

AN ANALYSIS AND CLASSIFICATION OF WHITE SPRUCE COMMUNITIES IN RELATION TO CERTAIN HABITAT FEATURES¹

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Abstract

Physiognomy, ratio between percentage moss and herb cover, significant associations between species, and soil texture were used to group vegetation samples containing white spruce into community types.

The averages of the "measured mean" pH, the minimum pH, and the maximum pH of three soil layers, the height growth of the white spruce trees, and the nitrogen content of the white spruce foliage of the community types were compared by *t* test. When a significant difference showed that the samples were drawn from different populations, this was taken to justify the acceptance of the community types as distinct entities with regard to the features investigated.

Of the five community types originally recognized, only three were retained. They were respectively the *Equisetum pratense* type, the *Equisetum arvense* type, and a very variable community type typified by a more or less developed moss-herb-shrub vegetation.

Nomenclature

The nomenclature of Grout (1928-1940) was used for the Musci. Where possible, the nomenclature of Fernald (1950) was followed for the Pteridophyta and the Spermatophyta; wherever this was not possible, Rydberg's (1922) was used.

Introduction

In the course of study on the effects of environment on the incidence of a root-rotting disease complex in white spruce (*Picea glauca* (Moench) Voss) in Saskatchewan, it became apparent that a classification of plant communities containing white spruce was needed which would (1) facilitate the study of habitat conditions in the various community types as they relate to disease; (2) provide knowledge of the various ecological features to help define conditions at the time of infections, because the ecology of the stand has changed when the disease becomes apparent; and (3) describe the vegetation types of disease prone areas so that stand management plans may be formulated.

Moss (1953), in his account of the forest communities in northern Alberta, treated the entire white spruce vegetation as a single plant association in which he recognized four faciations; a needle cover faciation, a grass-shrub faciation, a shrub-herb faciation, and a feather-moss faciation. Most of these faciations do not occur in the area investigated. As a result this classification cannot be applied in Saskatchewan. Rowe (1956) attempted to arrange sites along a moisture gradient by arranging the species in five moisture preference classes and then according to the presence of species of each moisture class, calculating a vegetation moisture index for each site. This method takes into account only one ecological factor, and it is deemed inadequate in ordering

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the vegetation samples in a manner that would serve the purpose mentioned above.

This paper presents an attempt to group 50 samples of white spruce stands into a few abstract communities, with reference to soil pH, the height growth of white spruce, and the nitrogen content of the white spruce foliage. The particular factors chosen were considered important with regard to certain forest-pathological aspects of this study.

Methods

The study sites are located at Candle Lake, Saskatchewan, which is situated approximately 65 miles northeast of Prince Albert, at 45° latitude and between 105° and 106° longitude. The landform is the Wapawekka Hills Upland, represented by gently to strongly rolling morainic plains with an elevation of 1800–2500 ft (Acton *et al.* 1960). Muskeg and fluvio-glacial deposits commonly occur. Pondered caps are fairly common, and many sites have reworked glacial till. The soils are of the grey wooded type, and generally belong to the "Waitville association" (Mitchell *et al.* 1950). The region belongs to the Mixedwood Section of the Boreal Forest (Rowe 1959).

A few points need to be emphasized in considering the choice of location of the study sites and the methods of vegetation analysis used. As a result of stand history, sharp boundaries between plant communities exist, which represent to some degree different stages in the development and succession. Also there are sharp boundaries as a result of topography (Dansereau 1957). Even if most habitat factors are continuous variables, there is the possibility that the total effect does not change gradually; associated changes of more than one factor and local steepening of gradients often result in radical changes in vegetation as the ecological tolerance of the species has been exceeded. Goodall (1954) demonstrated the continuous variation of vegetation but recognized that points representing stands may tend to form clusters in multidimensional space. These clusters correspond to units of vegetation classification systems. Poore (1955*a, b, c*), using a different system, demonstrated that most stands which he investigated tended to fall into groups of similar composition.

As a result of these considerations it was decided to attempt to group the sample plots in a number of community types.

As it was impractical to establish the sample plots completely at random, the stands for this study were chosen subjectively with the purpose of obtaining a fair representation of the communities, containing white spruce, occurring in the region. Fifty sample plots were established at random within these stands. The size of each sample plot was 50 × 50 ft as it was found that the soils were too variable to use larger units. These sample plots were used as basic units within which all measurements were made.

The percentage cover of each component of the vegetation was measured by means of 10 line intercepts, each 20 ft long, which were run at random across each plot (Brown 1954). The presence of species that occurred on the plot but were not intercepted by the lines were recorded. To investigate if small scale non-random patterns were present within the sample plots the line-intercept data were analyzed according to a variance method developed by Greig-Smith (1957) and Kershaw (1959).

Different methods were used in grouping the vegetation samples. First, the samples were tentatively grouped according to physiognomy. Where it was obvious that physiognomy alone was not sufficient to subdivide the vegetation, other features such as soil texture and species composition were utilized to attain a grouping. Second, the associations between 37 species were examined for each pair of species, by comparing the number of "observed together" with the number of "expected together" assuming random distribution. The significance of departure from the expected value was calculated from a 2×2 contingency table and tested by the chi-squared test. Only positive and negative associations for which $P \leq 5\%$ are considered. Third, the percentage total moss cover was plotted against percentage total herb cover. The samples were then grouped according to definite clusters of points in the diagram.

The trees on all plots were tallied for diameter at breast height and the data converted to area of cross section. The total basal area was calculated on a 1-acre basis.

Height growth curves were constructed from four or five dominant trees on each sample plot. The trees were felled and sectioned at 5-ft intervals; the growth rings were counted at each interval, and from these data the growth curves were constructed. The numerical value of the growth rate during the "intermediate stage" (Baker 1950), measured in feet per year, was determined, and this "Intermediate Height Growth Index" (I.H.G.I.) was used as an index of site quality.

The soil profiles of all sites were described in detail regarding depth and thickness of all horizons, estimate of soil texture, and soil colors on air-dry samples (Munsell color charts). Soil samples were prepared as a paste according to Doughty (1941), and the pH measured with a Beckman pH meter with a combination glass electrode. This was done either immediately in the field, or in the field laboratory within a few hours after sampling. The "measured mean" pH and the range of pH was determined on each sample plot (van Groenewoud 1961)

Foliage for analysis was taken only from the top 4 ft of the trees to minimize differences in the chemical composition due to different locations of the foliage (Leyton 1956, 1958; White 1954; Meyers and Brunstette 1946). To minimize the error which results from seasonal fluctuations in the composition of the foliage (White 1954; Tamm 1955; Nakatsuka 1952; Olsen 1943; Mitchell 1936; Sampson and Samish 1935; Meyer 1928; Ramann and Barcer 1910) the sampling was performed during the winter. The tree tops were shot down with a 0.22 caliber rifle with a telescopic sight. The foliage of these tops was kept at -18°C until it could be further processed. The spruce needles were dried at 60°C . The scales and other contaminations were then removed by hand and the dust adhering to the foliage was removed with an air jet at 60 p.s.i. The samples were ground in a Wiley mill and stored again at -18°C until the actual analysis could be performed. The nitrogen content was determined by the micro-Kjeldahl method. The results were corrected for moisture content of the samples at the time of analysis. Because a preliminary study revealed considerable variation in foliage composition within a site, 10 samples from each of the 50 sample plots were analyzed.

The averages of the "measured mean" pH for each group of plots were compared by a *t* test for each of three soil horizons. As the number of samples for each group was different, a weighted mean *t* was calculated according to an approximate method of Cochran and Cox (1944). Similarly the means of the minimum and maximum pH for the three soil layers, the I.H.G.I., and the nitrogen content of the foliage were compared statistically. A significant difference between the means shows that the samples were drawn from different populations and justifies the acceptance of these community types as distinct entities with regard to the factors investigated (comparable to Poore's "noda" (Poore 1955c)).

To verify a hypothesis by Brinkman (1936), the relationship between tree cover and percentage cover of the moss layer was investigated by plotting basal area of the trees against percentage moss cover, and by calculating the correlation coefficient.

Results

Upland stands with white spruce reveal little differentiation in species composition but a wide variety in percentage cover of the different species of mosses and herbs.

The variance analysis of the line-intercept data gave no indication of any small scale non-random pattern within the boundaries of the sample plots.

By using the physiognomy as a basis for grouping, three main vegetation types could be recognized: (a) A community type with predominantly *Equisetum* species for a ground cover (Figs. 1, 2, and 3). (b) A community type with almost continuous moss cover of *Hylocomium* and *Calliergonella* species and an almost complete absence of herbaceous species (Fig. 4). This type is identical with Moss's (1953) feather-moss faciation. (c) A community type characterized by a more or less developed herb-shrub vegetation above a feather-moss layer. The most common herbs are *Rosa acicularis*, *Linnaea borealis* var. *americana*, *Petasites palmatus*, *Cornus canadensis*, *Fragaria vesca*, *Mitella nuda*, *Mertensia paniculata*, *Maianthemum canadense*, *Pyrola secunda*, *Geocaulon lividum*, *Aralia nudicaulis*, *Lathyrus ochroleucus*, *Trientalis borealis*, *Pyrola asarifolia*, *Vaccinium vitis-idaea* var. *minus*, and *Arctostaphylos uva-ursi*. Stands belonging to this community type occupy large areas. This type shows the greatest variability within its limits. There is no distinct delimitation between this community type and the feather-moss type (b) (Figs. 4, 5, 6, and 7).

The results of the significance tests of the associations between species (Fig. 8) support the decision to group the samples with *Equisetum* species apart from the others. Little justification exists on the basis of "significant associations found" (Fig. 8) to recognize stands with a continuous moss cover as members of a separate vegetational unit. This community type, however, was tentatively retained to compare statistically the means of aforementioned features with those of other types.

The vegetation tables revealed two different types of vegetation within the group of stands with *Equisetum* species. In one group *E. arvense* is dominant; *E. pratense* is dominant in the other group. This division is also evident in the diagram of significant associations between the species (Fig. 8). The two community types occupy different soils; the *E. arvense* communities occur on loam



FIG. 1. White spruce community with *Equisetum pratense* along a lake shore.
FIG. 2. White spruce community with *Equisetum pratense* at the edge of a marsh.
FIG. 3. White spruce community with *Equisetum arvense* at the edge of a marsh.



FIG. 4. White spruce stand with continuous layer of the mosses: *Hylocomium splendens* and *Calliergonella schreberi*.

FIG. 5. White spruce community with slightly developed herb layer; *Cornus canadensis*, *Petasites palmatus*, *Linnaea borealis* var. *americana*.

FIG. 6. White spruce community with moderately developed herb layer.

FIG. 7. White spruce community with well developed herb layer.

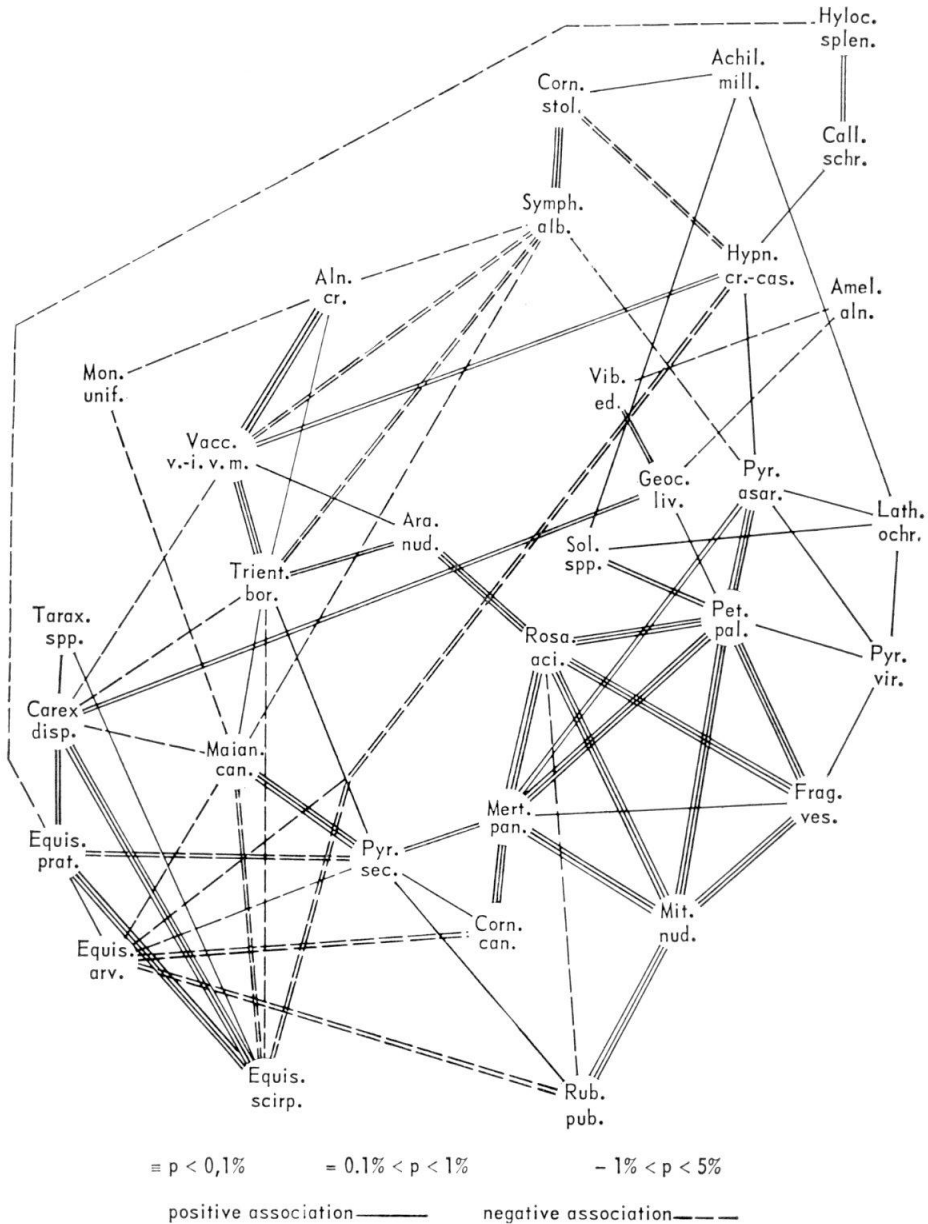
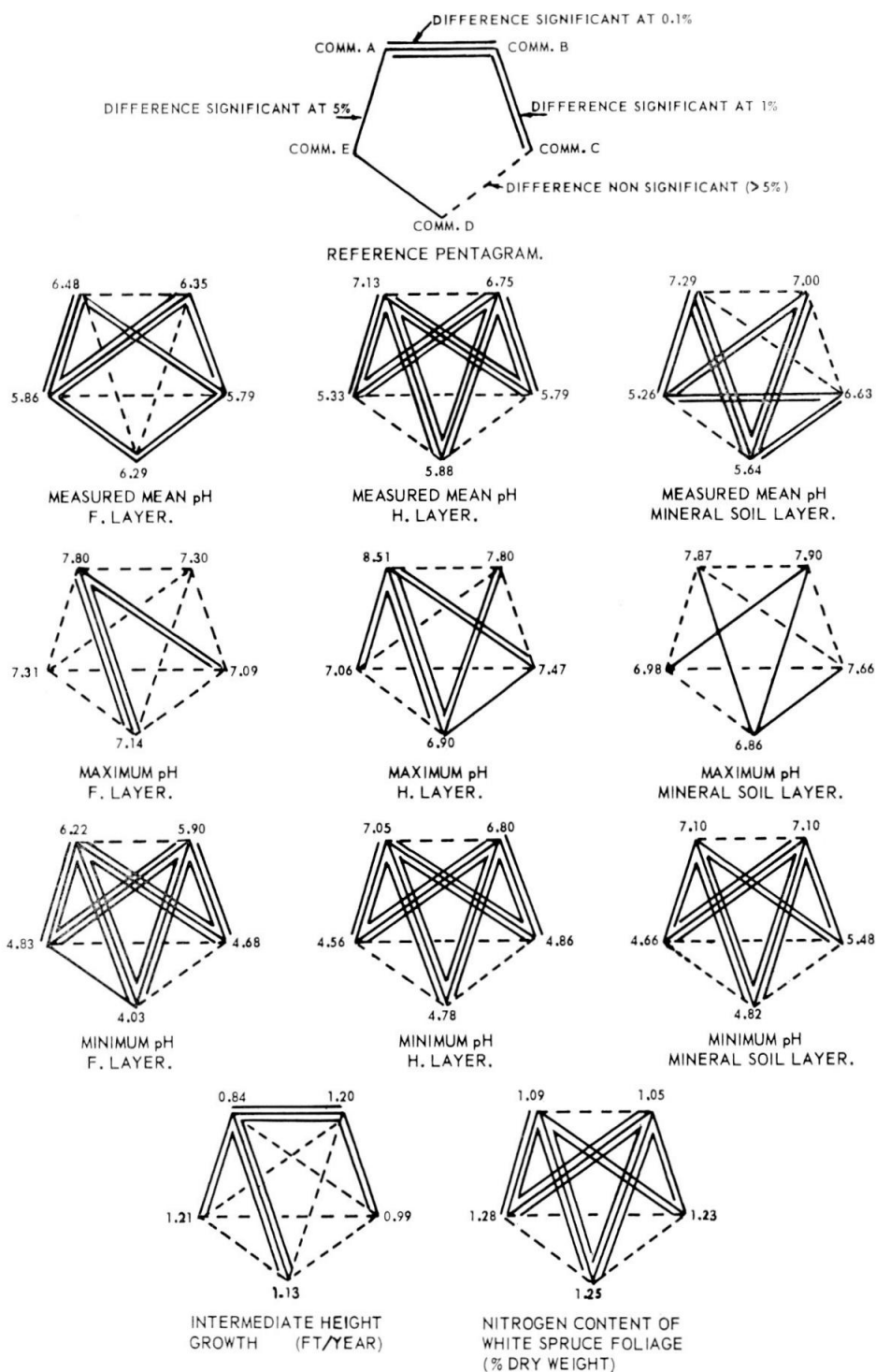


FIG. 8. Significant associations between species. No significant associations were found with *Picea glauca*, *Linnaea borealis* var. *americana*, *Arctostaphylos uva-ursi*, *Vicia americana*, *Viola renifolia*.



or clay soils, and the *E. pratense* communities occur on sandy soils with a deep Ao horizon and a fluctuating water table.

The plotting of percentage total moss cover against percentage total herb cover showed a definite clustering. One group corresponded to the feather-moss type. The communities with *Equisetum* species yielded points which were clustered together. The herb-shrub sites yielded two clusters of points; one group with a ratio of percentage moss cover over percentage herb cover of 20/60 and one with a ratio of 75/75. These two groups did not fit any other division but they were tentatively retained to be statistically compared for soil pH, height growth of the spruce, and nitrogen content of the white spruce foliage.

The diagram of the association between species (Fig. 8) shows several tendencies in the distribution of the vegetation, but based on these associations no further division could be made.

The results of the statistical analysis of the soil pH, height growth, and nitrogen content of the foliage are condensed in Fig. 9.

A comparison of the "measured mean" pH's of the community types shows that the difference between the two *Equisetum* community types (communities A and B) is not significant.

The "measured mean" pH of either *Equisetum* types, however, is significantly different from those of the feather-moss and the herbaceous types (communities C, D, and E). The differences between feather-moss and herbaceous types are not significant. The maximum pH relationships do not show a consistent pattern, while the minimum pH relationships show a distinct pattern which is consistent with that of the "measured mean" pH's.

A comparison of the I.H.G.I.'s shows that the two *Equisetum* types are significantly different in this respect. The height growth is greater in the two herbaceous types than in the feather-moss types. The differences, however, are not significant.

The nitrogen content of the white spruce foliage in the two *Equisetum* types was not significantly different. Both, however, were significantly different from the feather-moss and the herbaceous types. The nitrogen content in the feather-moss and in the herbaceous types were high and not significantly different.

The scatter diagram, showing the relationship between total basal area of the trees and the percentage moss cover, indicated a strong association between the two. The correlation coefficient was 0.7 with a significance level of 0.1%, indicating that 47% of the variation in the moss cover can be related to variation in the basal area. Considering the range of sites investigated this may be regarded a high correlation.

Discussion

The *Hylocomium-Calliergonella* type (community C) is easily recognizable according to physiognomy and is distinct in the scatter diagram of the moss-herb cover ratio. It was, however, not significantly different from the herbaceous types (community D and E), when the pH of the soil, the I.H.G.I., and

FIG. 9. Pentagrams showing mean values for each feature and each of five community types, and significance levels of the differences between the means.

the nitrogen content of the foliage of white spruce were considered. Moss (1953) recognized this community type as a separate unit (feather-moss faciation). When significant positive and negative associations between species were considered (Fig. 8) the *Hylocomium-Calliergonella* type was not evident; in fact, there were few significant associations, positive or negative, of other species with either *Hylocomium splendens* or *Calliergonella schreberi*. Both moss species have wide ecological amplitudes. Rowe (1956) placed them in high moisture preference classes; in this study it was found that these species flourished in a wide range of moisture conditions. It is true that both species can occur and thrive on moist soil, but it is doubtful whether they receive any moisture from the mineral soil (Tamm 1953). Stålfelt (1937) reports that *Hylocomium* is one of the few plants that can survive complete air drying. This is another indication of its wide ecological amplitude. *Hylocomium splendens* and *Calliergonella schreberi* occupy approximately the same range of habitats. Their optimum development, however, does not coincide. The highly significant correlation ($r = 0.7$, $P = 0.1\%$) between the moss cover and the basal area of the trees suggests that competition is an important factor in the distribution of these mosses. Most of the sites with a continuous moss cover have a very high tree root concentration in the uppermost soil horizons, which, as a result, are very dry. Profile development is generally shallow and weak. This dry condition coupled with low light intensity (as a result of the dense canopy) depresses the herbaceous species and favors the mosses.

Moss (1953) regards the feather-moss faciation as the association climax, and includes *Equisetum* spp., *Cornus canadensis*, and various other species. He postulates that the other faciations he mentions eventually develop into this stage. White spruce in the feather-moss communities is very susceptible to a root-rotting disease complex, which tends to decrease the basal area, with accompanying changes in vegetation (van Groenewoud 1954, 1956). This suggests that in Saskatchewan a development as indicated by Moss is unlikely. The feather-moss communities are not stable communities and they can not be regarded as climax vegetation. Intermediates between the *Hylocomium-Calliergonella* communities and those with a well-developed herbaceous and shrub cover are rather abundant (Figs. 5 and 6); nevertheless these are not intermediates in a developmental series but are relatively stable communities, except in the case of regeneration after fire or cutting. The intermediate communities occupy different places along various environmental gradients. This is also suggested by the increase of the I.H.G.I. for community types C to E (Fig. 9).

The association diagram (Fig. 8) shows several different plant groupings. This is due partly to the pattern in plant distribution within individual stands, and it demonstrates that some species predominantly inhabit the same range of habitats. Dawson (1951) and Greig-Smith (1957) have pointed out the effects of plot size on measures of association between plants. According to Dawson (1951) association can mean two things: individuals of one species change the environment in such a way as to make it more favorable to individuals of the other species; and a certain environmental factor or combination of factors may affect two species in a similar way or in opposite ways which would result in positive or negative associations. The size of the plots used

(50 × 50 ft) eliminates the effect of spatial exclusion. The significant positive and negative associations found are thus the result of interspecific relations, the effects of the environment, or a combination of these.

Kershaw (1959) suggested three causal factors of small-scale pattern in vegetation: morphological, sociological, and physiographical causes. Whitford (1949) considered clonal development of major importance in the development of aggregated distributions, and related the degree of aggregation to stand age. Vegetative reproduction by stolons or rhizomes, occurring from each of 25 herbaceous species which were examined, suggest that many species in the boreal forest are capable of forming aggregated distributions. The three causes mentioned by Kershaw (1959) often seem to be inseparable. Morphologically, almost all species investigated are able to form an aggregated distribution, but competition often prevents its formation. This seems to support Whitford's view. As Weaver (1930) pointed out, "The production of tillers is successful only when the secondary root system penetrates into moist soil and meets the increased demands of water". It is easily observed that species like *Geocaulon lividum*, *Petasites palmatus*, *Trientalis borealis*, and *Pyrola secunda* sometimes form dense aggregations under partly released white spruce because of the increased availability of soil moisture. As soon as root competition is decreased, the scattered plants produce abundant rhizomes, and an aggregated distribution on a small scale can result. *Hylocomium splendens* and *Calliergonella schreberi* do not react too quickly to changing conditions. To investigate the presence of any small-scale non-random pattern within the boundaries of the sample plots a variance analysis, using different length of line intercepts, was performed. No small-scale non-random pattern was found, although the species are morphologically capable of forming such a pattern. This agrees with Whitford's view (1949) about the relation between stand age and degree of aggregation and it supports the view that the stands chosen were relatively stable and not recently disturbed.

The relationships between species, as expressed by the diagram of significant associations, suggest that more than one factor is causal in the differences in distribution of the various species.

The various groups of species with significant associations are ecologically differentiated by different ranges of pH, moisture preferences, degrees of tolerance of competition, and probably several other factors. Interaction of these factors creates a wide variety of conditions, which are reflected by the wide range in abundance and performance of the different species (Figs. 3, 4, 5, and 6). The continuous variability that exists within the large and variable community type lends itself to ordination rather than to classification. Ordination was used in the deciduous forest stands of the North Central States (Curtis and McIntosh 1951) and in the mallee vegetation of Australia (Goodall 1954) and proved most satisfactory. The moisture content of the soil near lakes, creeks, or swamps is the only factor of the environmental complex that can be considered as being naturally discontinuous. The capillary moisture is able to rise only to a certain height above the phreatic niveau, depending on the texture and structure of the soil. If the soil surface away from the water's edge is sloping upwards, there is a sharp break in moisture content with distance from

the edge of the water which can easily be observed if a trench is dug perpendicular to the water's edge. The discontinuity in the moisture gradient is accompanied by other changes in the soil, for instance, profile, pH, and nutrients. This discontinuity in environmental factors is primarily responsible for the existence of the two distinct community types (A and B) with, respectively, *Equisetum arvense* and *Equisetum pratense* as dominants in the herb layer. Together, these types are distinct physiognomically, in the scatter diagram where the percentage moss cover was plotted against basal area, and in the association diagram. They are also significantly different from the other community types when pH of the soil, and the nitrogen content of the white spruce foliage are considered. They are separated from each other by significant differences in species composition, texture of the soil, and height growth of white spruce. These community types can be considered, therefore, as separate entities with regard to the factors mentioned and are comparable to Poore's *noda* (Poore 1955c). The possibility that intermediates could be found along a gradient of soil textures needs further investigation.

The stands with a continuous moss cover (Fig. 4) and those with herb and shrub layer (Figs. 5, 6, and 7) could not be accepted as belonging to separate types. Tentative groupings showed no significant differences. It seems logical, therefore, to group them all together in one community type with a wide ecological amplitude and floristic variation. The relationships between the communities belonging to this type will be the topic of another paper.

A comparison of the nitrogen content of the spruce foliage and the growth of white spruce in the different community types reveals some interesting facts. There is a large difference between the nitrogen content of the foliage in the communities with *Equisetum arvense* and *Equisetum pratense* (A and B) and that of the upland communities (C, D, and E). Both community types with a gley soil (A and B) have a low nitrogen content in the foliage (respectively 1.09 and 1.05%). There is, however, a large difference between the height growth of the trees in these two types. The community type with *Equisetum arvense* occurs on clay or loam soils with low pore space and permeability. The white spruce in this type are very slow growing (mean I.H.G.I. 0.84). The community type with *Equisetum pratense* occurs on sandy soils with a high permeability, permitting fluctuation of the phreatic niveau, replenishment of nutrients, and better aeration. The white spruce trees in this type grow very fast (mean I.H.G.I. 1.20) yet have as low a nitrogen content in the foliage as trees on *E. arvense* sites. The nitrogen content of the foliage of the trees on all upland sites is high (respectively 1.23, 1.25, and 1.28) even in the communities with a tree growth as slow as that in the *Equisetum arvense* community type.

Of the five community types originally recognized, only three are retained as being significantly different with reference to soil pH, the height growth of white spruce, and the nitrogen content of white spruce foliage. They are respectively the *Equisetum pratense* type, the *Equisetum arvense* type, and a floristically very variable type with a wide ecological amplitude.

The significance of these community types, in relation to the root-rotting disease complex mentioned before, will be considered in a forthcoming paper.

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