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jedoch einen grösseren Anteil der Variation und sind näher korreliert mit Standortsfaktoren als die Achsen der anderen Ordinationen.

Die Gruppenanalyse (cluster analysis) beruht auf dem "verallgemeinerten Abstand" ( $D^2$ ). Sie erlaubte zwar eine Klassifizierung der schweizerischen, nicht aber der kanadischen Vegetationsaufnahmen. Unterschiede der Mittelwerte von Licht- und pH-Verhältnissen in diesen Gruppen sind in den meisten Fällen statistisch gesichert.

Die Methode der Differentialarten-Gruppen ergab eine Klassifizierung sowohl der schweizerischen als auch der kanadischen Aufnahmen. Die Gruppen der schweizerischen Aufnahmen waren (statistisch gesichert) verschieden in bezug auf ihr pH, aber nicht auf die Lichtverhältnisse. Die Gruppen der kanadischen Aufnahmen unterschieden sich in keinem der untersuchten Standortsfaktoren (statistisch gesichert).

Die Kombination zweier Methoden, einer ordinerenden mit einer klassifizierenden oder einer Gruppenanalysemethode, die auf der Ordination beruht, erwies sich als wirksamste objektive Arbeitsweise für die Ordnung der Vegetationsaufnahmen.

Vegetation data collected in *Abies* forests in Switzerland and *Picea* forests in Saskatchewan, Canada, were organized by three ordinating methods, 1. principal component analysis of the covariance matrix, 2. an ordinating method based on the  $D^2$  statistic, and 3. principal component analysis of the transformed  $D^2$  matrix, and by two grouping methods, 1. the Zürich-Montpellier method of differential species-groups, and 2. a cluster analysis based on an ordination.

The relationships found to exist between habitat features and the axes of the ordinations follow the same pattern for all ordinations. All axes were ecologically significant. The axes of the ordination resulting from the principal component analysis of the covariance matrix, however, account for a larger portion of the variation and show a closer relationship with the habitat factors and other site features than the axes of the other ordinations.

Cluster analysis, based on the  $D^2$  statistic, produced grouping of the Swiss vegetation samples but not of the Canadian samples. Differences between mean levels of light and soil pH in those groups were in most instances statistically significant.

The Zürich-Montpellier method distinguished groups of sample plots in both the Swiss and Canadian data. In the case of the Swiss data, the groups of plots were significantly different with reference to soil pH, but not with reference to light conditions. The groups of Canadian sample plots were ecologically not significantly different.

The combination of an ordinating technique with a classification technique or a cluster analysis, based on the ordination, was shown to be a powerful, objective method for vegetation analysis.

## 2. Introduction

In an earlier study (VAN GROENEWOUD 1965) of the ecological conditions associated with the occurrence of a root-rotting disease complex in white spruce (*Picea glauca*) stands in Saskatchewan, Canada (VAN GROENEWOUD 1956), an attempt was made to design a classification of plant communities containing white spruce, which would show a significant correlation with certain habitat factors and other site features.

The classification of these communities was considered of extraordinary importance as it would aid in the study of the conditions prevailing in the different community-types and it would help to define the habitat conditions at the time the trees become infected. The disease is usually discovered only

after trees have died, by which time the ecological conditions (e.g. light and water) often have changed (VAN GROENEWOUD 1965). A classification also would be valuable by describing the vegetation-types associated with the disease complex, which would be of great help in locating disease prone areas.

A tentative classification of the vegetation samples into five groups based on physiognomy, statistically significant associations between species, ratio between percentage moss and herb cover, and soil texture was drafted. The averages of the quantitative measures of several habitat features of these groups were compared by "t" tests. If the samples proved to be drawn from different populations these groups were accepted as distinct entities with regard to the factors investigated. The groups are comparable to Poore's noda (POORE 1955, a, b).

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

The last community-type represents at least 80% of all white-spruce stands present in the area investigated. It contains the stands that suffer most from the forementioned disease complex. It appeared essential to investigate the possibilities of improved methods to order vegetation samples, in such a manner that an ecologically significant system does arise.

The object of this study was to evaluate the potentialities of different approaches, to elucidate the principles involved, and to demonstrate the potentials of different combinations of various biometric and other methods presented in this dissertation.

No attempt was made to explain, in detail, the mathematical procedures involved, because most ecologists are not experts in mathematical statistics. The separate methods are more fully described elsewhere (HARMAN 1960, IHM 1964, RAO 1952). It is, however, of vital importance to the ecologist to know what is achieved by using these statistical procedures and to understand how the analysis is performed. Therefore, emphasis has been placed on explaining the principles involved, wherever possible elucidating these principles by geometrical representations. The methods are illustrated with an example of principal component analysis of hypothetical data in appendix V.

The data were collected in forests in Saskatchewan, Canada, and in Switzerland. The Canadian sites are located at Candle Lake, approximately 65 miles north-east of Prince Albert at 54° latitude and between 105° and 106° longitude. The landform is the Wappewekka Hills Upland, represented by gently to strongly rolling morainic plains with an elevation of 1800 to 2500 feet

(ACTON *et al.* 1960). The precipitation is approximately 15.5 inches (38.75 cm) of which approximately 6 inches (15 cm) falls during the summer. The soils are of the grey-wooded type, and generally belong to the «Waitville association» (MITCHELL *et al.* 1950). The region is part of the Mixedwood Section of the Boreal Forest (ROWE 1959).

The Swiss forests studied are located in the proximity of Roggwil, Langenthal (Kanton Bern) and Murgenthal (Kanton Aargau), between 47°21' and 47°16' latitude and between 7°48' and 7°54' longitude. They are situated on moraine deposits of the Riss period. The soils are mottled podzolized brown earths, and pseudogleys of the brown earth group (PALLMANN *et al.* 1943). The precipitation is approximately 116 cm of which 49% (56.8 cm)<sup>1</sup> occurs in the summer (MEYER 1949). These forests belong to the *Quercus-Abietetum* and partly to the *Melico-Fagetum* (FREHNER 1963). Some of these forests were described by Meyer as *Mastigobryeto-Piceetum abietosum* (MEYER 1949, 1954).

### 3. Nomenclature and terminology

The nomenclature of BINZ-BECHERER (1961) was followed for the *Pteridophyta* and the *Spermatophyta* in Switzerland. The nomenclature of BERTSCH (1959) was used for the Swiss *Musci*.

Where possible the nomenclature of FERNALD (1950) was followed for the Canadian *Pteridophyta* and *Spermatophyta*; elsewhere, RYDBERG's (1954) nomenclature was followed. The nomenclature of GROUT (1928–1940) was used for the Canadian *Musci*, with the exception of *Calliergonella schreberi*, which is replaced by *Pleurozium schreberi* (Willd) Mitt.

The terms principal component, principal factor, and principal axis have the same meaning. The term factor, however, can easily be mistaken in ecological work for a habitat factor, which it is not. Therefore, the term principal factor is not used in this publication. The term factor is used exclusively in the sense of habitat factor. Wherever other features of these habitats or plant communities were included in the analysis (e.g. height-growth of the white spruce trees, nitrogen content of the white spruce foliage) the term features is used.

### 4. Theoretical considerations

Investigations of the ecology of vegetation can be divided into three stages (ELLENBERG 1954):

- (1) Description;
- (2) Organization (ordination and classification);
- (3) Interpretation.

#### 4.1 Description

A sample consists of a small portion separated from some large population, about which certain information is sought. The problem is to gather adequate

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<sup>1</sup> 116 cm = 46 inches, 56.8 cm = 22.6 inches