coniferous types. The rich types are represented by *Tilia americana* forests, *Acer saccharum* forests, *Quercus rubra* forests, and *Populus tremuloides-Quercus* sp. forests, all showing representatives of the rich flora of the mesic *Tilia-Acer* forest. The coniferous forest types are represented by *Populus tremuloides-Quercus* sp. forests and closely related *Pinus resinosa-Pinus banksiana* forests, *Pinus banksiana* forests on sandy outwash soils, and *Abies balsamea* forests in a young stage of development. Of these types the *Pinus banksiana* forest is floristically the best defined.

INTRODUCTION

The present study was not undertaken for phytosociological purposes only. The fieldwork was done between 1962 and 1964 to determine the composition of the vegetation types in the region and to put the present vegetational pattern in a context that could be used in interpreting the pollen assemblages that record the development of bog vegetation in a small pond (Janssen 1967). The region investigated, an area about 50 miles long and 24 miles wide in northwestern Minnesota, belongs to the extension of Rowe's (1959) Great Lakes-St. Lawrence forest region across the international boundary. This transitional belt between the deciduous forests in the south and coniferous boreal forest in the north, called Lake Forest by Weaver and Clements (1938), includes both conifers (*Tsuga canadensis*, *Picea glauca*, *Abies balsamea*, *Pinus strobus*, and *P. resinosa*) and deciduous trees (*Acer saccharum*, *Fagus grandifolia*, *Tilia americana*, *Betula lutea*, *Ulmus* spp., and *Quercus* spp.). Towards the south the coniferous elements drop out; towards the north they prevail.

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In the boreal forest *Pinus resinosa* and *P. strobus* are absent, and only a few deciduous elements remain (Fig. 1).

The conifer-hardwood region in Minnesota belongs to Braun's (1950) hemlock-white pine-northern hardwoods region. All of the above species are present except *Tsuga canadensis* and *Fagus grandifolia*. Between the conifer-hardwood region and the prairie is a narrow belt of deciduous forests. This may be considered a northwestern extension of the Big Woods section of Braun's maple-basswood forest region. It contains the same tree species present in the conifer-hardwood region except for the conifers. However, it does not have such tree genera as *Carya*, *Juglans*, and *Celtis*, which occur farther south in the state. In the transition between the narrow deciduous forest belt and the prairie, there locally occurs a *Quercus macrocarpa* savanna, in which shrubs play an important part.

The phytosociological data in this study cover vegetation types in the conifer-hardwood, deciduous, and savanna formations mainly in townships T143-144N, R32-41W (Fig. 1). This is essentially McAndrews' (1966) Itasca transect, but without the prairie sections. Data obtained from a region outside the Itasca transect (bog communities from the Lake Agassiz lowland) have been in-

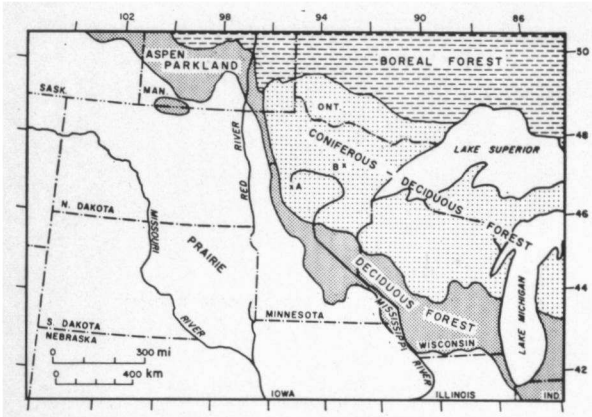


FIG. 1. Map of major vegetational formations of Minnesota and adjacent areas, showing location of Itasca State Park area (A) and Myrtle Lake (B).

cluded to show the contrast with lowland vegetation types in the Itasca State Park region. These data are from the Myrtle Lake region in north-central Minnesota (Koochiching County, T163-165N, R23-26W). The vegetation in the Itasca transect is related to these surrounding formations, namely the boreal forest formation, the prairie formation, and the deciduous forest formation.

This study is not the first attempt to classify the vegetation of northern Minnesota. Cooper (1912), working on Isle Royale in Lake Superior adjacent to northeastern Minnesota, described plant communities mainly for successional considerations. In fact, most of the older literature deals with climax problems (Cooper 1912, Bergman and Stallard 1916, Lee 1924, Kell 1938). Some of the presently described vegetation types may be found

in these studies. The types described in the present study, however, are not based on successional or ecological features, although such features will be considered because they are so striking.

LOCATION, CLIMATE, AND SOIL

Most of the relevés were taken in an area 45 by 10 miles in Hubbard, Clearwater, Becker, and Mahnomen Counties (Fig. 2), with a concentration near Lake Itasca in Itasca State Park (Fig. 3). The area is deeply covered by calcareous drift deposited during the Wisconsin glaciation. The Big Stone Moraine of the Des Moines Lobe is composed of silty till, whereas the Itasca Moraine of the Wadena Lobe consists of sandy loam till (Wright 1962). The textural differences are reflected in the soil types, respectively Waukon-Barnes and Nebish-Rockwood (Arneman 1963). Both soil types have a forest profile, but on the Itasca Moraine the soils have been leached to a greater depth and are therefore less fertile. The least fertile and most droughty soils are found in outwash plains (Allway and McMiller 1935). In the Itasca area are two large areas belonging to these soil types, the Twin Lakes and Lake George outwash plains, as well as several less extensive outwash areas in smaller drainageways.

West of the deciduous forest formation at the crest of the Big Stone Moraine are mixtures of forest and prairie soils (Buell and Cantlon 1951), in the *Quercus macrocarpa* savanna formation of McAndrews (1966). Because of the high degree of cultivation here the only forests existing today are farm woodlots. Relevés 148, 149, 151, 152,

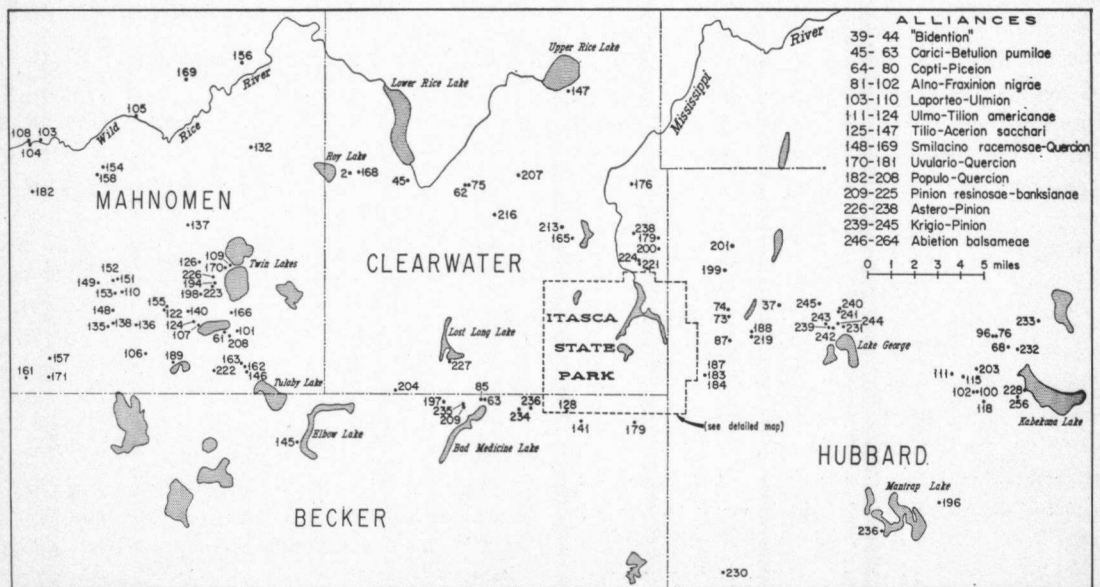


FIG. 2. Map showing location of relevés in area near Itasca State Park.

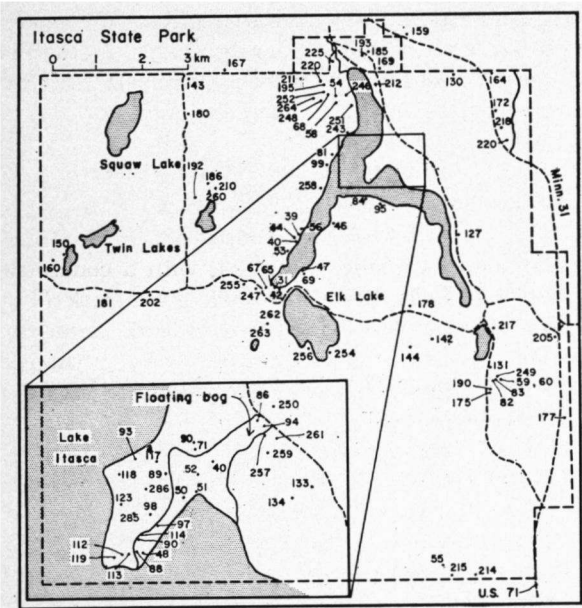


FIG. 3. Map showing location of relevés in Itasca State Park.

153, 154, 157, 158, and 161 belong to this category. Relevés from groves on the Erskine Moraine west of Mahanomen County proved to fit badly in the ordination of plots to the east and accordingly have been omitted (see further comments).

VEGETATION ANALYSIS

This survey does not include all vegetation types in the region. Types were selected that were most likely to be important in the interpretation of the pollen diagram. The survey deals with forests, but in addition data have been included from lowland vegetation types that are part of the successions in lake filling and in which trees may be absent. Not included in this study are submerged vegetation, upland pioneer vegetation, lowland and upland shrub types, and roadside communities. The vegetation was studied between June and September. The early spring flora may therefore be insufficiently represented, especially in the *Acer saccharum* forests.

For the study of the vegetation composition a single plot analysis was used. These vegetation plots were studied using the methods of the Zürich-Montpellier school of phytosociology (Braun-Blanquet 1951). Quantity of the various species was estimated according to the following combined 7-point scale of cover and abundance. A second symbol indicates sociability.

Indices of cover-abundance

5. Covering more than three-quarters of the area
4. Any number of individuals covering one-half to three-quarters of the area
3. Any number of individuals covering one-quarter to one-half of the area
2. Very numerous or covering at least 5% of the area
1. Plentiful but of small cover value
- + . Sparsely present, cover very small
- r. Single occurrence

Indices of sociability

- .1 Growing one in a place
- .2 Grouped or tufted
- .3 In troops, small patches, or cushions
- .4 In small colonies, extensive patches, or carpets
- .5 In great crowds, pure populations

A relevé consists of an annotated list of the vegetation on a relatively large plot that must fulfill three criteria.

1. The plot should be large enough to contain all the species of the community. The minimum size is determined by selecting a small plot, tallying the species encountered, then enlarging the plot until no new additions to the tally list can be made. The minimum size in forests will be larger than in herbaceous vegetation (cf. Ellenberg 1956). In my study, plots in forests usually measure 225 or 400 m².

2. The environmental complex, e.g. direction of exposure, should be constant, as far as can be seen without measurement.

3. The vegetation in all the strata should be as homogeneous as possible, as far as can be inspected visually. All the species (except single occurrences) should occur in every part of the plot. This means, for instance, that usually the fringe of a forest, where it borders a creek or a road, has not been included in a plot, because here lowland species, especially roadside species, may penetrate the forest. If the trees are large it may be difficult to fulfill the requirement of homogeneity in the tree layer. Then only a few trees are present in the relevé, and estimates of cover are useless. In these cases the size of the plots was expanded, while homogeneity in the other vegetation layers was maintained if possible. It becomes increasingly difficult, however, to scan such a large area in inspecting the homogeneity of the shrub and herb layers. Estimates of cover in these vegetation layers therefore are based upon

the original size of the plot. The degree of cover refers to the projections of the circumferences of the individual species on the ground.

The relevés have been arranged according to presence or absence of the species. Relevés that have a great number of species in common have been placed together. Species have been placed in sociological groups, which consist of species that show comparable sociological amplitudes (Iversen 1954, Scamoni and Passarge 1959). Sociological groups were used by Doing (1962) to characterize wood and shrub communities in the Netherlands. They are approximately equivalent to ecological groups (Duvigneaud 1946), because both reflect environmental conditions. As Scamoni and Passarge (1959) and Doing (1962) point out, however, they include the factor of competition, unlike ecological groups.

In practice, sociological groups were established by plotting all the relevés more or less randomly on a large sheet of paper and then shifting the columns and rows by trial and error until groupings were obvious. Basically this is a numerical method carried out by hand. The results are displayed in three tables (envelope under rear cover) which may be placed in echelon. The biggest departure from arrangement on the basis of presence/absence is in Table 1, where the unit labeled "transition" shows a position in the arrangement also based on geography and assumed succession. The left column in each table lists the plant species arranged in sociological groups. Each species occurs only once in the column. The composition of the sociological groups in each table is the same, except for omissions from one table because of absence or very low presence. An exception to this rule is made in group 8, which has the largest sociological amplitude. In this group occur species that are common in almost all the forest types in the region. Moisture is probably the limiting ecological factor for group 8 in the forest analyzed in Tables 1 and 2; for those of Table 3, it is the nutrient content of the soil. The species involved probably do not react in the same way to these factors. Therefore in Table 3 the species of group 8 have been arranged in a different way.

Species that show a very low presence in a table have not been included in the sociological groups, but their occurrences have been listed on the right side of each table.

At the top of each table are data about the location of the relevés, the structure of the vegetation, the exposure, the size of the relevés, and the number of species in each relevé. In case there is more than one tree or shrub layer, separate

height and cover values for these layers are indicated by 1, 11, and 111. The counties, indicated by abbreviations, are Hubbard, Clearwater, Mahanomen, Becker, and Koochiching.

Juvenile tree stages may occur in the shrub and herb layer of the forest, and juvenile shrubs may occur in the herb layer. In these cases an "h" (herb) or "s" (shrub) is added after the notation of cover/abundance-sociability. For several species this is so common that a special row in the tables has been added; the species names in the sociological groups then have been provided with a notation T, S, or H for tree, shrub, or herb layer.

In some cases more than one stratum in the tree layer may be recognized. If a species occurred in the overstory, the notation is underlined (e.g. 5); if in the understory, it is roofed (e.g. $\hat{3}$).

An "x" is used in case a species occurred in the sample plot but in an environment not typical for the site. Most commonly this applies for species occurring on stumps in otherwise lowland habitats.

IDENTIFICATION OF PLANT COMMUNITIES

Plant communities have been identified by combining sociological groups. Related communities have most of the sociological groups in common. In some cases the sociological amplitude is so narrow that the group is made up of species that are (locally) confined to a particular community. A glance at the tables shows how complex the interrelations of the communities are. The most striking feature is a gradient running through the three tables from the left top to the right bottom. Most of the species are not absolutely restricted to one segment of the vegetation. In many cases species are present outside their main occurrence. Moreover, it is often difficult to draw sharp boundary lines between neighboring communities. The communities that are floristically best characterized are the most specialized ones: forests on acid organic soils and forests on very poor sandy outwash soils. Other communities are floristically gradational into each other. The overall impression from the tables is that the vegetation is essentially a continuum in which delimitation of plant communities can only be arbitrary. This concept of vegetation is essentially that of Gleason (1926); it has been developed by workers at the University of Wisconsin (Curtis and McIntosh 1951, McIntosh 1958, Curtis 1959) and others.

It often has been claimed that the possibilities in recognizing distinct plant communities depend on the method followed. The Zürich-Montpellier system is said to be subjective because only homo-

geneous sample plots are selected (Goodall 1963). The clear distinctions between the plant communities thus may be a result of leaving aside transitional vegetation. On the other hand, much of the basis for the continuum might be the result of studying large stands in a large area rather than smaller homogeneous vegetation plots in a restricted area. In spite of the fact that the field methods common in continental Europe have been used in the present study and that the area is restricted in size, overlap of sociological amplitudes is more common than groups that are confined to particular units. The continuous nature of the vegetation pattern therefore is more striking than the discontinuities in the tables. Poore (1955a, 1955b), applying continental methods to Scottish *Nardus stricta*-*Carex* vegetation, came to the same conclusion.

This procedure of arranging the relevés is not exactly the same, however, as that used by the Zürich-Montpellier school of phytosociology, in which plant communities are established on the basis of characteristic and differential species, and in which a hierarchic classification is erected that comprises units of lower and higher rank. In the tables presented here, correlation among the various plant species is established by means of sociological groups. Such a procedure is essentially an ordination of the data as opposed to a classification (Goodall 1954) and is, in fact, the same way of working out the data as developed at the University of Wisconsin. The method of establishing correlations is much more primitive, however. It does not make use of the highly evolved statistical methods of the Wisconsin group, nor does it allow presentation of the data in a multidimensional picture showing environmental gradients (Bray and Curtis 1957, Maycock and Curtis 1960, Bakuzis 1960). It is difficult to press a multidimensional scheme of relationships into a linear scheme (Gams 1941, p. 206, 212). This drawback is best illustrated in Table 3, where a sharp floristic break is present between relevés 245 and 246. As mentioned above, two environmental gradients are involved here. In the table as it is now the transition from the *Pinion resinosa*-*banksianae* to the *Astero-Pinion* and *Krigio-Pinion* is best illustrated. The *Pinion resinosa*-*banksianae* shows such a transition to the *Abietion balsameae* as well but along another gradient. This way of presentation, however, has the advantage, in common with the Zürich-Montpellier approach, that the species composition of each vegetation plot remains visible.

There is a possibility that the continuous nature

of the vegetation is not largely a result of the methods followed, but that it also may be explained by features of the vegetation itself. In western Europe natural and seminatural vegetation no longer exists, for remnants of forests frequently have been split up in space during 5,000 years of agricultural practice. This has favored development of distinct communities. In contrast, in the Upper Midwest intensive agriculture has been active for only about 100 years. Stands have not been separated so much nor so long. Under such circumstances the continuous nature of the vegetation is more noticeable.

The establishment of sociological groups is the main purpose of this study. It would be contrary to the concept of a continuum to try to delimit definite plant communities. However, the continuum as presented in the tables is not completely continuous. At many places distinct concentrations of occurrences can be seen. They may be called noda (Poore 1955b) or clusters (Goodall 1954). It is around these noda that lines can be drawn to delimit plant communities. Solid lines were used where the noda are clearly outstanding and where occurrences are clearly clustered, and dotted lines where the delimitation of noda is uncertain, usually because of a low presence of the species. Obviously this can be done in an arbitrary way only. It helps, however, to focus on the noda to read the tables more easily.

The nodal concept of the community also is recognized by Tüxen (1955, p. 159), who stressed the type character of the community: "Das Klare und Präzise an einem solchen Typus ist immer sein Kern, nicht sein Rand. Es gehört zum Wesen eines Typus dass er keine scharfen Grenzen haben darf." So defined it is congruent to Goodall's clusters, and it comes close to the concept of continuum. An ordination of grassland stands in Saskatchewan by Looman (1963), based on continental premises, seems to indicate, however, that vegetational clusters may well be separated from each other.

The procedure here used, leading to the recognition of clusters, may be compared with that of recent statistical approaches. Lambert and Williams (1962) described an analysis that blends their earlier described normal association analysis (R analysis: plots arranged on the basis of species; Williams and Lambert 1959) with their inverse association analysis (Q analysis: species arranged according to plots in which they occur; Williams and Lambert 1961). Shifting rows to arrive at sociological groups is essentially a Q

type of analysis, and shifting columns is an R type of analysis.

An additional advantage in delimiting plant communities is that it is easier to refer to them, a matter much more difficult in a scheme stressing the continuum. The same point has been made by Goodall (1963).

It remains to be seen whether clustering would appear if we did not insist on the homogeneity of the plots studied. Such a requirement results in a loss of information (Goodall 1963), but it may be defended because this simplification enables us to evaluate the factors of the environment more easily.

In order to show the floristic correlations, the various plant communities are classified in a hierarchic system. In some cases the sociological groups are treated the same way, but only to two levels. At the top of each table is a scheme of plant communities arranged on different levels. This scheme is by no means the only one that can be made by combining sociological groups. It may be possible to combine the sociological groups in a different way, resulting in communities showing a different species composition. The combinations here presented have been made according to what seemed to the author the most logical way. The procedure used is as follows:

Communities that are best defined floristically, physiognomically, and ecologically have been put as much as possible on the level of the alliance. Such a treatment is contrary to the procedure of the Braun-Blanquet methods *sensu stricto*, in which communities so defined are put on the level of the association (Braun-Blanquet 1959). Their placement on the alliance level, however, makes the system better balanced upwards and downwards. Moreover, many of the units are comparable to units recognized in Europe that are also strongly characterized ecologically (e.g. *Alno-Fraxinon* v.v. *Alnion incanae*).

The communities have been named in the traditional way common in continental Europe. One might question whether this is justified. In the classical continental approach the association is identified by characteristic species and the sub-association by differential species. In my scheme such a strong connection is not present. I favor the European approach, however, because the principle of establishing and classifying communities on the basis of floristics lies very much at the base of continental ecology. The alternative would have been using common names. This, however, would introduce confusion with communi-

ties established on the basis of other characteristics.

In the following pages a description will be given of the recognized plant communities. It would be easy to do this by making formal statements about differential species and characteristic species of classes, orders, alliances, and associations. There are two main reasons to avoid such an approach, however.

1. The sociological groups may be combined differently into other plant communities that are no less valid than the ones here established. Under such circumstances it would be irrelevant to assign such groups formally to plant communities.

2. There is no proof that the composition of the sociological groups is the same in another area. In a different climate with a slightly different flora the changed competitive conditions may result in a different make-up of the sociological groups. Some examples may illustrate this. In our tables *Ledum groenlandicum* is restricted to moss heath and to *Larix laricina* and *Picea mariana* forests on peat. Approximately 100 miles towards the north, closer to the boreal forest formation, however, it is not uncommon to find *Ledum* in *Pinus banksiana* forests on well-drained mineral soils. The same applies for northern Ontario (Hustich 1955). *Pinus banksiana* itself, moreover, is more commonly associated in the north with species that are typical for bogs in our region. It may even occur on shallow peat (M. L. Heinselman, *personal communication*). In Wisconsin Curtis (1959, p. 224) states that *Pinus banksiana* may achieve as high as 100% dominance in certain bogs. In Newfoundland (Damman 1964) *Picea mariana* forests are present on well-drained mineral soils associated with species that in the Lake Itasca area are either typical upland or lowland species.

Pinus strobus in our region is strictly an upland species, but on the fringe of its distribution area it occurs in bogs (Curtis 1959, p. 205, 223). The sociological groups therefore may have only a local validity, and it does not make sense to assign them formally to plant communities valid over a larger region.

The sociological groups thus will tell us in principle how species are correlated with each other in this part of Minnesota only. Because of the local value of the sociological groups, one might question whether units of higher rank should be recognized on the basis of this local low-intensity study. The history of the erection of the vegetational system in Europe has been that first the units of lower rank were recognized from local studies; later, when a sufficient number of such studies was

available, units of higher rank were established. In the present study, units of high rank have been delimited and named so that they may be easily compared with the vegetation in other regions. For the same reasons van Donselaar (1965) described classes and units of lower rank in the savannas of Dutch Guiana.

The shifts in the sociological groups that occur in other areas do not affect the basic structure of the system. An investigation of the literature shows that the main trends evident in the Itasca tables is valid elsewhere in the forested regions of the Upper Midwest. In the Wisconsin studies, for example, any character of the vegetation (usually the importance value) is plotted against an environmental gradient (Curtis 1959). Species may be arranged in groups that show the same distribution along the gradient. Many such groups are more or less similar to the Itasca sociological groups. In such an arrangement, however, the species appear to be more tolerant towards environment than in the Itasca study. But even in the restricted area of the Itasca transect the arrangement of the sociological groups begins to blur. In Table 2 in part of the relevés belonging to the *Diervilleteo-Quercion*, species of sociological group 6b, 6c, and 7b occur that otherwise are characteristic for the *Ulmo-Tilion* and *Laporteo-Ulmion*. This happens mainly in the relevés from the most western part of the transect, situated in McAndrews' *Quercus* savanna. According to McAndrews (1966), west of the Big Stone Moraine there is an abrupt drop in precipitation from 23-25 inches/year in the deciduous/hardwood forest to 18.3 inches/year in the prairie, because of an orographic effect. The vegetation pattern would have been clearer if the relevés west of this boundary were excluded. West of the *Quercus* savanna there is on the Erskine Moraine a southern outlier of the aspen parkland of Manitoba, and the blurring of the arrangement is even stronger. This may indicate that the pattern of vegetation arrangement as is shown in this paper is in detail not much applicable beyond the formation.

The variations in the sociological groups that occur in other regions are very interesting, but an evaluation lies beyond the scope of the present work.

The sociological groups comprise species that show more or less the same requirements towards the environment. Apart from competition they therefore may be considered ecological groups. In the present study no measurement of the environment has been made. But one may commonly make general statements about the ecology of

the sociological groups by comparing the communities of the Itasca study with approximately the same vegetation types from which data on the environment are known. Many features in the tables, however, remain ecologically unexplainable at present.

LOWLAND COMMUNITIES

The lowland communities may be divided into three major units by means of five sociological groups. (1) The class *Kalmio-Chamaedaphnetea* contains species from sociological group 1 only. (2) The order *Fraxinetalia nigrae* has species combinations of sociological groups 2, 3, 4, and 5. (3) An intermediate group of communities has the exclusive presence of sociological group 2 but in addition quite a number of representatives of groups 1, 3, 4, and 8. This is a very heterogeneous group, comprising both well-developed forests and herb vegetation. Because of these structural and physiognomic differences, it seems better not to unite them all in a class or even an order. It will be provisionally termed the "*Thelypterideto-Piceetea*" from *Dryopteris thelypteris* (group 2d), which shows a high presence here.

Kalmio-Chamaedaphnetea

Most of the relevés for this class come from the Myrtle Lake region, an extensive patterned peat bog on the bed of the former glacial Lake Agassiz in north-central Minnesota (Heinselman 1963). This area is mainly covered by muskeg poor in species; trees, where present, are commonly stunted and widely spaced. Typical for this type of vegetation are representatives of sociological group 1b.

The relevés can be divided into the *Lariceto-Chamaedaphnetum* (group 1c) and the *Piceto-Chamaedaphnetum* (group 1f). Representatives of group 1a are abundant in hollows of string bogs (Heinselman 1963); this group may be analogous to the European *Scheuchzerietalia palustris*, which also contains *Carex limosa* and *Scheuchzeria palustris* and occurs in similar habitats. The data are too scanty, however, to unite the few relevés of group 1a into an association.

Chamaedaphne calyculata seems to find optimal conditions in open situations; *Ledum groenlandicum*, however, shows the reverse trend and is especially abundant in the last two relevés of the *Piceto-Chamaedaphnetum*, where *Picea mariana* shows its highest cover and provides the most shade. *Andromeda glaucophylla* is most abundant in the *Lariceto-Chamaedaphnetum*. According to Cooper (1912) and Stallard (1929) it favors

especially the wetter sites, whereas *Chamaedaphne* occupies the drier parts in a bog. They and Conway (1949) agree that *Andromeda* is characteristic of the younger parts of the moss heath formation. My table shows essentially the same.

The *Kalmio-Chamaedaphnetea* have been described in several boreal regions of North America. Heinselman (1963) calls this type the *Sphagnum*-black spruce-leatherleaf muskeg: his table comparing *Picea* types in the Agassiz lowland shows an absence of the species of group 2, as in our tables. The muskegs are also known from various parts of Canada, e.g. Alberta (Moss 1953), Ontario (Hustich 1955), Manitoba (Ritchie 1960).

"*Thelypterideto-Piceetea*"

The relevés found in this group of communities come mostly from the smaller basins in the Itasca area. Species from sociological group 3 and even 4 occur on peats in the marginal zones close to the upland, indicating that the nutrient content of the substrate must be higher than in the *Kalmio-Chamaedaphnetea*. The number of species per relevé is higher. *Larix laricina* and *Picea mariana* form much denser stands and are much taller.

The arrangement of the relevés shows essentially the course of lake filling in the minor basins in the Itasca area. Ecological data from comparable bogs (Kurz 1928, Conway 1949, Clausen 1957) indicate that the accumulation of peat is accompanied by decreasing base content of the soil, decreasing pH, and decreasing moisture. Our tables show how the species combinations change in response to the changing environmental conditions.

Alliance 1: The "*Bidenton*"

The *Bidenteto-Typhetum latifoliae*. This association is sometimes found at the edge of the floating mat (see also Kurz 1928, Gates 1942, and Conway 1949), at the inlets of small streams, and in depressions of cultivated areas, presumably in a base-rich environment. Indeed work on cattail marshes in Michigan (Segadas-Vianna 1951) indicates a high pH and a high content of bases in the soil. The *Bidenteto-Typhetum* represents the most eutrophic stage in the hydrarch successions.

The community is not optimally represented in the table. The cattail marshes in depressions in cultivated areas have not been studied systematically, so it seems better to describe this type only as an association and not an alliance.

Sociological groups 2a, 2c, 2d, and part of 3a (*Typha latifolia*, *Bidens cernua*, and *Impatiens capensis*) are especially represented. The same species occur in cattail stands in Michigan (Segadas-Vianna 1951) and Wisconsin (Curtis 1959). *Phragmites communis*, commonly dominant in comparable vegetation in Europe (*Scirpeto-Phragmitetum*), does not play an important part in the vegetation here. Where *Phragmites communis* occurs, however, it occupies the same sites as *Typha latifolia*

at the edge of the mat (e.g. Floating Bog at Itasca State Park). *Typha* mats with much *Phragmites* have been described in north-central and northeastern Minnesota (Stallard 1929).

Alliance 2: The *Carici-Betulion pumilae*

This alliance can be divided into two associations, the *Cariceto-Betuletum pumilae* and the *Saliceto bebbianae-Laricetum*, by means of sociological group 1c, 2c, part of 3a, and *Betula pumila*. It is striking that the sociological amplitude of group 1c shows the same range as it does in the *Kalmio-Chamaedaphnetea*, probably because of similar moisture conditions.

Compared with the *Bidenteto-Typhetum latifoliae*, the appearance of species from group 1 indicates that the habitat is increasingly deficient in nutrients. In spite of the features in common with the *Carex* mat, the *Laricetum* is definitely a later stage in the succession than the mat. The table shows floristic differences as well, for the *Cariceto-Betuletum* still has representatives from group 2a that are lacking in the *Saliceto-Laricetum*. This points perhaps to rather eutrophic conditions, because this group occurs also in the *Bidenteto-Typhetum latifoliae*. The *Saliceto-Laricetum*, however, shows strong ties with the *Picea mariana* forests (group 1d, 1e, 1f, 2f, 3b, and 3c). These sociological groups accentuate the fact that generally the soil in the *Larix* forests shows a lower pH than the soil in the pioneer mat (Conway 1949). Species in all these groups thus respond first to base content of the soil. In contrast with this, the groups that unite the *Saliceto-Laricetum* with the *Cariceto-Betuletum* must be indicators of another factor—probably moisture, for *Larix* forests are usually as wet as sedge mats.

The *Saliceto-Laricetum* could have been combined with the *Copti-Piceion* to make a unit of higher rank, but union with the *Cariceto-Betuletum* is preferable because both have the conspicuous *Betula pumila* shrub layer. Moreover, *Larix laricina* may be present in the sedge mat, although widely spaced. Finally the *Laricetum* forest generally lacks upland species of group 8 and higher that are present in *Picea mariana* forests.

Alliance 3: The *Copti-Piceion*

This unit represents the final stage in the hydrarch succession. Because of the accumulation of organic matter, the environment is rather dry, so two groups of upland species occur: (1) ubiquitous species that occur in almost every upland vegetation type (group 8), and (2) upland species that are typical for conifer forests (groups 14, 16-22).

Data from Conway (1949) indicate that the mean pH in *Picea mariana* forests is not lower than that found in *Larix laricina* forests, so the two lowland forest types, the *Saliceto bebbianae-Laricetum* and the *Copti-Piceion*, have many groups in common. Despite this, the *Copti-Piceion* has several species (of group 2g) that are characteristic for the whole alliance in this region. As a result the *Copti-Piceion* is one of the best-defined vegetation types.

The alliance may be divided into two associations, the *Habenarieto-Piceetum* and the *Dryopterideto cristatae-Piceetum*. The latter is characterized by group 4, which contains species with a wide sociological amplitude in the eutrophic *Fraxinetalia nigrae*. Moreover, species from *Typha* marshes are more abundant, especially *Impatiens capensis*. The *Dryopterideto cristatae-Piceetum* thus might occur on more eutrophic sites than the *Habenarieto-Piceetum*. Another feature that accentuates the differ-

ence is the presence of groups 2f and 2c in the *Habenarieto-Piceetum*, which ties it to the *Saliceto-Laricetum*. Which ecological factor is reflected by these groups is unknown. In the *Habenarieto-Piceetum* almost no species from group 3a occur, probably because of the extremely dry and acid character of the environment. In part of the *Dryopterideto cristatae-Piceetum* this group (3a) is present. The sociological groups 3a, 3b, and 3c probably are ecologically not very homogenous. A detailed environmental analysis therefore is not yet possible.

Thuja occidentalis is generally recognized as closely related ecologically to *Fraxinus nigra* (Gates 1942, Clausen 1957, Christensen, Clausen, and Curtis 1959). Indeed in the *Copti-Piceion* it coincides with group 4, thus stressing the more eutrophic character of that tree compared to *Picea mariana*. Oxygen, pH, and specific conductivity in ground water in *Thuja* soils (Wilde and Randall 1951) affirm this. In the tables the vegetation types with *Thuja occidentalis* are not clearly represented by characteristic species combinations. Unlike the *Alno-Fraxinion* they do not include the shade-intolerant group 5b. But they cannot be so easily distinguished from *Picea mariana* forests, which also include shade-tolerant species. In the *Dryopterideto cristatae-Piceetum*, *Thuja* may be the dominant tree, but here *Picea mariana* may be dominant with the same species composition. Some differences may be made by sociological group 3a. This pattern, however, is not exactly congruent with the presence of *Picea* and *Thuja*. Moreover, *Thuja* occurs in a relevé with a species composition otherwise found in *Larix* forests. In relevé 39 it is even associated with species from the *Bidenteto-Typhetum*. This relevé, however, originates from a site (Bohall Creek) close to the water's edge, where a *Thuja* forest might be degrading. These findings are in agreement with the opinion of Conway (1949) that *Picea* as well as *Thuja* may be dominant in less acid peat. According to her, *Picea mariana* is not acidophilous but can tolerate acidity to a degree impossible for *Thuja*. On less eutrophic sites *Thuja* thus is absent (*Habenarieto-Piceetum*). On more eutrophic sites it is a matter of chance rather than environment which tree becomes dominant. In our region *Thuja* is not present on the uplands.

The difference in species composition between the *Copti-Piceion* and the *Piceeto-Chamaedaphnetum* agrees well with a species list given by Heinselman (1963) for poor and good spruce sites. The *Copti-Piceion* resembles Heinselman's black spruce-alder-herb type, but there is no relationship with his black spruce-feather moss type, because of the absence of several species from groups 3, 14, 17, and 22—species that may be common in the *Copti-Piceion*.

The group of relevés labeled "transition" in the table poses a problem. Here are mixtures of *Picea*, *Larix*, and *Thuja* forests that show in the understory quite a bit of *Chamaedaphne calyculata* and *Andromeda glaucophylla*. This and the location of the relevés in the Myrtle Lake area would favor arrangement in the *Kalmio-Chamaedaphnetea*, although *Kalmia polifolia* is absent. The presence of several species from groups 2 and 3, however, would point towards the "*Thelypterideto-Piceetea*." In this assignment, the block of relevés would fit best between relevés 54 and 55. The block is better placed immediately after the *Kalmio-Chamaedaphnetea*, however, mainly because they have the same geographic location. Leaving it out of the "*Thelypterideto-Piceetea*" then results in a better picture of the succession in the Itasca transect. Part of the *Chamaedaphne* vegetation

of Segadas-Vianna (1955) from Quebec and Ontario may be placed in this transitional group on account of the joint occurrence of species from groups 1b and 2.

It is surprising that *Chamaedaphne* scarcely occurs in relevés of the Itasca transect. It is a very acidophilous species. According to Conway (1949), it does not occur in areas with a pH above 5.0, and it is not shade tolerant. As soon as *Larix* becomes dense, *Chamaedaphne* is shaded out and is replaced by *Ledum groenlandicum*. The same relations have been observed in the *Kalmio-Chamaedaphnetea*. As a result *Chamaedaphne* is greatly encouraged in open situations, often after disturbances such as fires (Catenhusen 1950). Our *Larix* and *Picea* forests might be too dense for *Chamaedaphne*. Conway points out, however, that an increase of *Chamaedaphne* happens only when the pH is low enough already. This would explain why our *Cariceto-Betuletum*, which is very open but not acidophilous enough, does not contain moss heath species like *Chamaedaphne*. In the Itasca State Park area there is a possibility that *Chamaedaphne* does not get a chance to establish itself because of the absence of such disturbances.

It is tempting to compare the *Piceeto-Chamaedaphnetum* with oligotrophic ombrogenous bogs of western Europe. Raised bogs, like the *Piceeto-Chamaedaphnetum*, are poor in species. But in Atlantic Europe no trees occur. The later stages of the succession in the Itasca transect might be compared with the more eutrophic *Sphagno-Alnion* and *Betulion pubescentis* types in western Europe. Except for the trees *Larix* and *Picea*, which are unusual in a bog in western Europe, we find in both continents several ecological equivalents, e.g. *Betula pubescens*, *Betula pumila*, *Frangula alnus*, *Rhamnus alnifolia*, and *Alnus glutinosa*-*Alnus rugosa*. Even some of the species are the same, e.g. *Menyanthes trifoliata*, *Potentilla palustris*, *Oxycoccus quadripetalus*, *Calla palustris*, and the more eutrophic *Dryopteris thelypteris*, *Lysimachia thyrsiflora*, and *Calla palustris*.

The equilibrium between the environment and the species composition of the *Larix laricina* and *Picea mariana* forests in the Itasca State Park area is not a very stable one. Supply of nutrients may upset the delicate balance, turning the vegetation into more eutrophic types. These relationships may be seen at several places in the park area: in small lowland areas there is a relation between the type of upland vegetation and the lowland vegetation. If the bog is surrounded by a deciduous type of forest, the runoff, rich in bases, results in a broad marginal vegetation of *Fraxinus nigra* (e.g. at Bear Paw Peninsula). Pine forests, on the other hand, favor the existence of bog vegetation. Indications for the same relationships have been found in the bog history of a small pond during the last 4,000 years (Janssen 1967).

This also may be the reason that the finest examples of bogs are found within the park boundaries, where pine has been protected from the logging operations since the turn of the century. Many of the smaller depressions in *Populus tremuloides* woods or in cultivated areas are covered by eutrophic *Typha* marshes, *Alnus* lowland shrubs, or *Fraxinus nigra* forests. Such a change from a bog to a *Typha* marsh at the time of the logging of the pine forests may be seen in the above-mentioned historical vegetation study of a small pond.

Severe fires, droughts, and drainage of the basin all contribute to the destruction of the bog flora (Curtis 1959, p. 236, Catenhusen 1950). A striking example is part of Bog D in Itasca State Park. After the construction of a road the *Larix* trees close to the road died off, and

eutrophic species, especially *Alnus rugosa*, expanded considerably.

The Fraxinetalia nigrae

The *Fraxinetalia nigrae* constitute lowland forests of *Fraxinus nigra* and *Ulmus americana*, occurring on azonal A-G soil profiles (Buell and Borman 1955, Fraser 1957). It may be characterized by sociological groups 3, 4, and 5. No representatives of group 2 occur. Curtis (1959) describes these communities under "northern wet-mesic forests." In his species list, however, a number of species from group 2 occur.

Two alliances may be recognized.

Alliance 4: The *Alno-Fraxinion nigrae*

This is the type of vegetation known as marginal fen (Conway 1949), recognized in Minnesota by Kell (1938). The *Fraxinion nigrae* occurs on shallow peat in the marginal zone between bogs or sedge mats and the upland, and it is present on peat at all sites where nutrients are available, e.g. along creeks. As might be expected the pH is neutral to slightly acid. In many cases the peat has been transformed into amorphous muck by oxidation (Curtis 1959, p. 238), and as a result the pollen grains in the peat are strongly corroded, often beyond recognition. The alliance is best characterized by sociological group 5c. Species generally present in the "*Thelypterideto-Piceetum*" (group 3) are found. It has group 4 in common with the *Dryopterideto cristatae-Piceion*.

The alliance may be divided into two associations: the *Fraxinetum nigrae* (group 5a), in which *Ulmus americana* is absent, and the *Ulmeto-Fraxinetum nigrae*, in which group 5a is absent and *Fraxinus nigra* and *Ulmus americana* both share the tree layer. In this community, species from group 6b and 6c begin to be present. This is a division easily observed in the field, for the *Fraxinetum nigrae* often forms a belt closest to the bog, whereas the *Ulmeto-Fraxinetum* usually is found close to the upland, often on wet mineral soils.

Lowland shrub of *Alnus rugosa*, also a community in a mucky environment rich in oxygen (Wilde and Randall 1951), possibly may find its most natural place in this alliance. A list of species occurring in alder thickets in Wisconsin (Curtis 1959) contains many that are typical for the *Fraxinetalia nigrae*. However, the *Alnus rugosa* shrub vegetation has not been sufficiently studied to assure its proper place. It might arise in case of clear cutting of *Fraxinus nigra* forest or as an initial stage after bog destruction.

The *Alno-Fraxinion* is closely related to the European *Alnion incanae*, which may occur also on thin layers of peat. It shows among the dominant trees the same two genera, but also the same richness in ferns. It also occurs on gley soils (cf. also the *Sanguinaria-Arisaema* type of Wilde (1958) in Wisconsin).

Alliance 5: The *Laporteo-Ulmion*

This alliance is characterized by sociological group 5d. Although *Fraxinus nigra* still is important, *Ulmus americana* plays a bigger role in the canopy than in the preceding alliance. All the relevés come from the floodplain of the Wild Rice River in Mahanomen County, the only river in the area big enough to form a real floodplain. In none of the relevés was peat present in the uppermost layer of the soil, which is too young for the development

of a profile. This situation is comparable to that in the European *Alnion incanae* and *Ulmion* communities. Unfortunately a line through the alliance divides it into parts with and without a number of general upland herbs. The part with these species (tentatively named *Osmorhizeto-Ulmetum*) even comprises groups 9 and 7b. This ties it to the *Uvulario-Aceretalia*. This connection is stronger and more consistent than that to the lowland communities. Groups 3b, 3d, 4, and 5c may be present in part of the *Laporteo-Ulmion*, but this happens in an inconsistent way. It is therefore not possible yet to distinguish clearly between the *Fraxinetalia nigrae* and the *Uvulario-Aceretalia*. More relevés are needed to clear the systematic position of a possible *Ulmion* besides the *Fraxinion*. The species composition of this alliance and the *Alno-Fraxinion* resembles that of Dansereau's *Acereto-Ulmetum laurentium* and *Aceretum rubri* in Quebec (Dansereau 1959).

DECIDUOUS UPLAND FORESTS

The Uvulario-Aceretalia

The *Uvulario-Aceretalia* may be described as forest types that generally are recognized as mesic deciduous forests of *Tilia americana*, *Acer saccharum*, *Ulmus americana*, *Fraxinus pennsylvanica*, *Quercus rubra*, *Quercus macrocarpa*, and *Populus tremuloides*. The species found in these communities have a generally southern distribution. The Itasca region is almost at the northwestern edge of the rich deciduous forests. The species composition is therefore much impoverished when compared with stands southeast from here, e.g. the Big Woods of Daubenmire (1936). Another reason for this impoverishment of the flora is that many of the mesic stands are in a young stage of development. About 50 years ago the conifer-hardwood region was the object of extensive logging, which removed many of the pines from the uplands. This and the destruction of pine seeds by the fires favored an increase in the areal extent of *Populus tremuloides*, which spread easily from root suckers, and of *Betula papyrifera* (Spurr 1954, Buell and Buell 1959).

About 1920 protection against fires became effective, and tree species less well adapted to fires than pine have become increasingly important, such as *Abies balsamea*, *Acer saccharum*, and *Tilia americana* (Heinselman 1954). They form a closed canopy of young trees, above which the pines, *Populus tremuloides*, and *Quercus macrocarpa* may tower. Not all of these stands are in such a young stage. Some examples exist of mature forests in which no sign of such an overstory is present. These stands are found in protected sites— islands, peninsulas, or between neighboring lakes, where fires occur less frequently than elsewhere (see also Daubenmire 1936).

The deciduous forest formation of course has no

overstory of pine, but here protection against fires has resulted in the same trend towards mesic conditions. Young mesic stands here often surround old trees of *Quercus macrocarpa* and *Populus tremuloides* (McAndrews 1966).

The order may be characterized by sociological group 9a.

Alliance 6: The *Ulmo-Tilion americanae*

This alliance comprises among the mesic forest types stands that are most pronouncedly related to the *Ahno-Fraxinion*. This is expressed in sociological group 6. In groups 6a and 6b we find species that have their main distribution in the *Fraxinetalia* and *Ulmo-Tilion*. Group 6c connects only the *Laporteo-Ulmion* with upland forests, but the right side of the sociological amplitude of this group extends into the *Tilio-Acerion*.

Another feature that stresses the relation with the *Ahno-Fraxinion* is the occurrence of group 18b, mainly *Abies balsamea*. This tree occurs in the *Ulmo-Tilion*, often in a lower tree layer below the canopy of *Tilia* and *Ulmus*. Seedlings of *Abies* also are often present.

Group 7 may be called typical for the alliance, especially group 7b. Group 7a shows a main distribution in this alliance, but it extends also in the *Tilio-Acerion*.

It must be stressed, however, that most of these groups are not restricted to the *Ulmo-Tilion*. Some extend into the *Tilio-Acerion*, and several are found in rich *Quercus-Populus* forests. Many stands are not in a juvenile stage but contain mature trees. An overstory of pines or aspens is absent. Often we find these stands near lakes, which may prevent extreme air temperatures (Rosendahl and Butters 1928). The difference from the *Tilio-Acerion* may be explained also by soil differences. Buell and Bormann (1955) describe a *Tilia-Abies-Fraxinus nigra* stand on an A-G soil. This is common in *Fraxinus nigra* forests, but in this case *Tilia* is associated with it. It is therefore not impossible that the *Ulmo-Tilion* is best developed on such soils. It also would explain the floristic connection with lowland forests in a most natural way. Two stands in the Itasca region occurred on sandy soil rather than on till soil. The *Tilio-Acerion* then would occur on the better drained soils.

The alliance has been divided tentatively into two associations on the basis of group 6b (excluding *Ulmus americana*). In the *Matteucieto-Tilietum* group 6b is present, but it is absent in the *Ulmeto-Tilietum americanae*. However, it must be readily admitted that this basis is too narrow to support strongly the delimitation of these associations. There is a possibility that some of these stands are relics from a deciduous forest that preceded the present mixed forest (McAndrews 1966). Pollen analysis of a small pond in this forest type would settle this. There is one on the Bear Paw Peninsula.

The alliance resembles the *Aceretum saccharophori-Ulmosum* of Dansereau (1959).

Alliance 7: The *Tilio-Acerion sacchari*

In this alliance *Acer saccharum* is the dominant tree, along with *Tilia americana* and *Quercus rubra*. It is usually a young forest, with the preceding stage of *Pinus strobus* and/or *Populus tremuloides-Quercus macrocarpa* still present (Buell and Cantlon 1951). Some of the relevés even contain herb species associated with an earlier stage (see alliance 8).

Notwithstanding the immature stage of the stands, the alliance is clearly defined by sociological group 11.

Group 10 (also present in the *Smilacino-Quercion*) and group 9b (also present in the *Ulmo-Tilion* and *Smilacino-Quercion*) reach highest values here. Because of the dense character of these forests, the shrub and herb layers are not well developed. In these layers often the most abundant plants are seedlings of *Acer saccharum* itself. Seedlings of *Tilia*, however, are fairly rare.

The alliance comes closest to the southern mesic forest of Curtis (1959), which occurs between prairie and conifer-hardwoods in Wisconsin, and to the Big Woods in south-central Minnesota (Daubenmire 1936). These forest types, as well as the *Tilia-Acerion*, are characterized by *Acer saccharum* and *Tilia americana* as their major dominants. Also, they lack *Tsuga canadensis* and *Betula lutea*, which are typical constituents of the forest to the east and northeast. However, in the Itasca area this forest type is much impoverished: *Carya*, *Celtis*, and *Juglans*, for example, are absent. The Big Woods contain most of the species found in the *Tilio-Acerion*, but they also show species that in the Itasca region are optimal in the *Ulmo-Tilion* or even in the *Fraxinetalia* (e.g. *Cryptotaenia canadensis*, *Laportea canadensis*).

Alliance 8: The *Diervilleto-Quercion*

This alliance comprises forests of *Populus tremuloides*, *P. grandidentata*, *Quercus macrocarpa*, and *Q. rubra*. *Tilia americana* is less common than in the *Ulmo-Tilion* and *Tilio-Acerion*. The group of species that comes to full development here is sociological group 13. The number of shrubs is high. As a whole group 13 therefore may be typified as a group comprising pioneer species. Several species are known to reach their optimum in the regeneration shrub stages after clearing of a forest, e.g. *Rosa* and *Rubus* are important on abandoned fields. *Corylus americana* is an important shrub at the prairie-forest margin (McAndrews 1966) in a *Quercus macrocarpa* savanna. All of these shrubs give their forests a young, secondary character.

In a number of relevés *Pinus strobus* or *Populus tremuloides* comprises the overstory, but never *Pinus resinosa*.

The species of group 13 are not present throughout the two alliances. From right to left in the table, in the direction of the *Tilio-Acerion*, more and more species of group 13 drop out. Group 13 can be divided into a number of subgroups along this line. In the *Tilio-Acerion* at last most of the species of group 13 are absent, except group 13a-1, which comprises the species that are most likely to persist, namely the overstory species. The table shows also that at the same time conditions are increasingly mesic. Two suballiances are recognizable, the *Smilacino racemosae-Quercion* and the *Urnulario-Quercion*.

The *Smilacino racemosae-Quercion* is characterized by group 9a (the group typical for the *Urnulario-Aceretalia*), and by at least one other mesic group that is present also in the *Tilio-Acerion*. This suballiance may be divided into the *Sanguinarieto-Populetum* (group 9b) and the less mesic *Querceto-Populetum tremuloides* (group 10). Seedlings of *Acer saccharum* may be present, though not in such quantities as in the *Tilio-Acerion*. The divisions in the *Smilacino racemosae-Quercion* may be considered as steps in a succession leading towards the highly mesic *Tilio-Acerion*. In *Populus* and *Quercus* forests on good sites and in some *Pinus strobus* forests, protection from fires would result in an increase in the number of mesic species and at the same time an elimination of the pioneer fire species. Indeed *Pinus strobus* is generally considered as among the pines occurring on the better sites, with loams

or sandy loams rich in bases (Curtis 1959). The succession from these pioneer forests towards the mesic *Tilio-Acerion* happens in the conifer-hardwood formation but also in the deciduous forest belt on the Big Stone Moraine, which is marked by soils especially favorable for mesic forest types. In fact, relevés from this area are heavily represented in the *Smilacino racemosae-Quercion*. Successions there since the federal land survey have been studied by McAndrews (1966).

The time elapsed since fires were a major ecological factor is short, and in the present *Tilio-Acerion* an overstory of *Populus*, *Quercus*, and *Pinus strobus* is still present. Pioneer species from this former forest are almost gone, however. An overstory of white pine above a nearly closed forest of mesic species also has been reported from northern Wisconsin (Curtis 1959, p. 212).

The *Uvulario-Quercion* can be divided into the *Uvulario-Populetum* and the *Corneto canadensis-Populetum*. The first association is unspecific. It comprises group 9a, characteristic for the order to which it belongs, and in addition only general upland forest species (groups 8 and 13). The *Corneto canadensis-Populetum*, however, shows for the first time a group of species (14) that more commonly occur in coniferous forest, though coniferous trees are generally absent. Moreover, besides *Quercus macrocarpa* and *Populus tremuloides*, the association is characterized by *Quercus rubra* in the canopy and *Acer rubrum* in the shrub layer (group 13a-2). *Acer rubrum* less often attains tree size: *Quercus* forests containing *Acer rubrum* trees are more commonly found in the deciduous belt south of our area, but there it includes *Ostrya virginiana*.

The *Corneto canadensis-Populetum* occupies a position exactly between coniferous forests (group 14) and the mesic deciduous forests (group 9a). Analogues in Quebec are the *Quercetum albae* and *Quercetum boreale* (Dansereau 1959).

CONIFEROUS UPLAND FORESTS

This group of communities has most genera and several species in common with the European *Vaccinio-Piceetea* Br.-Bl. 39. We have here a parallel class that might be called *Vaccinio-Piceetea boreo-americana* (Braun-Blanquet 1959). The sociological group that is characteristic for most of the coniferous forests is group 16.

Two orders may be recognized, namely the *Corno canadensis-Pinetalia*, characterized by group 14, and the *Arctostaphylo-Pinetalia*, characterized by group 21. Braun-Blanquet recognizes the *Vaccinio-Piceetalia* in Europe, Asia, and northern North America and the *Gaultherio-Piceetalia* in the northern United States and southern Canada. The latter order includes more representatives of the Ericaceae than the former. According to this our two orders are equivalent to the units described by Braun-Blanquet. However, there are differences in species composition. Although no characteristic species of the *Gaultherio-Piceetalia* are given by Braun-Blanquet, the order seems to show a similarity to the *Copti-Piceion* of this study. It therefore seems better to apply new names for

the orders described here. Because of the presence of conifers, the class is confined to the conifer-hardwood formation.

The Corno canadensis-Pinetalia

Alliance 9: *Populo-Quercion*

This alliance consists of forests of *Populus tremuloides*, *Quercus macrocarpa*, and *Pinus banksiana*. Compared with preceding communities, it has much less *Quercus macrocarpa*, however. *Pinus banksiana* may play a large part in the canopy of the forest, but it does not form pure stands. It is combined with either *Populus tremuloides* or *Pinus strobus*. Coniferous trees may even be absent, but relevés showing this composition are included in the order because they include groups 14, 15, and 16, which are typical of most coniferous forests. Only one association could be distinguished, the *Galieta-Populetum*, on the basis of group 16.

Several relevés of *Populus tremuloides* forests lack representatives of group 16, so they have not been included in the *Galieta-Populetum*. They do belong within the *Corno canadensis-Pinetalia*, however, because group 14 is present, but group 9a of the *Uvulario-Aceretalia* is not.

The *Populo-Quercion* is the richest alliance in the order. *Pinus strobus* may be present, even dominant; in these cases group 9a may occur. It is the only alliance in the order in which group 13a is present. The *Populus-Quercus* forests in the *Diervilleteo-Quercion* and the *Populo-Quercion* alliances have the same tree dominants, but floristically they seem to be tied to either the rich mesic deciduous forests or to the coniferous forests.

A similar situation exists in Michigan (Benninghoff and Cramer 1963) where *Populus grandidentata* forests show, besides relics of pioneer vegetation, species characteristic for poor and good sites. Gates (1930) described *Populus* stands with a species composition typical for "pine lands" and "beech maple soils." In Minnesota and Wisconsin this relation has been amply discussed by Kittredge (1938). It has been a point of frequent discussion in the past whether this part of the state is heading for an *Acer saccharum-Tilia americana* or an *Abies balsamea-Picea glauca* climax (Buell and Gordon 1945, Buell 1956, Buell and Martin 1961). According to Kell (1938) *Acer* forests would develop in fine-textured soils and *Abies-Picea* forests on coarser textured ones. There is in a general way a soil difference between the *Populo-Quercion* that tends to occur on sandy till or outwash and the *Smilacino-Quercion* on the heavier till of the Big Stone Moraine; but soil data from each individual relevé are needed to settle this.

Pteridium aquilinum is especially abundant in the *Populo-Quercion* and in the next alliance, the *Pinion resinosae-banksianae*. This is also true in *Populus* forests in lower Michigan (Gates 1930) and in the *Populetum tremuloides*, *Betuletum papyriferae*, and *Betuletum populifoliae* in Quebec (Dansereau 1959), which are also pioneer forests that offer much light to the ground flora.

The *Populo-Quercion* may be considered as a vicariant of the European *Vaccinio-Quercion*.

Alliance 10: The *Pinion resinosae-banksianae*

This alliance, which consists of forests of *Pinus resinosa* and/or *P. banksiana*, is floristically difficult to define. The only species that differentiate it from the *Populo-Quercion* are the two species of group 17, including *Pinus*

resinosa itself. The other groups present in this alliance occur in the *Populo-Quercion* as well.

In contrast to *Pinus strobus*, the two other pine species are less shade tolerant, but they are better adapted to the drier sites, which show a lower base content. As a result, these stands of pine are usually found on sands or loamy sands (Rudolph 1957). *Pinus banksiana* extends farther to the nutrient-deficient dry portion of the gradient than *P. resinosa*.

Most of the present mature *Pinus resinosa* forests that are protected in Itasca State Park belong to this type. They are widely recognized as a pioneer forest maintained by fires (Spurr 1954). This also applies to most of the *Populus* forests. Moreover, the *Pinion resinosa-banksiana* and the *Populo-Quercion* occur on the same soil types. These features in common may help to explain why the floristic differences between the *Pinion resinosa-banksiana* and *Populo-Quercion* are so small. The only difference is the occurrence of the dominant *Pinus resinosa*. The two species are alternately dominant in the same community, according to Curtis (1959, p. 469), as a result of the lower intensity of presettlement fires, which did not destroy pine seeds of *Pinus resinosa* and *Pinus strobus* in the same manner as the heavy slash fires did during lumbering of the pine forest. Reproduction of the pine forest today seems to be difficult because of protection from mild fires (Spurr 1954). The species composition of the *Pinion resinosa-banksiana* does not exclude a possible succession towards an *Abies balsamea* forest.

Alliance 11: *Abietion balsameae*

Abies balsamea and *Picea glauca* forests are usually at a very young stage in development. Seedlings and saplings of *Abies* are very abundant, and all the stands of this type are reproducing vigorously. Floristic ties with the *Pinion resinosa-banksiana* are still strong. Some of the relevés show a similar species composition except for *Abies balsamea* and *Picea glauca*, which occur in all the layers of the forest except the highest one—still occupied by *Pinus resinosa* (exclusively in this alliance) or *Pinus strobus*. This relationship with a former pine stage appears to exist in all the sites occupied by *Abies* forest type. A site that has been continuously occupied by *Abies balsamea* virtually does not exist (Buell and Niering 1957).

In part of the *Abietion balsameae* the pioneer sociological group 13b is still present. In the more advanced stages, however, several species occur that are characteristic for *Abies* forests in this part of the state (group 20). On the basis of this the *Trientaleto-Abietum* has been recognized. Some of the immature stages then may be arranged under the *Abietum balsameae rosetosum*, indicating the strong pioneer character of these forests. In the most advanced stage group 13b has gone, and we find a renewed occurrence of two species of group 3 that occur on peat (see also Buell and Niering 1957). The appearance of these species on mineral soil may be explained by the increasing dampness of the vegetation, probably related to the dense cover of these forests.

It is not surprising that group 13b is absent. As mentioned already, this group constitutes a pioneer group adapted to heliophilous conditions. Because of the shade of *Abies* this group is the most likely one to go. There is also a decrease in importance in group 8. A sub-association *Abietum balsameae mitelletosum* has accordingly been recognized.

The *Arctostaphylo-Pinetalia*

In contrast to the *Abietion balsameae*, where light is a limiting factor, in this order soil is limiting. The *Arctostaphylo-Pinetalia* occur on dry outwash sands. *Pinus banksiana* is almost the only tree present. The characteristic groups are 21a and 21b, the latter to a less extent. The outwash sands on which the order occurs belong to the mineral soils with the lowest nitrogen and moisture content. Also they show a low pH (Allway and McMiller 1935). The divisions in the order are probably a result of these soil factors.

Alliance 12: The *Astero-Pinion*

In this alliance sociological group 8c drops out of the general upland forest species. Also group 14, characteristic for most of the coniferous forests in the area, is absent. It is found at the margin of the Lake George outwash plain or in smaller occurrences of outwash sand in the region.

Alliance 13: The *Krigio-Pinion*

In the *Krigio-Pinion* more general upland forest species disappear (group 8b). The only ones that remain are *Fragaria vesca/virginiana* and *Maianthemum canadense* (group 8a). Most of the shrub layer so conspicuous in the preceding communities has gone, and the poor edaphic conditions even affect *Pinus banksiana* itself, which becomes more widely spaced. The understory is characterized by a low heath of ericaceous shrubs, in which lichens are common. At the same time a set of new species appears, among which are several dry prairie species.

Relevés of this type are all situated in the center of the Lake George outwash plain east of Itasca State Park. This area constitutes the most extensive outwash plain in the region. According to Allway and McMiller (1935), in a comparable area in the southern part of the county the federal land survey recorded *Pinus banksiana* forest in 1860 but prairie in 1871. It is not impossible that fire is the main reason for such a shift in vegetation type, for *Pinus banksiana* is a tree highly adapted to fire for its reproduction (Rudolph 1958). Perhaps at the same time fires also swept the Lake George outwash plain, returning much of the forest to prairie or pine savanna. The prairie species present in the *Krigio-Pinion* may be considered as relics from this period.

Two associations may be recognized in the order: *Krigiето-Pinetum*, characterized by group 21d, and the *Senecio-Pinetum*, in which group 21d is absent but groups 21b and 21c are present.

The order resembles in species composition the *Pinetum banksiana* in Quebec, where it occurs on the same soil types (Dansereau 1959). Dansereau also mentions the infiltration of prairie elements from the west. Towards the north in boreal and arctic regions this community becomes mixed with species from the *Copti-Piceion* (*Ledum groenlandicum*, *Picea mariana*), e.g. *Piceetum ledosum*.

(sensu Dansereau). In the Upper Midwest this type is found in southeastern Manitoba (Ritchie 1961), where *Ledum groenlandicum* occurs especially on gley soils with a high water table. In our region this usually is not so, but because of the location of these vegetation types in low-lying plains a high water table might affect the minor vegetation. The rare occurrence of *Ledum* in a *Pinus banksiana* stand just north of Itasca State Park might be explained in this way.

In Ritchie's study *Arctostaphylos uva-ursi* and *Lithospermum canescens* (A) are present on dry soils. *Linnaea borealis* and *Pteridium aquilinum* (B) do not occur on the driest soils. *Cornus canadensis* and *Vaccinium myrtilloides* (C) come third in tolerance to moisture deficiency. This behavior is also reflected in the table of the *Vaccinio-Piceetea*. Group A is characteristic for the *Arctostaphylo-Pinetalia*, group B constitutes species absent in the *Krigio-Pinion*, and group C has species that are even absent in the order.

The divisions of the order of the *Arctostaphylo-Pinetalia* probably thus reflect differences in soil moisture superimposed on the general deficiency of nutrients. The *Krigio-Pinetum* in such a scheme would be extremely dry. The same dependency towards soil moisture has been reported by Stallard (1929). According to him, the water content of the superficial soil in stands with shrubs (*Astero-Pinion*) is higher than that in *Pinus banksiana* stands without shrubs (*Krigio-Pinion*).

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