ACTA FORESTALIA FENNICA

192

AN ECOLOGICAL STUDY OF UPLAND FOREST SITE CLASSIFICATION IN SOUTHERN FINLAND

EKOLOGINEN TUTKIMUS ETELÄ-SUOMEN KANGASMETSIEN KASVUPAIKKALUOKITUKSESTA

Jussi Kuusipalo

SUOMEN METSÄTIETEELLINEN SEURA 1985

Suomen Metsätieteellisen Seuran julkaisusarjat

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Publications of the Society of Forestry in Finland

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Seloste

EKOLOGINEN TUTKIMUS ETELÄ-SUOMEN KANGASMETSIEN KASVUPAIKKALUOKITUKSESTA

To be presented, with the permission of the Faculty of Mathematics and Natural Sciences of the University of Joensuu, for public criticism in Auditorium Y 2 of the University, Yliopistokatu 2, Joensuu, on 26 March 1986, at 12 o'clock noon.

HELSINKI 1985

KUUSIPALO, J. 1985. An ecological study of upland forest site classification in southern Finland. Seloste: Ekologinen tutkimus Etelä-Suomen kangasmetsien kasvupaikkaluokituksesta. Acta For. Fenn. 192: 1–78.

The vegetation and a number of physical and chemical soil properties were studied on a random sample of closed upland forest stands in southern Finland. The material consists of a total of 410 sample plots. Two-way indicator species analysis (TWINSPAN) was carried out in order to produce a hierarchical clustering of samples on the basis of the vegetation data. Discriminant analysis and analysis of variance were applied in order to find environmental correlations of the vegetation clustering. The vegetation was found to indicate the nutrient regime of the humus layer well, but to a less extent the properties of the sub-soil. The understorey vegetation was found to be jointly dependent on site fertility and on the properties of the tree stand, especially on the tree species composition. Although the forest vegetation appears to be distributed rather continuously along an axis of increasing site fertility, relatively unambiguous classification can be based on the appearance of indicator species and species groups.

The results of the study were interpreted as indicating that operational site classification done using the vegetation is rather good method for classification in closed forest stands. Different methods produce relatively consistent, natural and ecologically interpretable classifications. The results also imply that the vegetation cover and the humus layer develop concurrently during the development of the ecosystem, but the differentiation of the site types is regulated simultaneously by a number of interacting factors ranging from minerological properties of the parent material to the topographical exposition of the site. As the plant cover depicts all these primary factors simultaneously, only a relatively rough ecological site classification can be based on the vegetation.

Tutkimusaineisto käsittää 410 satunnaisesti otostettua, puustoltaan sulkeutunutta metsikköä, jotka sijoittuvat Etelä-Suomen metsäkasvillisuusvyöhykkeen kangasmaille. Näytealoilta analysoitiin pintakasvillisuus sekä mitattiin puusto ja kasvupaikan viljavuustunnuksia. Näytealat luokiteltiin kasvillisuuden perusteella soveltaen rinnasteista indikaattorilajianalyysia (TWINSPAN). Erottelu- ja varianssianalyysin avulla selvitettiin kasvillisuuden jakautumisen riippuvuuksia ympäristötekijöistä. Pintakasvillisuuden havaittiin heijastavan humuskerroksen ravinnetasoa varsin hyvin; vastaavaa riippuvuutta mineraalimaan ravinteisuustunnuksista ei havaittu. Pintakasvillisuuden rakenne on riippuvainen paitsi kasvupaikan viljavuudesta, myös puuston ominaisuuksista, erityisesti puulajisuhteista. Vaikka metsäkasvillisuus näyttää muodostavan selvän jatkumon viljavuusgradientilla eikä tietylle kasvupaikalle tyypillisiä lajiyhteisöjä voida erottaa, suhteellisen yksiselitteinen kasvupaikkaluokitus on mahdollista muodostaa tarkastelemalla eri kasvilajien ja lajiryhmien kasvupaikkavaatimuksia ja indikaattoriarvoa.

Tutkimuksen tulokset osoittavat, että pintakasvillisuuteen perustuvaa operationaalista kasvupaikkaluokitusta voidaan soveltaa varsin menestyksellisesti kivennäismaiden sulkeutuneissa metsiköissä. Eri menetelmät johtavat suhteellisen yhdenmukaisiin, luonnollisiin ja ekologisesti tulkintakelpoisiin luokituksiin. Tulokset näyttävät viittaavan siihen, että kasvupaikan kasvipeitteen ja humuskerroksen ominaisuudet ovat kiinteässä riippuvuussuhteessa toisiinsa, muotoutuen ekosysteemin sukkession myötä kullekin kasvupaikalle tyypillisiksi. Kasvupaikkojen erilaistumista säätelevät samanaikaisesti hyvin monet abioottiset ympäristötekijät, mineraalimaan minerologisista ominaisuuksista kasvupaikan topografisiin suhteisiin. Koska pintakasvillisuus on riippuvainen samanaikaisesti hyvin monista abioottisista ympäristötekijöistä, kasvillisuuden pohjalta ei ole mahdollista edetä kovin tarkkaan ja pienipiirteiseen kasvupaikkaluokitukseen.

ODC 542+114.521+187
ISBN 951-651-069-8
Arvi A. Karisto Oy:n kirjapaino
Hämeenlinna 1985

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PREFACE

This study constitutes part of a project being carried out in the Finnish Forest Research Institute, Department of Soil Science, in co-operation with the Department of Biology at the University of Joensuu, into the classification of upland forest soils. I started working on this study in summer 1982 while employed by the University of Joensuu. In the years 1983–84, I continued to work on the theme while employed as a research assistant and a junior researcher by the Academy of Finland. The study was supported financially by the Academy of Finland.

I received considerable advice during the stages of the study from Prof. Eino Mälkönen, head of the Department of Soil Science, and invaluable assistance in collection and treatment of the material from Mr. Pekka Tamminen, L. F., and Mr. Teuvo Levula, researchers of the Department of Soil Science. I have also received considerable help in carrying out the field work for the study from Mr. Jorma Korhonen and Mrs. Riitta Heimala-Raimas. Prof. Eddy van der Maarel of the University of Uppsala, Institute of Ecological Botany, helped in theoretical questions involded in estimating the optimal level of classification. Other sources of contribution to the study include the staffs of the Department of Biology at the University of Joensuu, the Department of Soil Science at the Finnish Forest Research Institute, and the Institute of Ecological Botany at the University of Uppsala. Prof. Eino Mälkönen and Doc. Pertti Huttunen have read the manuscript and made valuable comments. Mr. John Derome of the Department of Soil Science kindly checked my English.

I would like to thank those responsible for providing funds for the study, the persons mentioned above, and all who have contributed towards the completion of the present work. I am extremely grateful to my family for the understanding and support.

Joensuu November 1985

Jussi Kuusipalo

1. INTRODUCTION

The Finnish forest site type system is based on A. K. Cajander's (1909a, 1921, 1926, 1949) theory, according to which the understorey vegetation reflects the major soil and other important site features accurately and reliably enough to be used in estimating the conditions that control site fertility. In southern Finland, topographical variation is minimal, till soils are predominant and there are few forest-forming tree species. However, forestry is faced with a wide range of production and stand responses, and site classification must separate out the conditions that control these responses. It is easier to check forest vegetation when classifying stands than to measure the important but often subtle and obscured soil features that control stand development. However, the Finnish forest site type system is generally considered to be incomplete, and requires further development and testing under the conditions prevailing in the intensively managed forests of today (Vuokila 1980, Kuusela 1982).

A site classification system which is applicable in practical forestry must consist of a reasonable number of distinct site classes only (Cajander 1949). This is the reason why there is a wide range of variation in important soil and other features within each of the Cajanderian site types. However, the forest site type system is also widely applied in botanical, zoological and other biological research. The system is frequently used as a framework in stratified sampling, or in studies dealing with different types of forest ecosystem. It is quite clear that biological research in the field of forestry needs a more accurate classification system for allocating the study objects (stands) into different ecosystem, or habitat, types.

The descriptions of the different site types are primarily based on undisturbed, mature forests, which nowadays can seldom be found. Most of the present forest stands represent younger successional stages of the different forest site types than those described in forestry textbooks. From a botanical point of view, the descriptions of the site types are more or less qualitative, and seldom include any unambiguous recognition criteria (Cajander 1926, Kalela 1961, Lehto 1969). Under these conditions, site determination is clearly highly subjective (Kuusela 1982). The main reason for this is Cajander's emphasis on forestry practice: a great number of different types of plant community are included in a few site type classes with wide limits (Cajander 1921). There is an obvious need for an unambiguous, easily applicable key for reliable site determination.

The Finnish forest site type system is essentially unidimensional. The types are ranked in a series ranging from dry-and-poor to fresh-and-rich; such an ecological series represents the main axis of vegetation response to habitat (Keltikangas 1959). Climatical variation is taken into consideration by a zonal system in which parallel site type series are described separately for each vegetation zone (Kalela 1961). However, there is a lack of knowledge about the ecological gradients that control the upland (i.e. mineral soil) forest vegetation in Finland. Multidimensional systems with more than one direction of variation, as well as hierarchical classification systems which also imply multidimensional configurations, have been found to be useful tools in the ecological interpretation of vegetation pattern (Gauch & Whittaker 1981).

The present study is based on the collection and analysis of ecological data from an essentially random sample of relatively mature upland forest stands throughout some central forestry areas in southern Finland. Preliminary methodological studies of this material have been published earlier (Kuusipalo 1983a, 1983b, 1984a, 1984b, 1985). The stands are first classified on the basis of vegetation composition using two-way indicator species analysis (TWINSPAN) (Hill 1979a). Studies carried out on the relationships between operational vegetation units and the important site properties provide a basis for testing the ecological correlations of vegetation. The theoretical implications of the findings are discussed with special reference to the structuring and organizing processes that affect the plant community composition. The findings are also evaluated in the light of Cajander's forest site type theory, the major aim being to test the applicability of the Finnish site classification system in present forest conditions. Finally, the present work can be regarded as an attempt to develop the Finnish forest site type system towards more proper ecosystem classification.

The "null hypothesis" of the present study is that the variation in the vegetation composition cannot be adequately explained by site variables. This cannot be tested in the statistical sense, but is inferred by an appraisal about whether there is any edaphically interpretable variation in the vegetation gradient superimposed by logic internal to the numerical method used. Additional objectives of the study are:

(1) To determine, objectively, the major discontinuities in the forest vegetation continuum and their relationship to the underlying environmental gradients; following this, an operational scheme is elaborated for different forest habitat types and their relationship to edaphical conditions.

(2) To propose some adjustments to the site classification criteria presently applied in southern Finland, and to propose a model of an unambiguous key for allocating forest stands successively to operational site type classes.

2. THE FINNISH FOREST SITE TYPE SYSTEM

The Finnish forest site type system was developed under the leadership of A. K. Cajander, who based his theory on wide field experience in Fennoscandian and Siberia (Cajander 1903, 1904, 1909a, 1909b, 1913). Already in these early papers Cajander recognized that only a few plant species are able to dominate in the relatively extreme conditions of the main boreal ecosystems -forests, mires and meadows. These species are well adapted to a certain range of site conditions and are capable of competing in their typical habitats. The co-occurring species have to adapt themselves not only to the site conditions but also to the dominant species. Hence it follows that altough the site conditions may change more or less gradually, discontinuity occurs in the vegetation. In stable communities the composition of the vegetation results from competition through a long time scale and hence contains information about the ecosystem itself. The variation in disturbed temporary (successional) communities, on the other hand, is connected with the information about the instability of the ecological situation. According to Frey (1978), Cajander was the first to take stable communities as the basis for the classification of vegetation, characterizing the site type as a cluster of successionally related communities around a mature or normal community type which indicates site quality, and which is to be recognized and related to the successional communities by vegetation composition.

Cajander thus established his theory on the concept of plant community (Pflanzenvereine) as a fundamental vegetation unit (Cajander 1921, Kalela 1954). This concept is used in a strict sense of mature and stable plant community, which is characteristic of a certain range of variation in site conditions. The Cajanderian concept closely resembles the systematic viewpoint of Braun-Blanquet (1928), in which individual communities are related to community types by certain features of structural and compositional similarity. Gleason (1926) considered that while the existence of a plant community depends upon the selective forces of its particular environment and the surrounding vegetation, the environment is in fact not stable and changes constantly in time and continuously in space. Therefore, in his view, no two communities can be considered alike or closely related to one another. An intermediate view, originally presented by McIntosh (1967), admits that although vegetation discontinua are evidently found in nature, continuity can always be found when comparison is made between similar stands.

Cajander (1909a) considered that the understorey vegetation of boreal forests is a more sensitive indicator of the environment and its potential productivity than the tree layer. After disturbance of the tree layer, the understorey vegetation re-attains a new equilibrium within a relatively short period of time. Knowledge of successional processes and interspecific relationships allows one to group various disturbed or successional stands in relation to the stable communities of the site types. One of Cajander's basic aims was that his forest site types should be identifiable independently of the successional stage and tree species composition of the stand (Cajander 1921). In spite of the vigorous effect of the tree layer upon the lower vegetation strata, the understorey vegetation always consists of enough species to permit definition of the site type. It should be noted here that the forests of the Fennoscandian region are composed of only a few tree species, each of them capable of dominating over a wide range of site conditions with different understorey associates.

Cajander (1926) makes a clear distinction between primary and secondary site factors. Primary site factors, i.e. macroclimate and the basic properties of the soil, remain active even though all the vegetation, including the tree stand, is removed from a site. The site type system, which employs understorey vegetation as an indicator of site quality, should predict the biological productivity that the site can support. The biological productivity, or fertility, of a site is a combined effect of primary site factors (Keltikangas 1959). The relationship between site type and forest growth has been investigated by Ilvessalo (1920) and others. Valmari (1921), Ilvessalo (1923, 1933) and many others studied the relationships between the site type and the physico-chemical properties of the soil. These studies indicate that in many areas the site types can be arranged in a sequence of increasing productivity ranging from dry-and-poor to fresh-and-rich. According to Kujala (1938), such an ecological series (*sensu* Cajander 1903) represents the main axis of the vegetation response to habitat. Secondary site factors may affect the composition of the understorey vegetation considerably, but only temporarily: the site type remains unchanged (Keltikangas 1959, pp. 207–208).

Tamm (1920, Tamm & Petrini 1922) disagreed with Cajander's opinion that the tree stand is of secondary importance in determining the site type. In addition to its effect on light conditions, the tree stand, especially the tree species composition, strongly affects the composition and physico-chemical properties of the humus layer. The Uppsala school (see Trass & Malmer 1978) emphasized the decisive role of site history in the formation of plant communities. For example, after a forest fire almost all the plants on the site are totally destroyed. Site conditions also change after clear-cutting and the subsequent treatments, and all forest plants are heavily suppressed. Many plant species may need more than one cutting interval to re-attain their initial abundance in the stand (Sarvas 1937). In Finland, slash-and-burn cultivation was practiced on a wide scale right up until less than a century ago (Soininen 1974). Combined with frequent natural forest fires, it had a strong effect on the forest soil. At the present time the soil is probably changing gradually towards a more acid and nutrient-poor state. In addition, forest fires control the regeneration of many important forest plants (Oinonen 1967a, 1967b, 1967c, 1968, 1969). The vegetation characteristic of a site type, or even the site type itself, is perhaps in a dynamic state, and is actually undergoing a gradual change.

The Finnish forest site type system is essentially unidimensional: the site types form a sequence which represents the main dimension of variation in site conditions. One important point to remember is that the site types have been distinguished primarily to meet the needs of forestry (Cajander 1921). Cajander himself pointed out that all botanically interesting types should not be described as forest types if they are economically unimportant; on the other hand, botanically relatively homogenous types should be divided if the distinguishable segregates differ as regards silvicultural treatment (Cajander 1921). There should be only a reasonable number of classes if the number of management prescriptions is to be reasonable (Cajander 1926). Hence the forest site types are relatively widely delimited. Cajander and his successors, however, differentiated them into subtypes and variants (Cajander 1916, 1926, Kujala 1936, Kalela 1952, Keltikangas 1959). The forest site type system is thus strongly deductive: there is an assumed normal series with typical types, and the untypical stands are considered as minor deviants from the normal types.

Kujala (1938) considered that when one proceeds to a different geographical area, each of the site types may be replaced by another, ecologically similar but vegetationally somewhat deviating site type. Kalela (1954, 1958, 1960, 1961) emphasized the decisive role of macroclimate by distinguishing regional (climatic, zonal) plant communities from local (edaphic, azonal) communities. The macroclimate within each vegetation region (Kalela 1961) is relatively homogeneous, and the region is characterized by the prevalence of the same site types in ecologically similar localities. Regionality now holds a position of major importance in the Finnish forest site classification (Koivisto 1971). As emphasized by Oksanen (1984), Kalela's (1961) introduction of zonal variants did not actually diminish the fundamental unidimensionality of the system; on the contrary it produces strictly unidimensional series for each vegetation type.

In the Estonian forest site classification a two-dimensional system based on moisture and lime-content gradients is used (Frey 1978). Jones & al. (1983) utilize two-dimensional ordination diagrammes in their classification of Canadian forest ecosystems. The *Pyrola* type found on clayey soils in Finland can be regarded as an exception to the normal state of unidimensionality. The description of esker slope vegetation by Jalas (1950) can be considered as an attempt to introduce an additional gradient into the forest site type system: the forests of sunny esker slopes are treated as variants of normal, level-ground forest types. This and other more recent developments of the forest site type system are primarily botanical in scope (Jalas 1961, Hämet-Ahti 1963, Mäkirinta 1968, Oksanen 1984). From the forestry point of view, however, these developments have largely been ignored or treated as ”vicariant”, rare forest types, which are in practice included in the most closely related types.

According to Cajander's (1926) definition, a forest site type is characterized by ”mainly identical floristic composition and similar ecologico-biological nature”. He based his descriptions of normal plant associations of the site types primarily on the ecological character of the site which is reflected in the relative abundance, presence and absence of certain species and ecological species groups (Cajander 1949); the early descriptions are based mainly on species composition (Cajander 1916). There are only a few published vegetation tables for the site types, e.g. the synoptic table in Kalliola (1973). The methodology is mainly described in general terms (Cajander 1949, Keltikangas 1959). Ilvessalo (1922), Kujala (1921) and many other of Cajander's successors used Norrlin's (1870) abundance scale, which also consists mainly of qualitative descriptions. Tuomikoski (1942) stresses floristic composition and presents more explicit definitions and practical procedures. The role of ”indicator” or ”guide” species is especially emphasized in forestry textbooks (Lehto 1969). The qualitative nature of the descriptions arises from the deductive nature of the system: a great number of plant association types representing different successional stages and variants of the ”normal” types are included in a few wide classes.

The descriptions of the site types are primarily based on the assumed ”normal” plant associations characteristic of mature, undisturbed forests. Recent silvicultural activities are, however, so intense that such stable plant communities can seldom be found. Nowadays about 80 % of the actual forest stands represent younger successional stages of the forest site types described in the Cajanderian classification system (Kuusela & Salminen 1983). Identification of the site type in a present-day forest stand can thus be regarded as a projection of the actual vegetation to an ”ideal” Cajanderian type. Site determination under these circumstances is quite clearly highly subjective. According to Kuusela (1982), the differences in the proportions of different site types between the two latest national forest inventories cannot be explained by anything else than a change in the definition criteria applied in the field. Fertilization, soil preparation and other treatments cause additional confusion. There is evidently a lack of clear, unambiguous criteria for site determination.

Cajander (1921) stressed that the number of site types has to be kept relatively small. In fact, there are only three important forest site types in southern Finland: the *Vaccinium* type (VT) covers 27.8 %, the *Myrtillus* type (MT) 35.3 % and the *Oxalis-Myrtillus* type (OMT) 13.5 % of the forest area; mires (nowadays mostly drained) cover 19.2 % of this area (Ilvessalo 1956). Whether the number is sufficient or too small depends upon the user's viewpoint: forestry (planning of regeneration procedures, soil treatments etc.) may need more accurate classification than for instance forest taxation (Karjula & al. 1982, Piironen 1984). A continuous index based on height-over-age curves for different tree species has several advantages and drawbacks (Gustavsen 1980, Vuokila 1980, 1982, 1983, Vuokila & Väliaho 1980, Hägglund 1981, Kilkki & Ojansuu 1981, Kuusela 1982). Biological research in the forestry sector obviously needs a more accurate and natural classification system than forestry practice. Adapting classification systems which are primarily designed for practical use to meet the needs of scientific studies is not justified. However, even a purely technical classification must be incorporated in or at least comparable with an universal, scientific classification. A good example is the mire type system used in Finland (Heikurainen & Pakarinen 1982).

According to Frey (1978), the main idea of Cajander's site type theory lies in the typification of a limited number of ecosystem types through the expression of site conditions in stable plant communities. The site type is thus an abstraction based on a series of individual stands which show some convergence caused mainly by climatical and edaphical factors. As observed by Whittaker (1962): "The site type approach is thus carried to its logical conclusion; it is a classification not simply of communities, but of sites characterized by groups of related communities." Cajander (1949) and his successors (see Keltikangas 1959) emphasized that the forest site type system lies on such a firm theoretical basis that the classification needs no fundamental adjustments. Attempts to question the fundamentals of the forest site type theory have often received strong criticism, usually that the nature of the forest site type is not understood correctly (see Keltikangas 1959). On the other hand, supporters of the system frequently stress that the description of the forest types is not yet complete (Cajander 1949, Keltikangas 1959). The incompleteness of the system has often been forgotten both in criticism and defence, as well as in practical application of the types.

3. MATERIAL

3.1. Study areas

The operational unit used in the preliminary selection of the study areas was a 10 × 10 km sheet of the basic ordnance survey map (1:20 000). The selection was done on those sheets where the basic mapping of quaternary deposits had already been performed at that time (Korpela & Niemelä 1980). The sampling was limited to the southern boreal vegetation zone (Ahti & al. 1968), and to the forest vegetation region of South Finland (Kalela 1961). The regional variation within the zone was considered by selecting the study areas from different geological and climatical regions in the central forestry areas of southern Finland. The location of study areas I–III is presented in Fig. 1. The following physiographical descriptions are mainly based on the Atlas of Finland (1960). The effective temperature sum refers to the cumulative sum of the daily mean temperatures during the growing season, and was computed by taking into account the altitude above sea level (Raitasuo

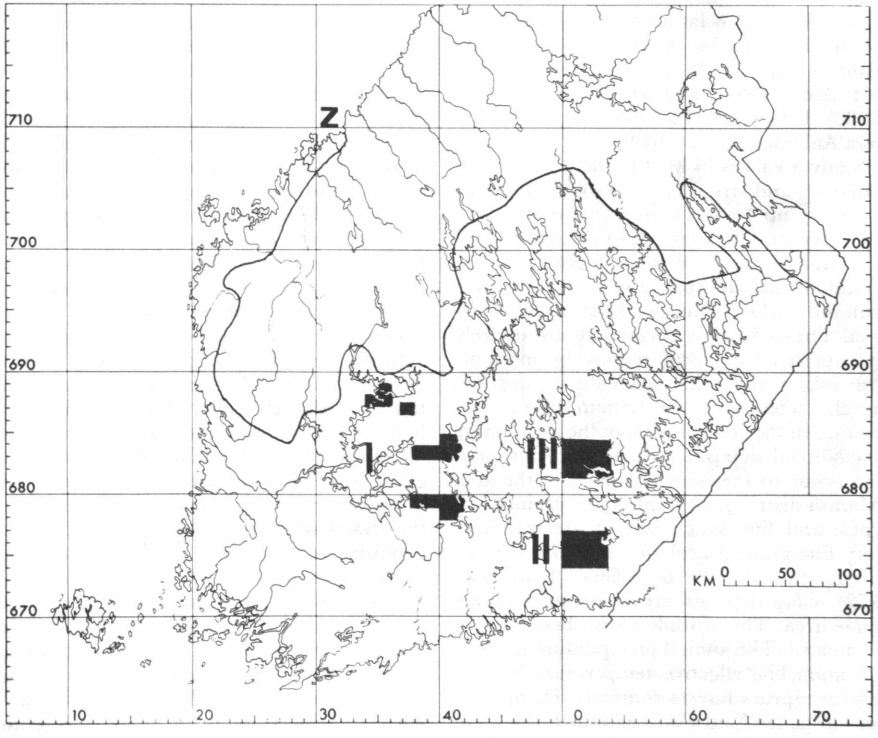


Fig. 1. Location of the study areas. Z = border of the northern boreal vegetation zone (Ahti & al. 1968).

Table 1. Number of sample plots in each site class (Kuusela & Salminen 1969) and stand type (dominant tree species).

Stand type	Study area I	II	III	Total
Dry and subdry sites	18	43	16	77
Damp sites	58	79	84	221
Rich sites	52	19	41	112
Spruce stands	85	73	69	212
Pine stands	43	68	72	176
Total	128	141	141	410

1983). Some basic data for the forests in each area are given in Table 1. In Finland, the most important forest-forming tree species are Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), which are called "pine" and "spruce" in the following. In the present paper, the nomenclature of the plant species follows Hämet-Ahti & al. (1980) (vascular plants), Koponen & al. (1977) (Bryophyta), and Ahti (1980) and Hawksworth & al. (1980) (lichens). Soil terminology mainly follows Aaltonen & al. (1949).

Study area I is located to the west of Lake Päijänne, and stretches from southern Häme (Lammi) up to the border of the southern boreal vegetation zone (Mänttä and Vilppula). Granodiorite and mica gneiss rocks are dominant in the southern parts and acid plutonic rocks in the northern parts of the area. The bedrock is covered almost entirely by superficial deposits, mainly by moraine. The eskers and other glaciofluvial deposits are characteristic of the Lammi district, but are rare in the central parts of the area. Large glaciofluvial deposits of sand and fine sand also occur in the northern parts of the area (Mänttä district). In Lammi, finegrained soil types, and fine sand and silt are common. Very fine-grained aeolian sediments also occur in the vicinity of eskers (Jauhiainen 1972). Clay deposits are uncommon in the whole area. The altitude varies between 90–195 m a.s.l. The annual precipitation is about 600 mm. The effective temperature is 1170 degrees. Spruce forests dominate. Damp sites (for terms, see Kuusela & Salminen 1969) are most common on mineral soils, but nearly as common are rich sites, which are largely concentrated in the southern parts of the area. The northernmost parts of the area belong to the Forestry Board District of Pirkka-Häme, where, according to Koivisto (1971), the average value of the relative volume increment is 92 (the corresponding value in the Uusimaa-Häme district is 100). The southern parts of the area are located mostly in the Forestry Board District of Itä-Häme, where the relative volume increment is 97.

Study area II lies between the towns of Kouvola and Lappeenranta, southwest of Lake Saimaa. Geologically, the area belongs entirely to the rapakivi granite region of southeastern Finland. Rapakivi granite weathers easily and differs from other forms of granite in its chemical composition (Piispanen 1977). Exposed areas of bedrock are rather rare. Till soils are mainly predominant. A large moraine formation, the First Salpausselkä, runs east to west across the area; in these parts of the area, deposits of sand and fine sand are common. Clay deposits also occur in places alongside the southern slope of the Salpausselkä formation. The altitude varies from 50 m up to 115 m a.s.l. The annual precipitation is about 650 mm. The mean effective temperature is 1330 degrees. Mostly spruce-dominated damp sites are predominant on the till soils, and subdry and dry sites dominated by pine are most common on the sandy soils of the Salpausselkä formation. The area lies entirely in the Forestry Board District of Etelä-Karjala, where the relative volume increment is 88 in average.

Study area III is located in the western part of the Lake Saimaa region, near to the town of Mikkeli. The area is geologically homogeneous: mica gneiss rocks prevail. Moraine soils are dominant, eskers and other glaciofluvial deposits are rare. Exposed areas of bedrock occur frequently, especially along the shores of Saimaa and other lakes. Clay deposits are uncommon in the area. The altitude varies between 100 m and 150 m a.sl. The annual precipitation is between 550–600 mm. The effective temperature is 1300 degrees in average. Pine forests and spruce forests occur in approximately equal proportions; damp sites predominate, but rich sites are also rather common. Pine forests are unusually common on damp and rich sites in this area, probably due to historical factors: slash-and-burn cultivation was practised widely in the area up until fairly recently (Soininen 1974). The area lies within the Forestry Board District of Etelä-Savo, where the average relative volume increment is 91.

3.2. Sampling and field work

3.2.1. Sample plots

The sample plots were located systematically using the center points of the coordinate quadrats (1 × 1 km) of the basic ordnance survey map. Every third center point was investigated preliminarily by field groups from the Finnish Forest Research Institute. The groups marked out the sample plots in cases where the sample plot was on forested mineral soil. Soil samples were collected from each sample plot. The tree stand characteristics were measured on all sample plots dominated by a stand of either pine or spruce, provided that the stand was at least 20 years old and was not defined as low-yelding (for definition, see Kuusela & Salminen 1969, p. 16). Only those sample plots representing closed forest stands were subjected to vegetation analysis. In practice, this refers to stands ready for final cutting and regeneration, and old thinning stands where the proportion of saw-timber stems is high (see Kuusela & Salminen 1969, Tamminen 1982).

The material used in the present study consists of vegetation analyses made on 410 sample plots during the summers 1982–84. Environmental data and tree stand measurements are available from 269 sample plots only (from study areas I and II).

3.2.2. Environmental measurements and soil sampling

The established sample plots were 16 × 16 m in size. Several environmental measurements (see Table 2) were made on each sample plot. The altitude of the site was determined, and the effective temperature sum was computed (Tamminen 1982). The topography of the site was observed in order to assess the moisture conditions: depressions and descents receive soil and surface water, whereas loss of water occurs on ascents and elevated land. Aspect and slope were measured and coded in the field. Since these topogenic site factors interact owing to the microclimatical conditions, a new joint variable (WARM) was constructed by combining these two variables as presented in Fig. 2. This variable has minimum values on steep NE slopes, maximum values on steep SW slopes and intermediate values in the various combinations of steepness and aspect lying between the two extremes (cf. Bradfield & Scagel 1984, p. 107).

The superficial deposit type was described in accordance with the RT classification (Aaltonen & al. 1949). A rough ordinal scale class variable was constructed in order to describe the effect of deposit type on site fertility: coarse glaciofluvial soils, i.e. gravel, sand and fine sand, are least fertile, coarse till soils which also contain finer fragments imply intermediate fertility, and finegrained till

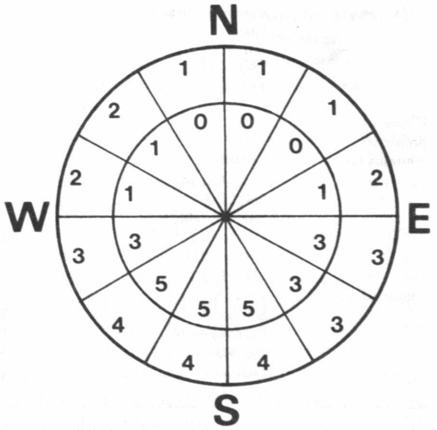


Fig. 2. Construction of variable WARM by combining aspect and slope.
(1) If slope is less than 5°, WARM = 2.5
(2) If slope is between 5° and 10°, WARM = value on the outer circle corresponding to the aspect.
(3) If slope is steeper than 10°, WARM = value on the inner circle corresponding to the aspect.

Table 2. List of the environmental variables.

CATEGORY	VARIABLE	ABBREVIATION	DIMENSION
Tree stand	Stand density	–	stems/hectare
	Medium diameter	–	mm
	Basal area	–	m^2/hectare
	Canopy coverage	SHADE	%
	Dominant species	PINE/SPRUCE	–
	Dominant height	–	dm
	Dominant age	AGE	a
	Site index	SI	dm (H_{100}) .
Physiography	Altitude	ALT	m a.s.l.
	Temperature	TEMP	effective cumulative temperature, d.d.
	Topography	TOPO	1: depressions, lower slopes 2: intermediate 3: hill tops, upper slopes
	Aspect Slope	WARM	see Fig. 2
	Superficial deposit type	SSOIL	1: coarse sand or gravel 2: coarse till 3: fine-textured material
	Soil type	STYPE	1: iron podzol 2: iron-humus podzol 3: brown soil, mull soil, traces of agricultural treatments
	Humus layer	HDEP	Thickness of raw humus layer, cm
		HUMUS	kg/hectare
	A horizon	AHOR	Thickness, cm
	Mull soil	MULL	1: absent 2: present
	Peaty mor	PEAT	1: absent 2: present
	Soil thickness	BEDROCK	1: thick soil 2: shallow soil (< 30 cm)
Soil texture	Stoniness	STONES	% soil volume (Viro index)
	Cumulative percentage of different fractions	–	% soil volume (see the text)
	Clay	CLAY	% soil volume
	Silt + clay	FSAND	% soil volume
	Degree of sorting	DDES	S (see the text)
	Md particle size	MDPS	mm, median
Chemical properties			
– humus layer	Total N, P, K, Ca, Mg	N, P, K, CA, MG	% air dry material
	Soluble P	PSOL	mg/100 g air dry material
	Exchangeable Ca, Mgm K	CAEX, MGEX, KEX	mg/100 g air dry material
	Ash content	ASH	% dry material
	pH (H_2O)	PH	
– mineral soil	Total N	NMIN	% air dry material
	Soluble P	PMIN	mg/100 g air dry material
	Exchangeable Ca, Mg, K	CAMIN, MGMIN, KMIN	mg/100 g air dry material
	Loss-on-ignition	LOI	%
	pH (H_2O)	PHMIN	

soils together with silty and clayey soils are the most fertile (Ilvessalo 1933, Urvas & Erviö 1974). The thickness of the superficial deposits was coded merely by determining whether the bedrock was lying near to the ground surface (<30 cm) or not. The stoniness of the mineral soil was measured and transformed into volume percentage by the method and formula of Viro (1952).

The soil type was described from soil profiles mainly in accordance with Troedsson & Nykvist (1973). Since many of the sampling sites have earlier been subjected to agriculture, attention was paid to locating signs of slash-and-burn cultivation (charcoal particles in the uppermost layer of the soil profile) or other activities (e.g. tillage). Soil type was then recoded into a three-class ordinal scale variable to describe the moisture regime and fertility of the soil. Iron podzols with a grey-white A horizon and reddish B horizon are typical of dry and subdry sites, whereas dark, humic podzols are characteristic of damp sites. Brown soils or podzols covered by mull or moder are characteristic of rich sites; in addition, man-modified soils with a clear ploughed layer or signs of slash-and-burn cultivation were also considered to indicate considerable fertility. The structure of the humus layer was described by measuring its thickness and constitution (raw humus, moder, mull or peat). The thickness of both the A and B horizons was also measured, when identifiable.

Four mineral soil samples were collected separately from the 0–30 cm and 30–70 cm layers from pits dug at the corners of the sample plots. Soil texture was analyzed by the Geological Survey of Finland (Korpela & Niemelä 1980). The mineral soil samples were sieved through a series of sieves corresponding to the soil particle size classification devised by Aaltonen & al. (1949). The finest fractions were analyzed by the hydrometer method (Elonen 1971). The mean particle size (median), a parameter depicting the degree of sorting (S) (Seppälä 1971) and the relative proportions of different mineral soil fractions were calculated on the basis of the results from the particle size distribution analysis (see Virkkala 1969). Soil texture was analyzed separately on samples from the 0–30 cm and 30–70 cm layers. However, owing to the fact that data for the latter layer was frequently missing, only the surface soil texture is considered in the present study.

Humus samples were collected from 16 points located systematically along the sides of the sample plot using a soil auger (Ø 58 mm). Chemical analyses were performed on the humus and mineral soil samples in the Department of Soil Science, the Finnish Forest Research Institute, following the recommendations and standard procedures presented in Halonen & al. (1983). The pH was measured from water. Loss in weight on ignition was determined on the mineral soil samples, and ash content on the humus samples. Total nitrogen was measured by the Kjeldahl method, extractable cations with acidic ammonium acetate (1M, pH 4.65), and the readily soluble phosphorus by the molybdate-hydrazine method. Exchangeable and easily soluble nutrients (Ca, K, Mg and P) are given in mg/100 g air dry soil, and total nutrients, including nitrogen, in weight percentages of air-dry material.

3.2.3. Tree stand measurements

Field groups from the Finnish Forest Research Institute estimated the development class of the tree stand (Kuusela & Salminen 1969). Basal area of the tree stand was estimated by a relascope method and the breast-height diameters of the included trees were measured (Tamminen 1982). The dominant trees were sampled by defining 100 thickest trees per hectare by summing up, in decreasing order of breastheight diameter, the number of stems represented by each tree, until the cumulative sum reached the treshold value 100 (see Tamminen 1982, p. 6). In sampling of the dominant trees, the objective sample size was 3–10 stems.

The tree stand characteristics used in the present study are listed in Table 2. Dominant height refers to the average height of the dominant trees included in the sample. Dominant age was computed as the average of the dominant trees. Site index (H_{100}) refers to the dominant height at an age of 100 years, and was computed on the basis of height-over-age curves (Gustavsen 1980). This is an index which measures the potential growth rate of the stand and, to a certain degree, also describes the site fertility. The values of the tree stand characteristics are given plotwise. It should, however, be noted that the sampling area is not exactly the same as that of the soil sampling plots, since it depends upon the relascope factor used.

Canopy coverage values were estimated from the total basal area and percentage of spruce on the plot using a regression presented in Kuusipalo (1985, p. 190). The formula is based on a linear model in which canopy coverage, measured from hemispherical photographs taken on 40 sample plots included in the present material, was used as the criterion variable, and various tree stand characteristics, measured on each sample plot of the study material, were treated as the predictors. The model used in the estimation explains 75 % of the variance in the canopy coverage.

3.2.4. Description of the vegetation

The small-scale variation in the understorey vegetation was inventoried on each sample plot by drawing a rough map of the different vegetation patches, as determined by eye. Six vegetation sample quadrats, 2 × 2 m in size, were then marked out on the basis of the vegetation map in such a way as to give full representation of each different patch of vegetation. The abundance of different plant species growing on each quadrat was estimated separately in the field layer (vascular plants) and bottom layer (mosses and lichens) using direct estimation of percentage cover. The vegetation growing on larger stones, stumps, logs etc. was disregarded. The mean coverages of different plant species were calculated for each sample plot since the environmental data were also determined plotwise.

4. METHODS

4.1. Vegetation analysis

In vegetation ecology, different vegetation strata are often described separately (Barkman 1978, Bergeron & Bouchard 1983, see also Oksanen 1984). In the Braun-Blanquet approach (Westhoff & Maarel 1978), the different strata of a given stand are considered to form a single community. The different strata of forest vegetation are rooting in a common substratum and are therefore ecologically closely interrelated. The study approach employed in the present work accepts the Cajanderian concept that although the tree stratum belongs to the plant community together with lower strata, it should operationally be kept separated from the understorey vegetation in site characterization (Keltikangas 1959, pp. 210–211). Accordingly, the understorey vegetation is analyzed as a whole – the field layer and bottom layer together, but without the tree layer. The tree stand is treated separately, essentially as an external environmental factor.

From a theoretical point of view, the present study approach largely accepts the two principles originally stated by Ramensky (1926) and Gleason (1926):

(1) Species are distributed ”individualistically”, each according to its own way of relating to the environment. Ecological groups and character-species groups are primarily arbitrary groupings of species by similarity of distributional relationships: the limits of such groups and the number of species they are to comprise must be decided by the phytosociologist (Whittaker 1978a).

(2) If not affected by different disturbances or steep environmental discontinuities, plant communities integrate continuously. The number of community types into which a vegetation continuum is divided, and the locations of the boundaries of these types, are determined by the phytosociologist's choice of the characteristics he uses to define those types (Werger & Maarel 1978).

Accordingly, the plant communities and vegetation types are primarily seen as arbitrary segments of community-gradients.

In the present study, the basic method of vegetation analysis is two-way indicator species analysis (TWINSPAN) (Hill 1979a), which results dichotomous hierarchical clustering of both samples and species. The data are first ordinated using a reciprocal averaging algorithm (Hill 1973). The samples are initially divided into two clusters by breaking the ordination axis near its mid-point. The sample division is refined by a reclassification in which species with a maximum value are used to indicate the poles of the ordination axis. The division process is then repeated on the two sample subsets to give four clusters and so on, until the maximum number of divisions is reached. A corresponding species classification is produced, and the sample and species hierarchical classifications are used to produce an arranged data matrix. This ordered two-way table shows the species' synecological relations.

The method in its basic form is essentially qualitative. The quantitative information is retained by expressing it on a relatively crude scale of quantitative equivalents, so called ”pseudospecies” (Hill & al. 1975). The data are scaled using special cut levels, which are equivalent to the commonly used ordinal scales of coverage. Both ”real species” (presence/absence of a species) and ”pseudospecies” (a certain abundance class) can appear as indicator species. An indicator species is ideally one with clear ecological preferences, so that its presence or abundance can be used to identify the environmental conditions in question. In TWINSPAN classifications of the present study, the cover data were expressed on a logarithmic abundance scale by defining the pseudospecies cut levels to conform to the following coverage classes: 0=absence, 1=0–0.25 %, 2=0.25–1 %, 3=1–4 %, 4=4–9 %, 5=9–16 %, 6=16–25 %, 7=25–36 %, 8=36–49 % and 9=49–100 %. The subsequent parameters of the TWINSPAN programme were determined as follows:

the minimum group size for division =5, the maximum number of indicators per division =7, and the maximum level of divisions =6.

An eigenvector method of ordination, detrended correspondence analysis (DCA) (Hill & Gauch 1980) was used in analyzing the total vegetation data set in order to reveal the major vegetational gradients. This was performed using the programme DECORANA (Hill 1979b). The same ordination method was used also in expressing the vegetation types defined after the first phase of classification in the ordination diagramme. This was done simply by computing the class (vegetation cluster) centroids of species abundances, and then analyzing them with DCA as if they were ordinary samples.

4.2. Analysis of the environmental control of vegetation

In analyzing the relationships between vegetation and environmental conditions, it is usually a question of investigating the relationship between the occurrence of a set of species and a set of environmental characters in a set of samples. One possible method of doing this, canonical correlation analysis, is bound to be unsuccessful in many ecological situations, because the responses of species to quantitative environmental factors are generally nonlinear (Orlóci 1978, cf. Kuusipalo 1984b). A more convenient way of representing the species composition in complex data sets is by classification of the samples. The relationships between species and the environment can now be studied indirectly by identifying, separately for each group of samples, the set of environmental conditions that prevails in each sample group. In order to do this, the vegetation types defined by a TWINSPAN classification were treated as class variables, and the continuous environmental variables as response variables. A stepwise procedure of canonical discriminant analysis was used in order to find linear combinations of environmental variables which best discriminate between the vegetation types; Mahalanobis distances were used as selection criteria (Klecka 1975). In order to improve the interpretability of the discriminant functions, a VARIMAX solution was used to rotate the discriminant function axes so as to give coefficient values for the discriminating variables that are either close to 1 or close to 0 (Klecka 1975, Kim 1975). The final objective of the study was to test the ecological interpretability of the groupings. The statistical theory of discriminant analysis assumes that the discriminating variables have a multivariate normal distribution, and that they have equal variance-covariance matrices within each group. In practice, the technique is very robust and these assumptions need not be strongly adhered to (Morrison 1969).

Multivariate statistical methods such as discriminant analysis often reveal only the most obvious differences, while hiding the more subtle ones. The more subtle differences can be revealed by using the hierarchical structure of the sample classification. This structure allows more precise comparisons, namely by identifying the environmental variables that discriminate between neighbouring groups at different levels of hierarchy. These comparisons should show up variables that are associated with the major differences in species composition and the variables that determine the finer structure. Theoretically, these comparisons could be done by a stepwise application of discriminant analysis. Many environmental variables are, however, characteristically discrete. They include only two or a few classes and cannot be treated even as "semicontinuous" variables in multivariate statistical analyses. Furthermore, the group sizes are often too small for statistical comparisons, particulary at the lower levels of sample hierarchy.

The method which is particularly suited for the construction of simple discriminant functions for a given hierarchical classification of samples is DISCRIM (ter Braak 1982). The programme DISCRIM is a modification of the TWINSPAN programme, and can be regarded as its appendage. In TWINSPAN, the divisions of the samples are characterized in terms of indicator species. This facility of TWINSPAN is used in DISCRIM to characterize the groups of this classification in terms of additional, e.g. environmental variables. DISCRIM is suited primarily for the analysis of presence/absence data, but it can also handle quantitative variables such as temperature, i.e. variables that can not be absent. In this method, quantitative information is retained using "pseudo-attributes", which correspond to the "pseudospecies" used in TWINSPAN. The crude scale of quantitative equivalents is determined by "pseudo-attribute cut levels". DISCRIM uses two input data sets: the hierarchical classification vector produced e.g. by TWINSPAN, and the data file which contains values of discrete environmental variables for the corresponding samples.

An attempt was made in the present study to apply the programme DISCRIM to the ecological interpretation of a successive hierarchical classification of vegetation. Both qualitative (crude ordinal scale) and quantitative variables were used (see Table 2). Quantitative variables were transformed into ordinal scale by ranking the numbers in such a way that the cut levels determined the quartiles of the distribution of each quantitative variable. Three cut levels were needed: the median, and the upper and lower quartile thresholds of the ranked data.

4.3. Relationship between the vegetation and stand productivity

In order to test whether and how well the sample clusters produced by vegetation classification indicate the differences in stand productivity, the site index value (H_{100}) was computed for each sample plot using formulae presented for natural pine and spruce stands by Gustavsen (1980). The site index can be used in predicting the average level of tree production obtainable under different conditions. It should be noted, however, that the apparent productivity estimated with the help of site index also depends on stand density: a free-growing tree can reach its maximum height at an earlier age than it would when growing within a dense forest stand. Thus site index may indicate that a dense stand growing on a potentially rich site has the same productivity as a few trees growing on a relatively poor site.

In the analysis of variance, site index was treated as a criterion (response) variable and the set of sample clusters produced by the TWINSPAN classification was treated as an independent class variable. Due to the fact that the site indices for pine and spruce stands are not directly comparable (Vuokila 1983, p. 4), the main effects of both vegetation type (sample cluster) and tree species, and the interaction between them, were examined in the two-way analysis of variance. The analysis was followed by the multiple classification analysis (Kim & Kohout 1975), in which the average level of productive capacity indicated by site index was adjusted for the effect of the tree species in order to make sites dominated by pine and spruce comparable.

In addition, one-way analysis of variance with *a posteriori* contrast tests of the group means was used when comparing the productive capacity obtainable in sites represented by different vegetation types. This was done separately for pine and spruce stands. The least significant difference (LSD) procedure was used in the multiple range tests. This is essentially a Students *t* test between group means, and exact for unequal group sizes.

4.4. Computing work

Computing work was performed by the author at the University of Joensuu using facilities of the library programme packages CEP (Cornell Ecology Programs, Systematics and Ecology, Cornell University, Ithaca, New York), SPSS (Statistical Package for Social Sciences) (Nie & al. 1975) and SAS (Statistical Analysis System) (SAS User's Guide: Statistics, 1982, SAS Institute Inc., Cary, North Carolina). Final compilation of the vegetation analysis was done by the author in the Institute of Ecological Botany at the University of Uppsala with facilities provided by the Computing Centre of the Faculty of Mathematics and Natural Sciences, and the Uppsala Datacenter.

5. RESULTS

5.1. Species ordination

The entire vegetation data set (410 sample plots) was ordinated using detrended correspondence analysis of the programme DECORANA in order to preliminarily determine the major vegetation gradients. The species scores for the first three ordination axes are presented in Table 3. The first axis seems to reflect fertility gradient ranging from fresh-and-rich to dry-and-poor sites: with a few exceptions, the species seem to be in decreasing order of nutrient and moisture demands.

The second ordination axis is clearly connected with the degree of paludification of the site. In actual fact, this axis seems to imply a fundamental discontinuity rather than any continuous vegetation gradient: the very highest scores are associated with only a few typical mire plant species, whereas the variation range of the subsequent species scores forms only a minor part of the total variation. This axis separates clearly paludified sites from the more typical forest sites on mineral soil. It should be pointed out, however, that the genuine mire sites were *a priori* excluded from the material; sites covered mostly by mire vegetation (>75 %) growing on peat substratum deeper than 40 cm are defined as mire sites. On the other hand, sites characterized by a patchy occurrence of peat and mire plants, as well as those covered by only a shallow peat layer, were defined as paludified upland forest sites and, hence, included in the vegetation analyses.

The third ordination axis is difficult to interpret ecologically. However, with a few exceptions, high scores are mainly associated with species characterized by relatively low light requirements, whereas low scores characterize species which typically occur under a dense canopy dominated primarily by spruce. As a whole, species ordination of the total data set seems to support the concept of ideal unidimensionality of the Finnish forest site type system. When interpreted in ecological terms by considering the environmental preferences of different plant species, the most important ordination axis clearly reflects the fertility gradient governed by edaphical factors. The second axis separates paludified and, as such, vegetationally untypical upland forest sites from the more typical upland forest sites. The third axis do probably not reflect any primary site factors, or is at least of less importance in comparison with the preceding ones.

5.2. Preliminary hierarchical classification and ecological analysis

In order to reveal the major outlines of divergence in the vegetation pattern and its environmental control, those sample plots for which both vegetational and environmental data were available (n=269) were analyzed using the programmes TWINSPAN and DISCRIM simultaneously. This preliminary classification also serves as a test of the subsequent vegetation analysis carried out on the complete vegetation data set: classification can be considered reliable if the same method produces essentially equal results, independent of the size of the data set. The results are summarized in the dendrogramme in Fig. 3. Only the first four levels of the dichotomous hierarchical clustering are shown. The indicator species of each division, as well as the environmental characteristics which best discriminate between subsets of samples produced by each division, are presented in decreasing order of importance (for environmental characteristics, see Table 2).

As regards the major division of the data set, the fact that *Maianthemum bifolium*, *Melampyrum sylvaticum* and *Brachythecium* spp. are on the left side, and that *Calluna vulgaris* together with *Vaccinium vitis-idaea* (with more than 4 % coverage) are on the right side, illustrate the obvious difference between mesophilous and xerophilous vegetation. According to the simultaneous DISCRIM analysis, a relatively high pH is the best environmental indicator of the left side (subset 0), whereas the most important indicator of subset 1 appears to be the predominance of pine. Accordingly, the major division can be interpreted ecologically in such a way that subset 0 represents mesic, mostly spruce-dominated sites, whereas subset 1 represents more xeric, pine-dominated sites.

Table 3. The species scores for the first three axes of the DCA ordination of the complete vegetation data set (N = 410). Scores of the species with a low frequency are ignored.

First axis (ranked) Eigenvalue = 0.311		Second axis (ranked) Eigenvalue = 0.181		Third axis (ranked) Eigenvalue = 0.168	
Anemone nemorosa	761	Carex globularis	1225	Convallaria majalis	436
Angelica sylvestris	755	Sphagnum spp.	1119	Hieracium umbellatum	428
Hepatica nobilis	592	Polytrichum commune	317	Calamagrostis arundinacea	414
Oxalis acetosella	501	Aulacomium palustre	248	Lathyrus vernus	397
Veronica chamaedrys	469	Equisetum sylvaticum	177	Rubus saxatilis	379
Gymnocarpium dryopteris	461	Orthilia secunda	160	Pteridium aquilinum	360
Carex digitata	442	Dryopteris carthusiana	104	Hypochoeris maculata	348
Geranium sylvaticum	408	Lycopodium annotinum	86	Carex globularis	280
Melica nutans	387	Potentilla erecta	84	Geranium sylvaticum	273
Brachythecium spp.	386	Pyrola minor	79	Sphagnum spp.	257
Fragaria vesca	384	Anemone nemorosa	67	Melica nutans	206
Dryopteris carthusiana	359	Trientalis europaea	59	Festuca ovina	186
Viola riviniana	353	Deschampsia flexuosa	50	Trientalis europaea	152
Rhytidiadelphus triquetrus	259	Oxalis acetosella	39	Solidago virgaurea	134
Rubus saxatilis	197	Maianthemum bifolium	39	Cladina arbuscula	105
Equisetum sylvaticum	178	Gymnocarpium dryopteris	33	Deschampsia flexuosa	97
Maianthemum bifolium	128	Vaccinium myrtillus	23	Aulacomium palustre	87
Luzula pilosa	104	Luzula pilosa	16	Calluna vulgaris	72
Calamagrostis arundinacea	100	Vaccinium vitis-idaea	3	Angelica sylvestris	63
Melampyrum sylvaticum	81	Calluna vulgaris	−7	Viola riviniana	46
Trientalis europaea	60	Dicranum polysetum	−17	Hepatica nobilis	30
Orthilia secunda	40	Rhytidiadelphus triquetrus	−21	Vaccinium vitis-idaea	12
Convallaria majalis	27	Carex digitata	−26	Vaccinium myrtillus	6
Deschampsia flexuosa	−3	Pleurozium schreberi	−44	Equisetum sylvaticum	−8
Linnaea borealis	−6	Hylocomnium splendens	−55	Luzula pilosa	−24
Hylocomnium splendens	−21	Viola riviniana	−56	Orthilia secunda	−49
Vaccinium myrtillus	−41	Melampyrum pratense	−58	Pleurozium schreberi	−51
Pleurozium schreberi	−52	Melica nutans	−75	Hylocomnium splendens	−60
Sphagnum spp.	−58	Rubus saxatilis	−79	Brachythecium spp.	−73
Polytrichum commune	−63	Cladina arbuscula	−103	Dryopteris carthusiana	−87
Vaccinium vitis-idaea	−77	Cladina rangiferina	−113	Ptilidium crista-castrensis	−94
Dicranum polysetum	−93	Festuca ovina	−117	Oxalis acetosella	−140
Mealmpyrum pratense	−96	Geranium sylvaticum	−133	Dicranum majus	−149
Cladina arbuscula	−124	Calamagrostis arundinacea	−159	Gymnocarpium dryopteris	−158
Cladina ragiferina	−125	Hieracium umbellatum	−171	Anemone nemorosa	−218
Calluna vulgaris	−155	Convallaria majalis	−200	Dryopteris filix-mas	−227

In the second division, herb-rich sample plots (subset 00) are segregated from the remaining mesic sites of subset 0. The presence of mull in the uppermost soil layer, high pH and large loss-on-ignition, a considerable content of calcium, and a soil type typical of rich sites are the most informative environmental properties of subset 00. Accordingly, this subset clearly represents rich forest sites. On the contrary, abundance of raw humus is characteristic of subset 01, indicating moist but less fertile edaphical conditions.

Subset 1 is further divided into more (subset 11) and less (subset 10) xeromorphic vegetation types; the former is characterized by an abundance of lichens typical of dry-and-poor site conditions. The environmental attributes characterizing subset 10 indicate a somewhat higher moisture and soil fertility. Subset 11, on the other hand, is characterized by a frequent occurrence of exposed bedrock.

At the subsequent levels of classification, sample plots representing clearly nemoral forest sites (subset 000) are segregated from the remaining herb-rich sample plots of subset 00. Among the nemoral sites, vegetation

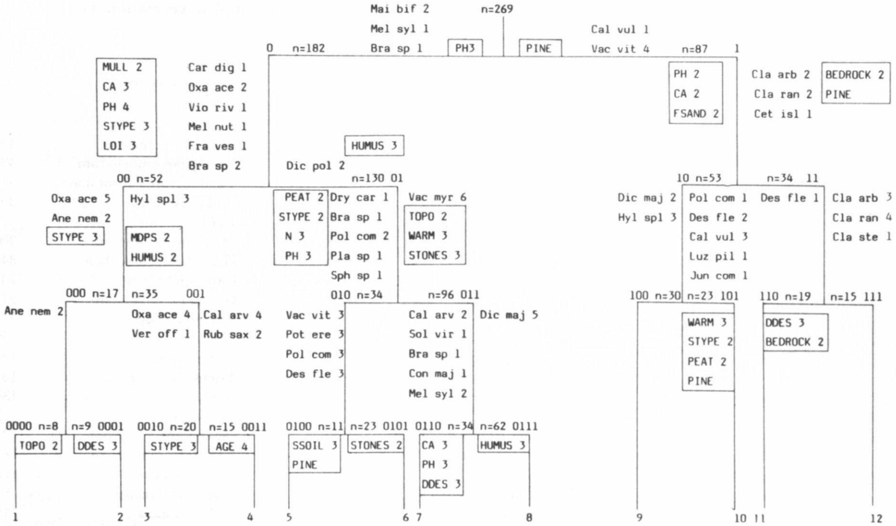


Fig. 3. Preliminary TWINSPAN classification of the vegetation data set, with a simultaneous DISCRIM analysis, on those sample plots for which both vegetation and environmental data are available (study areas I and II). Environmental variables which best discriminate between clusters at different levels of hierarchical vegetation classification are indicated by capital letters. Numbers after species and environmental attribute names give the pseudospecies and pseudoattribute cut levels (for further information, see Table 2 and Chapters 4.1. and 4.2.).

characterized by an abundance of *Anemone nemorosa* can be further distinguished (subset 0000). Compared with these subsets, subset 001 is characterized by a larger medium particle size of the mineral soil and a somewhat thicker layer of raw humus. Among sites included in subset 001, subset 0010 probably represents somewhat younger and hence dense spruce stands. This is reflected in the abundance of *Oxalis acetosella,* and in the absence of light-demanding plant species *Calamagrostis arundinacea* and *Rubus saxatilis;* subset 0011 is characterized by an older dominant age of the stand. The further division of subset 01 indicates differences in moisture conditions. Indicator species of subset 010 are plants typical of moist, even paludified forest sites. Subset 011 is characterized by a high abundance of *Vaccinium myrtillus* (coverage of more than 16 %). The environmental characteristics of subset 010 also indicate somewhat moister and more fertile conditions; these are the presence of peat, a relatively high nitrogen content and pH, and a soil type typical of moist sites. The topogeneous environmental attributes characterizing subset 011 support the above conclusions. Subset 010 is divided further into the pine-dominated, clearly paludified sites included in subset 0100, and the spruce-dominated, moist sites included in subset 0101. Subset 011 is further divided into subsets 0110 and 0111. Indicator species of the former prefer light and warm sites; on the other hand, environmental attributes indicate a considerable level of fertility. Subset 0111 is characterized by a comparatively thick humus layer; the indicator species *Dicranum majus* prefers shady conditions.

Differences in moisture and light conditions are probably the underlying reasons for the further division of subset 10. *Dicranum majus* and *Hylocomium splendens* are mosses typical of relatively shaded, moderately dry conditions obviously prevailing on sites included in subset 100; in this subset, spruce occurs frequently as the dominant tree species. *Polytrichum commune* indicates moist conditions, while the other indicator species of cluster

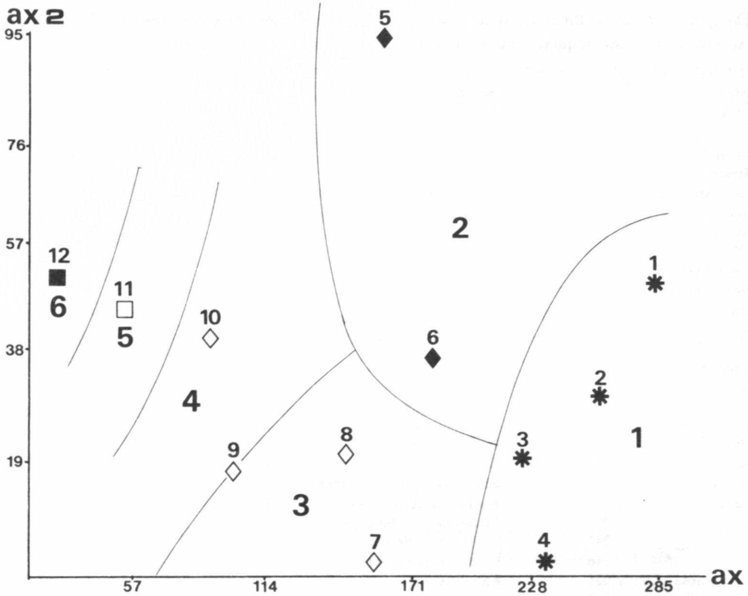


Fig. 4. DCA ordination of the 12 clusters produced by the TWINSPAN classification (Fig. 3); for interpretation of the ordination axes, see Table 4. The regions indicated by the large numbers show the approximative relationships between preliminary classification and clustering of the entire vegetation data set (see Appendix). Symbols for different subsets of clusters depict the approximative nutrient and moisture conditions of corresponding sites as follows. ✱ = mesic and fertile sites, ◆ = mesic and moist, intermediately fertile sites, ◇ = mesic and subdry, intermediately fertile sites, □ = xeric and subdry, infertile sites, and ■ = xeric, dry and infertile sites.

101 are characterized by relatively high light requirements. An abundance of xerophilous lichens is characteristic of subset 111. It would appear that the sites included in subset 111 are confined to sandy soils, whereas subset 110 is characterized by exposed bedrock and confined mainly to till soils.

A total of 12 clusters each representing somewhat different vegetation type and environmental conditions were distinguished in the preliminary classification. These clusters were ordinated using detrended correspondence analysis (Fig. 4). The scores of the most important species on the first two ordination axes are given in Table 4. The axes are rather easily interpretable, corresponding to the first two axes of the DCA ordination of the entire data set (Table 3). The first axis reflects the site fertility governed mainly by the nutrient status of the site; the highest scores are associated with demanding herbs, ferns and mosses, while the lowest scores are found with *Cladina* lichens and other xerophilous species. The second axis seems to be associated with the moisture regime: species typical of paludified forest sites have the highest scores, whereas the lowest scores are obtained with species which characterize relatively dry, warm sites.

According to the above, indirect ecological interpretations, the descending order of clusters 1–12 clearly forms a sequence ranging from poor to rich sites. Clusters 1–4, which represent the richest vegetation types, also differ with respect to the second axis. Clusters 5–8 are clearly segregated by the second axis, but indecisively by the first axis; they hence seem to indicate a more or less equal fertility,

Table 4. The species scores for the first two axes of the DCA ordination of 12 cluster centroids (Fig. 3, Fig. 4.). Scores of the species with a low frequency in original data material are ignored (cf. Table 3).

First axis (ranked) Eigenvalue = 0.449		Second axis (ranked) Eigenvalue = 0.081	
Anemone nemorosa	408	Carex globularis	378
Angelica sylvestris	373	Aulacomium palustre	364
Veronica chamaedrys	372	Sphagnum sp.	291
Carex digitata	363	Polytrichum commune	282
Oxalis acetosella	359	Pyrola rotundifolia	278
Hepatica nobilis	358	Potentilla erecta	270
Dryopteris carthusiana	357	Deschampsia flexuosa	180
Gymnocarpium dryopteris	346	Orthilia secunda	148
Melica nutans	346	Luzula pilosa	144
Fragaria vesca	339	Trientalis europaea	135
Viola riviniana	333	Rhodobryum roseum	132
Rhytidiadelphus triquetrus	314	Anemone nemorosa	127
Solidago virgaurea	304	Dryopteris carthusiana	124
Maianthemum bifolium	292	Viola riviniana	123
Equisetum sylvaticum	286	Calluna vulgaris	116
Rubus saxatilis	283	Vaccinium vitis-idaea	109
Luzula pilosa	282	Hepatica nobilis	108
Melampyrum sylvaticum	276	Rhytidiadelphus triquetrus	94
Calamagrostis arundinacea	266	Equisetum sylvaticum	93
Trientalis europaea	260	Maianthemum bifolium	88
Convallaria majalis	247	Cladina rangiferina	79
Dicranum majus	246	Dicranum polysetum	78
Daeschampsia flexuosa	221	Lathyrus vernus	50
Hylocomnium splendens	214	Oxalis acetosella	44
Linnaea borealis	179	Vaccinium myrtillus	28
Sphagnum sp.	156	Hieracium umbellatum	−8
Vaccinium myrtillus	148	Pleurozium schreberi	−29
Pleurozium schreberi	92	Melampyrum pratense	−73
Melampyrum pratense	38	Hylocomium splendens	−85
Vaccinium vitis-idaea	6	Calamagrostis arundinacea	−106
Dicranum polysetum	−7	Hieracium murorum	−144
Calluna vulgaris	−98	Pteridium aquilinum	−212
Centraria islandica	−134	Convallaria majalis	−496
Cladina ragiferina	−146	Empetrum nigrum	−616
Cladina arbuscula	−165	Festuca ovina	−774

but with different moisture conditions. Cluster 5, which represents vegetation typical of paludified forest stands, reaches highest scores on the second axis, "moisture gradient". Cluster 7, the indicator species of which are plants characteristic of warm and relatively dry sites, represents the lowest scores on this axis. As regards clusters 9–12, the second axis distinguishes between cluster 9 and the remaining clusters, which are separated from each other by the first axis (fertility gradient).

The major axis of the vegetational variation in the present material seems to be associated with the soil fertility gradient. The both extremes of this axis, the richest sites represented by clusters 1–4, and the poorest sites represented by clusters 11–12, can most clearly be distinguished. On the other hand, sites represented by clusters 5–10 are less easily distinguishable in terms of fertility characteristics, but seem to differ from eachother in their moisture regime.

5.3. Hierarchical classification of the entire vegetation data set

The complete vegetation data set consists of 410 sample plots representing different forest stands ranging from fresh-and-rich to dry-and-poor sites. As can be concluded on the basis of the preliminary vegetation analysis, TWINSPAN classification serves rather well in revealing the main direction of vegetational variation, allocating the richest and the poorest sites to the opposite poles of the axis. However, the major division of the vegetation data seems not to reflect any clear environmental discontinuity: in the DISCRIM analysis, environmental attributes indicate differences between subsets 0 and 1 primarily in tree species composition and secondarily in soil pH (Fig. 3). In addition, these two major subsets seem to include vegetationally fairly similar sites (see Figs. 3 and 4).

One important point to remember is that there are only a few plant species which are common to both dry-and-poor and fresh-and-rich sites; in other words, the ecological distance between poor and rich sites is very long in the present material. The relationship between actual ecological distances and corresponding measures of sample similarity appears to be linear only when the samples to be compared consist of a sufficient number of species in common. If two samples which are to be compared have no species in common, then the measured numerical distance between them is independent of the actual ecological distance (Gauch 1973).

The programme TWINSPAN uses reciprocal averaging ordination while ranking the samples to form a single axis. This axis should represent the major vegetation gradient. As a second step, the samples are divided into two clusters by breaking the axis near its mid-point. If the actual ecological distance between the poles of such an axis is very long, a subset of samples may appear near one pole, which all have a maximal numerical distance to the samples near to the opposite pole of the axis. Since the division point of the axis is determined on the basis of numerical distances, the TWINSPAN division of such an axis is arbitrary and may not represent the expected major discontinuity in the vegetation continuum.

The analysis of the entire vegetation data set was performed in two steps in order to avoid this kind of distortation in classification. In the first step, the entire data set was analyzed using TWINSPAN in order to distinguish a subset of samples representing either of the poles of the ordination axis, which differ most from the major part of the data set. This subset of samples was then removed from the remaining data. In the second step, the more homogeneous, truncated data set was reclassified, and the results of both classification steps were combined.

The first two levels of the dichotomous hierarchical classification of the entire data set (n=410) are presented in the dendrogramme in Fig. 5. The indicator species of each division are presented in decreasing order of importance; the numbers in parentheses indicate the occurrence of each species (or pseudospecies) in the left and right subset produced by each division. The most important indicator species in the first division is *Maianthemum bifolium*, with a coverage of more than 0.25 %. It is totally absent from only 8 % of the sample plots in subset 0, but is absent from 85 % of the sample plots in subset 1. In contrast, the indicators of subset 1, *Vaccinium vitis-idaea* with a coverage of at least 10 % and *Calluna vulgaris* (when present), represent xerophilous vegetation. Only 7 % of the sample stands in subset 1 are spruce-dominated, whereas the corresponding percentage in subset 0 is 80. This, and the subsequent divisions of subsets 0 and 1 show a fairly close resemblance to the results of the preliminary classification (Fig. 3).

In the second division, 96 sample plots are segregated from subset 0. The indicators of this subset (00), *Carex digitata, Brachythecium* spp. (mainly *B. curtum* and *B. reflexum*), *Oxalis acetosella, Melica nutans, Fragaria vesca* and *Viola riviniana,* are species typical of rich forest sites. The abundance of *Vaccinium myrtillus* in the sample plots of this subset is in most cases lower than 16 %, and the average number of species is clearly higher than in the remaining material. These 96 sample plots clearly represent the richest sites in the material, being comparable to subset 00 (clusters 1–4) of the preliminary vegetation classification (Figs. 3 and 4). In order to reduce superfluous floristical heterogeneity which could distort the results of TWINSPAN classification, the vegetation data set was truncated by allocating these 96 sample plots as a separate cluster representing sites characterized by a rich occurrence of demanding plant species. After this had been done, the remaining 314 sample plots were reclassified using TWINSPAN.

The dendrogramme resulting from reclassification is presented in Fig. 6. The ordered two-way table in the Appendix includes the

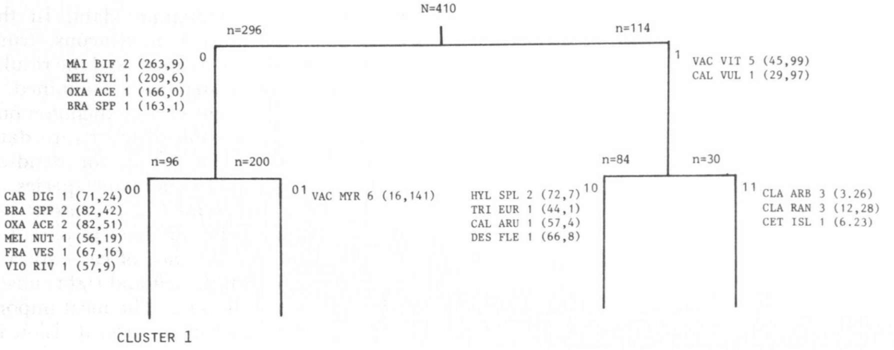


Fig. 5. Indicator species analysis of the complete vegetation data set (study areas I–III). Numbers after species names give the abundance value with which the species indicate each division (see Chapter 4.1.). Numbers in parentheses give the frequencies of each species in the left and in the right cluster, respectively. Subset 00 (cluster 1) is inserted on the left side of the arranged data matrix in the Appendix.

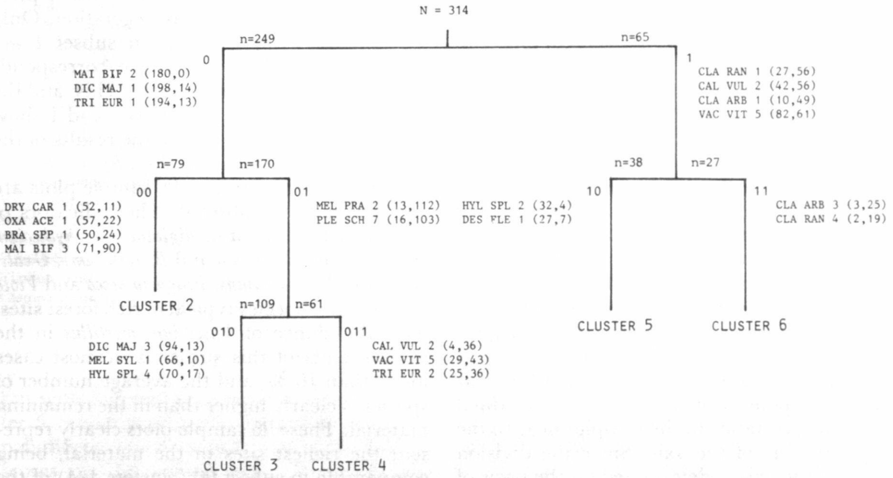


Fig. 6. Indicator species analysis of the truncated vegetation data set, with the richest sites (cluster 1) split off after the first TWINSPAN run (Fig. 5). For explanations, see Fig. 5. The sample plots assigned to clusters 2–6 are arranged on the right side of the data matrix in the Appendix.

sample and species hierarchical classifications, showing the species' synecological relations. Subset 00, which was split off after first TWINSPAN run, is inserted on the left side of the table and forms a matrix of its own. The rankings of species in these two data matrices are somewhat different, but show common features exposed by the RA ordination: with few exceptions, the species seem to be ranked in decreasing order of nutrient and moisture requirements, constituting a gradient ranging from demanding herbs, ferns and mosses down to xerophilous dwarf-shrubs, mosses and lichens. Most of the exceptions are rare species which occur sporadically in the material. In general, the ordination axis corresponds rather well with the major ecological gradient implicated in the unidimensional sequence of the Finnish forest site types.

The indicator species of the first division (Fig. 6) are partly the same as those in the first division of the entire data set (Fig. 5). *Maianthemum bifolium* is again the most important indicator species and, together with *Dicranum majus* and *Trientalis europaea*, characterizes subset 0. Two *Cladina* lichens, together with *Calluna vulgaris* and *Vaccinium vitis-idaea*, are indicators of subset 1. This division clearly separates xerophilous vegetation (subset 1) from the more or less mesophilous vegetation characterizing subset 0. The stands included in subset 1 are entirely pine-dominated. On the other hand, 32 % of the stands included in subset 0 are also pine-dominated.

In the second division, 79 sample plots (subset 00) are split off from subset 0. The most important indicators of subset 00 are *Dryopteris carthusiana*, *Oxalis acetosella*, *Brachythecium* spp. and *Maianthemum bifolium* (with a coverage more than 1 %). Subset 01 is characterized by a frequent occurrence of *Melampyrum pratense* and a considerable abundance of *Pleurozium schreberi* (with a coverage more than 25 %). It can be seen from the ordered table in Appendix that the number of species is larger in subset 00, and many of these species are moisture-demanding ferns, herbs and mosses. The second division hence seems to divide subset 0 into sites which are either more (00) or less (01) moist, the former probably also indicating a somewhat higher nutrient status.

The second division further separates subset 11, which indicates an extremely low moisture in the present material, from subset 10, which indicates somewhat moister conditions. This can be concluded from the dominance of lichens and the lack of mesophilous species in the former subset. However, the species composition of these two subsets appears to be rather similar.

In the third division, the largest subset (01) is further divided into two (subsets 010 and 011). The positive indicators *Calluna vulgaris*, *Juniperus communis*, *Vaccinium vitis-idaea* and *Trientalis europaea* are rather light-demanding species, whereas the negative indicators *Dicranum majus*, *Melampyrum sylvaticum* and *Hylocomium splendens* prefer shelter from direct sunlight. The differences between the species composition of these two subsets give the impression that the division is, in ecological terms, largely generated by the light factor. The difference in tree species composition gives support to this conclusion: spruce is dominant in 85 % of the sample plots in subset 010, but in only 7 % of the sample plots of subset 011.

The subsequent divisions are ecologically less easy to interpret, mainly due to the general drawback of divisive classification programmes: misclassifications tend to accumulate, and their appearance becomes more and more effective as the division process proceeds (Gauch 1982, p. 197). Some conclusions, however, can be drawn by interpreting the ordered vegetation table. Subset 000 clearly represents nemoral forest sites characterized by an abundance of *Hepatica nobilis*, *Anemone nemorosa* (especially subset 0000) and other rather demanding species. Small subsets containing *Sphagnum* spp, *Polytrichum commune* and other mire plants can be found in each of the six major subsets (e.g. 0010 in the left-hand matrix and 000, 00110 and 0111 in the right-hand matrix of the Appendix). These subsets include sites where paludification has taken place to some degree at least.

In the following, the produced six major subsets (00 in the left-hand matrix and 00, 010, 011, 10 and 11 in the right-hand matrix of the Appendix) are used as operational vegetation units, clusters 1–6. From the phytosociological point of view, these clusters hardly constitute any clear plant community types. The presented classification should instead be regarded as an operational tool for depicting in a more concise form the multidimensional variation which appears in the vegetation continua. From the classificatory point of view, it should be noted that these broad clusters cover the whole range of vegetational variation in the present material. This means that all variants, as well as each single outlier plot, are included in one of the six major categories, just as occurs in practice in the Finnish forest site type system. No attempt is made here to describe the whole variation range of the forest vegetation by means of a scale of broad classes. The aim is rather to find those major features of the vegetation which reflect the most important discontinuities in the major environmental gradients.

5.4. Ecological interpretation of the vegetation classification

The 269 sample plots from which environmental data were available were allocated into the six major clusters produced by the TWINSPAN classification of the complete vegetation data set. Some basic environmental data characterizing different clusters are given in Table 5. Canonical discriminant analysis was used in order to find the set of environmental variables which best discriminate between the clusters. The discriminating variables were selected by means of a stepwise procedure.

It was assumed that the tree stand, being the dominant vegetation layer, governs the understorey vegetation in a way which is partly independent of the site factors. This is mainly due to the fact that the density of the stand, as well as the tree stand composition, is affected not only by site properties but also by silvicultural treatments carried out in the stand and by the development class of the stand. Three different discriminant analyses were therefore performed. In the first one, only the primary site factors (*sensu* Cajander 1926) were incorporated in the analysis as environmental variables. In the second analysis, the estimated canopy coverage (Kuusipalo 1985) was added to the environmental variables to describe the effect of the tree stand on the light factor. In the third analysis, site index (Gustavsen 1980) was added to the set of environmental variables. This was done in order to determine how the estimated potential growth rate of the tree stand is related to the site characteristics.

The results of the first analysis are summarized in Table 6. The first two canonical discriminant functions are statistically significant; these explain the major part of the total variation. Rotated standardized discriminant function coefficients indicate the relative importance of each variable in measuring the environmental gradients underlying each function (for terms, see Kuusipalo 1984b).

The most important variables describing the first discriminant function are the total nitrogen content and pH of the humus layer. The total phosphorus content of the humus layer also shows rather strong positive association with the first function. This function clearly appears to be connected with the nutrient status of the site. The second function is negatively associated with the total calcium content of the humus layer; loss-on-ignition together with the variable describing the effects of aspect and slope (see Fig. 2) also indicate negative associations. On the other hand, however, the thickness of the humus layer is clearly positively connected with this function. The underlying environmental gradient may be connected to the degree of decomposition of the humus layer, which is affected by the calcium content of the parent material (see Mikola 1955, Bååth & al. 1980).

The third function appears to be connected to the textural properties of the soil. The most important variables explaining this function are the stoniness (%) and the proportion of fine-textured particles (<0.06 mm) in the mineral soil. Both variables are associated rather strongly with the thickness of the A horizon in the soil profile, but negatively with the clay content in the superficial deposits. The factor which best explains these different associations is probably the superficial deposit type: stones and boulders together with fine-grained mineral soil particles are found in till soils characterized by an uneven particle-size distribution. In contrast, sandy and clay soils are characterized by an even particle-size distribution, and their soil profile is often poorly developed.

In order to illustrate the relationships between the six clusters representing different vegetation types and environmental gradients interpreted from the above discriminant functions, the positions of the cluster centroids along each of the discriminant axes are given in Fig. 7. It should be noted, however, that there is considerable overlap between the clusters at each axis; this is because the complete data set was used, instead of selected sets of "typical" vegetation types.

It can be concluded from the uppermost line diagramme in Fig. 7, that the nutrient status of the site decreases in increasing order of the rank number of the vegetation clusters. Clusters 1 and 2, which are characterized by

Table 5. Ecological characteristics of the sample clusters.

		CLUSTER					
Biological characteristics		1	2	3	4	5	6
Dominant species %	Spruce	91	89	75	15	0	0
	Pine	9	11	25	85	100	100
Total basal area (m^2)	Mean	32	31	30	27	25	22
	SD	7	7	8	6	6	6
Percentage of spruce	Mean	83	85	75	14	20	7
	SD	24	25	30	18	27	9
Percentage of deciduous trees	Mean	8	5	3	3	3	1
	SD	10	8	6	6	6	3
Dominant height (m)	Mean	22	22	22	22	20	18
	SD	4	3	3	3	3	3
Dominant age (a)	Mean	70	78	90	91	100	90
	SD	20	22	23	26	29	24
Total number of plant species	Mean	32	24	19	20	17	12
	SD	5	4	4	4	4	3
Properties of the sub-soil		1	2	3	4	5	6
Superficial deposit type (%)	Till	81	83	84	75	88	45
	-coarse	70	78	81	75	88	45
	-fine	11	5	3	0	0	0
	Sand	11	8	16	25	12	55
	Silt, clay	8	9	0	0	0	0
Shallow soils (%, presence)		3	8	14	32	56	21
Stoniness (% soil volume	Mean	16	20	18	19	16	22
	SD	7	7	7	6	6	8
Silt and clay (% soil volume	Mean	34	33	27	26	26	24
	SD	19	17	11	12	11	6
Properties of the humus layer		1	2	3	4	5	6
Thickness of the raw humus layer (mm)	Mean	20	33	31	27	26	24
		10	12	11	9	7	9
Peaty mor (%, presence)		10	41	9	21	0	0
Mull and moder (%, presence)		50	4	0	7	0	0
pH	Mean	4.4	4.0	3.9	3.9	3.8	3.6
	SD	0.3	0.3	0.2	0.2	0.2	0.2
Total nitrogen (kg/ha)	Mean	454	637	528	463	412	416
	SD	221	234	207	94	105	145
Total calcium (kg/ha)	Mean	171	172	145	135	119	109
	SD	84	61	75	42	30	43

Table 6. The first three canonical discriminant functions and rotated standardized discriminant function coefficients of the analysis of six clusters and the set of environmental variables.
Canonical discriminant functions

Function	Eigenvalue	Percent of variance	Canonical correlation	Wilks' lambda	Chi-squared	D.F.	Significance
1	1.458 22	69.56	0.770 1957	0.573	142.26	48	0.0000
2	0.427 79	20.41	0.547 3743	0.818	51.27	33	0.0000
3	0.121 66	5.80	0.329 3401	0.918	21.94	20	0.3439

Rotated standardized discriminant function coefficients

	Function 1	Function 2	Function 3
N	0.698 57	0.190 20	–0.087 87
PH	0.647 72	–0.218 78	0.063 41
P	0.207 09	0.123 30	0.127 28
DDES	0.186 41	0.186 26	0.141 75
HDEP	0.360 95	0.588 11	0.229 83
CA	–0.094 11	–0.514 83	–0.107 54
LOI	–0.085 97	–0.259 89	0.112 56
WARM	–0.100 56	–0.236 75	0.006 03
STONES	–0.242 08	0.054 62	0.828 57
FSAND	–0.009 20	–0.006 83	0.792 43
CLAY	0.305 30	–0.005 22	–0.441 72
AHOR	–0.034 75	0.204 80	0.435 85
MDPS	0.038 47	–0.042 16	–0.174 96

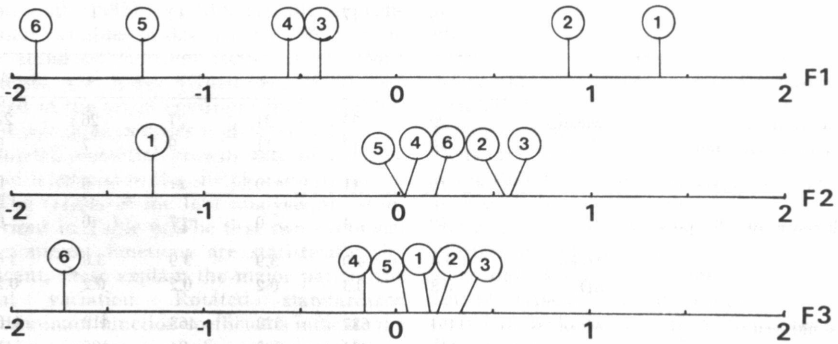


Fig. 7. Position of the cluster centroids on each of the separate discriminant functions of Table 6. F1 depicts the nutrient status of the humus layer. F2 is associated negatively with the total calcium content of the humus layer and positively with the thickness of the humus layer. F3 is related to the textural properties of the soil.

rich herb and grass vegetation, clearly form the most fertile site classes implied by high nutrient contents and pH of the soil. Clusters 3 and 4 represent clearly less fertile sites, although their vegetation also indicates relatively mesic site conditions. The xeric sites included in clusters 5 and 6 indicate even less fertile conditions. The latter, representing lichen-rich xerophilous vegetation, appears to form the negative pole of the nutrient gradient.

The second discriminant function (Fig. 7) ranks the clusters in such a way that cluster 1 is clearly separated from the remaining ones. This cluster, which represents demanding, rich grass and herb vegetation, appears to be characterized by rapid and efficient litter decomposition, thus resulting in a low level of raw humus accumulation. The aspect and slope of a site, as depicted by the variable WARM, may also affect the decomposition activity through microclimatical conditions. According to Jalas (1950), the vegetation of sunny esker slopes shows some affinities with the lime-rich forest vegetation. The third discriminant function clearly separates cluster 6 from the remaining clusters. The lichen-rich, xeric sites included in cluster 6 seem to occur mainly on sandy soils, whereas most of the remaining clusters represent forest sites on till soils (cf. Table 5).

In the second discriminant analysis (Table 7), the estimated canopy coverage (variable SHADE) was incorporated as an environmental variable describing the effect of the light regime on the understorey vegetation. The first three discriminant functions are statistically significant, the first one explaining the major part of the total variation. It would thus appear that the tree stand, particularly through its effect on the light conditions below the canopy, is one of the most important factors affecting the understorey vegetation. Canopy coverage seems to be rather independent of the fertility characteristics such as the nutrient contents and pH of the soil. It is most strongly associated with the medium particle size and stoniness of the mineral soil. These associations are probably due to the fact that the proportion of stones and fine-textured particles is higher in till soils, which are usually dominated by spruce and have higher stand densities than e.g. sandy soils.

The second discriminant function is characterized by an abundance of fine-textured mineral soil particles, higher organic matter content in the mineral soil, and also by a topographic position on sunny slopes. In addition, a rather high pH seems to be an important characteristic of this function. According to Sepponen (1981), the percentage of fine-textured particles (<0.06 mm) in the mineral soil correlates rather strongly with both the cation exchange capacity and field capacity. This function can be considered to reflect the moisture and nutrient gradient. The third function is associated with a high nutrient status: a high nitrogen content and pH are important contributing factors. However, the most significant factor is a low proportion of stones and boulders in the mineral soil.

The positions of the cluster centroids along the discriminant axes are presented in Fig. 8. It can be seen from the uppermost line diagramme that the canopy coverage decreases in increasing order of the rank number of the vegetation clusters. This can largely be interpreted by the tree species composition: spruce is dominant in clusters 1–3, whereas the stands included in clusters 4–6 are characteristically pine-dominated (see Table 5). The lowest stand densities are found in cluster 6, which represents dry-and-poor sites. On the other hand, the stands included in cluster 1 had the highest stand density, this cluster representing the most fertile sites in the present material. This function is very effective in separating the spruce-dominated clusters from the remaining clusters.

Clusters 1 and 6 form the opposite poles of the second discriminant axis (Fig. 8). This supports the interpretation that this function reflects the gradient of increasing moisture and nutrient availability. However, the function is not very effective in separating the remaining clusters from each other. The nutrient gradient is also clear in the third axis: cluster 1 forms the positive pole of the axis, cluster 2 also clearly lying on the positive side. The subsequent clusters cannot be separated reliably from each other by this function.

Inclusion of the site index with the environmental variables restored the major importance of the differences in soil fertility in the ecological interpretation of the vegetation

Table 7. The first four canonical discriminant functions and rotated standardized discriminant function coefficients of the analysis of six clusters and the set of environmental variables, including canopy coverage.

Canonical discriminant functions

Function	Eigenvalue	Percent of variance	Canonical correlation	Wilks' lambda	Chi-squared	D.F.	Significance
1	2.854 18	76.28	0.860 5473	0.480	187.65	48	0.0000
2	0.623 58	16.67	0.619 7383	0.780	63.82	33	0.0010
3	0.125 11	3.34	0.333 4645	0.876	33.71	20	0.0282
4	0.119 57	3.20	0.326 8084	0.981	4.85	9	0.8474

Rotated standardized discriminant function coefficients

	Function 1	Function 2	Function 3	Function 4
SHADE	0.960 48	–0.048 71	–0.007 63	–0.002 83
MDPS	–0.373 99	0.373 99	0.234 83	0.352 15
FSAND	–0.056 22	0.767 27	–0.390 76	0.568 22
LOI	–0.094 07	0.343 70	–0.083 41	–0.024 66
WARM	–0.199 80	0.287 97	–0.022 11	–0.008 66
STONES	0.370 14	0.182 33	–0.714 12	0.091 14
N	0.160 38	–0.040 88	0.576 70	0.155 59
PH	0.236 39	0.514 29	0.528 10	0.124 10
CLAY	0.019 99	–0.312 42	0.466 72	–0.235 69
HDEP	–0.044 22	0.011 76	0.145 93	0.710 71
CA	–0.028 36	0.048 72	–0.030 82	–0.649 25
AHOD	0.100 41	0.148 06	–0.291 51	0.306 26
P	0.040 25	0.167 43	0.109 24	0.285 85

classification. The results of the third discriminant analysis are summarized in Table 8. The first discriminant function, which covers more than 77 % of the total variance, can now clearly be interpreted as a fertility factor. Site index, together with a high nitrogen content and pH, is strongly positively associated with this function; the association with stoniness is clearly negative (for effects of stoniness on site fertility, see Viro 1947, 1953). However, the total calcium content of the soil is not correlated with the first discriminant function and its decisive variables (cf. Valmari 1921). This is probably due to the skewed distribution of the calcium content in the present material (Kuusipalo 1984a). The positive correlation between site index and total phosphorus content appears to be rather weak. It should also be noted that canopy coverage is not correlated with the first discriminant function.

The second discriminant function is strongly affected by canopy coverage, which in turn appears to be associated with the medium particle size of the mineral soil. This function is approximately the same as the first function in the preceding discriminant analysis (Table 7). The third function corresponds to the second discriminant function in the first analysis (Table 6). The apparent negative correlation between calcium content and the thickness of the humus layer, as well as the negative correlation between the total contents of calcium and phosphorus have been discussed by Valmari (1921), Wittich (1939), Viro (1953) and Mikola (1955).

The positions of the cluster centroids along the discriminant axes are presented in Fig. 9.

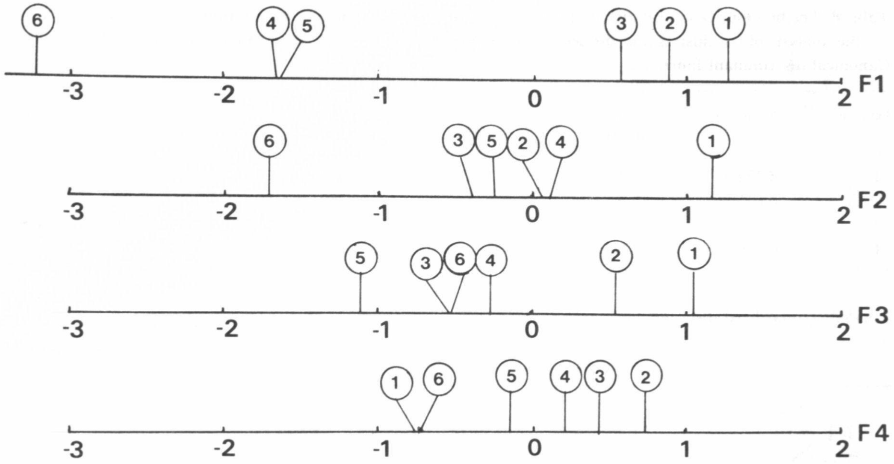


Fig. 8. Position of the cluster centroids on each of the separate discriminant function sof Table 7. F1 is related to canopy closure with –3.5 most open. F2 appears to reflect the moisture and nutrient gradient in the mineral soil. F3 is associated with a high nutrient status of the humus laver. F4 is statistically non-significant but can be related to F2 of Fig. 7.

The uppermost line diagramme indicates that site fertility decreases in increasing order of the rank numbers of the clusters (cf. Fig. 7). The most fertile sites have rich grass and herb vegetation characteristic of cluster 1, and the sites included in cluster 2 also indicate a considerable level of site fertility. The vegetational differences between clusters 3 and 4 can be attributed to the differences in tree species composition; the fact that the cluster centroids indicate that there is almost equal fertility, provides further support for this conclusion. Cluster 5 represents much less fertile subdry and dry sites, and the lichen-rich dry-and-poor sites of cluster 6 form the negative pole of the fertility gradient in this material.

The second line diagramme (Fig. 9) shows the positions of the cluster centroids along an axis of decreasing canopy coverage. The spruce-dominated stands of the clusters 1–3 are more shady than the pine-dominated stands of clusters 4–6 (cf. Fig. 8). The third axis separates the clusters partly differently than the ecologically corresponding second axis in Fig. 7. The thickness of the humus layer decreases on moving from mesic to xeric sites, with the exception that on the most fertile sites (cluster 1) the uppermost soil layer is composed of a mixture of mineral soil and mull or moder instead of a sharply delineated raw humus horizon.

5.5. Differences in stand productivity

It is assumed in the following that the site index (Gustavsen 1980) is a reliable indicator of site fertility, and is a measure of the potential capacity of the site to produce stemwood. When determining the relationship between the vegetation clustering and site index, the former was treated as an independent class variable and the latter as a continuous response variable in two-way and one-way analyses of variance. In the two-way analysis the dominant tree species was treated as a second factor, the cluster means for which being adjusted in a multiple classification analysis. This was done because the site index curves differ from one tree species to another (Gustavsen 1980). The results of the two-way analysis of variance with associated

Table 8. The first four canonical discriminant functions and rotated standardized discriminant function coefficients of the analysis of six clusters and the set of environmental variables, including canopy coverage and site index.

Canonical discriminant functions

Function	Eigenvalue	Percent of variance	Canonical correlation	Wilks' lambda	Chi-squared	D.F.	Significance
1	3.174 31	77.17	0.872 0318	0.461	197.42	52	0.0000
2	0.645 40	15.69	0.626 2957	0.759	70.44	36	0.0000
3	0.152 81	3.71	0.364 0816	0.875	34.18	22	0.0472
4	0.119 58	2.90	0.326 8120	0.979	5.37	10	0.8650

Rotated standardized discriminant function coefficients

	Function 1	Function 2	Function 3	Function 4
PH	0.589 74	0.107 05	0.098 32	–0.237 33
SI	0.545 62	–0.086 06	0.293 23	0.085 69
N	0.319 80	0.082 64	0.074 23	–0.298 74
SHADE	–0.006 61	0.966 51	–0.040 64	–0.084 53
MDPS	0.238 95	–0.452 31	0.349 17	0.195 24
HDEP	0.161 40	–0.112 56	–0.751 37	–0.024 71
SA	0.034 22	0.000 16	–0.642 81	0.049 23
P	0.176 74	–0.010 49	0.306 03	0.115 97
AHOR	–0.211 32	0.128 38	0.294 37	0.253 75
FSAND	0.0.026 34	–0.077 96	0.608 84	0.887 01
CLAY	0.231 98	–0.019 91	–0.259 68	–0.488 89
STONES	–0.325 16	0.458 47	0.164 00	0.481 08
LOI	0.058 94	–0.105 92	–0.019 84	0.349 93
WARM	0.027 54	–0.203 91	–0.037 86	0.270 93

multiple classification analysis are given in Table 9. In the one-way analysis of variance, *a posteriori* contrast test (LSD) for the cluster means was used when examining the differences between clusters. In order to avoid the interacting effect of the different tree species, the analysis was performed separately for stands dominated by spruce and pine. The results of the one-way analysis of variance with associated tests are presented in Table 10.

As can be seen in Table 9, both of the main sources of variation indicate significant effects on the criterion variable. The interaction, however, does not appear to be statistically significant. The total mean of the site index for the entire data set is about 250 dm. The deviation of each class mean from this grand mean is presented in the multiple classification analysis (column on the left side). The column on the right side represents the corresponding deviations adjusted for the effect of the tree species on the site index value. The adjustment naturally reduces the differences between the clusters, diminishing the site index values of the spruce-dominated stands of clusters 1–3 and increasing the values of the pine-dominated stands of clusters 4–6. The highest cluster mean occurs with fertile sites of cluster 1; the somewhat lower mean value of cluster 2 also indicates a considerable level of site fertility. The adjustment removes the clear difference between clusters 3 and 4: when the effect of tree species is kept constant, these two clusters indicate equal site fertility. Markedly lower cluster means are found with clusters 5 and 6, the latter being somewhat less fertile.

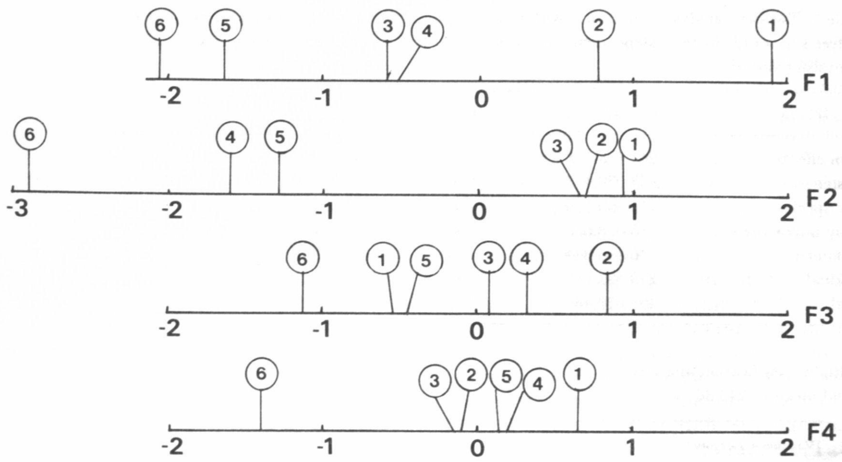


Fig. 9. Position of the cluster centroids on each of the separate discriminant functions of Table 8. F1 reflects site fertility as indicated by site index and nutrient status of the humus layer, with most fertile sites on the positive side. F2 is the same function as F1 of Fig. 8, being related to canopy closure mainly. F3 is associated positively with the thickness of the humus layer and positively with the total calcium content of the humus layer. F4 is statistically non-significant but can be approximately related to F3 of Fig. 7.

In the one-way analysis of variance (Table 10), the spruce and pine stands were analyzed separately. Since clusters 5 and 6 did not contain any spruce stands, they were excluded from the comparison concerning spruce stands. As can be seen from the resulting diagramme of the multiple ranges test, all the clusters differ significantly from each other and the cluster mean decreases in increasing order of the rank numbers of the clusters. Spruce obviously reaches its physiological growth limits on dry-and-poor sites. On mesic sites, the growth potential of spruce seems to decrease almost linearly on moving from rich vegetation types to poorer ones. As regards the pine stands, clusters 5 and 6 differ significantly from all the other clusters and form a fertility class of their own. Cluster 1 differs significantly from all the other clusters except for cluster 2. Other differences between the clusters are statistically non-significant. The results give the impression that there is a critical point, lying somewhere between subdry and dry sites, which corresponds to some kind of threshold in the site requirements of pine. The response of pine to the increasing nutrient supply on mesic sites is less marked than that of spruce. On poorer mesic sites the growth potential of pine is equal to that of spruce, while on fertile sites spruce seems to be superior.

The different Cajanderian forest site types can be related to site index classes: such tables for different tree species are given in Gustavsen (1980) and Vuokila (1983). The average site index value for spruce in cluster 1 is 29 m; in the Finnish forest site type system, the corresponding value comes between the *Oxalis-Myrtillus* site type and nemoral forest types. The group mean of cluster 2 is 27 m for spruce. The corresponding Cajanderian site type is the *Oxalis-Myrtillus* type. The group mean for spruce in cluster 3 is 25 m, which approximately corresponds to the *Myrtillus* site type. The group mean of cluster 4 for spruce is 24 m, which coincides with the average value of the site index in the *Myrtillus* site type; for pine, the group mean of 23 m means that cluster 4 should be allocated to a fertility class which is slightly better than the *Vaccinium* site type. The group means for pine in clusters 5 and 6 are 21 m and 19 m,

Table 9. Two-way analysis of variance with multiple classification analysis using sample clusters (6) and dominant tree species (2) as the independent variables and site index (dm) as the response variable.

Analysis of variance

Source of variation	Sum of squares	D.F	Mean square	F	Significance
Main effects	241 468.188	6	40 244.699	41.61	0.000
Cluster	88 939.453	5	17 787.891	18.39	0.000
Tree species	11 590.536	1	11 590.536	11.98	0.001
2-way interactions	5 028.656	4	1 257.164	1.30	0.271
Explained	246 496.844	10	24 649.684	25.49	0.000
Residual	249 523.625	258	967.146		
Total	496 020.469	268	1 850.823		

Multiple classification analysis
Grand mean = 249.86

Variable + category	N	Unadjusted devation	Eta	Adjusted for independents deviation	Beta
Cluster					
1	66	35.69		29.73	
2	46	20.58		14.98	
3	80	−5.22		−7.97	
4	28	−18.54		−7.63	
5	25	−45.50		−34.76	
6	24	−51.15		−38.80	
			0.68		0.53
Tree species					
Pine	104	−29.99		−12.35	
Spruce	165	18.90		7.78	
			0.55		0.23

Table 10. One-way analysis of variance with multiple range tests (LSD, p = 0.05) done separately for pine and spruce stands using sample clusters (6) as the independent variable and site index as the response variable.

PINE STANDS

Multiple range test

Cluster	Mean	6	5	4	3	2	1
6	198.71						
5	205.22						
4	230.50	*	*				
3	233.80	*	*				
2	234.60	*	*				
1	255.83	*	*	*			

Analysis of variance
F = 10.426*** n = 104

SPRUCE STANDS

Multiple range test

Cluster	Mean	4	3	2	1
4	218.25				
3	248.25	*			
2	274.81	*	*		
1	288.52	*	*	*	

Analysis of variance
F = 16.798*** n = 165

respectively. These site index values come between the *Vaccinium* and *Calluna* site types in the Cajanderian system.

5.6. Ecological gradients and site factors

Attempts were made in the present study to analyze ecological gradients and their significance in controlling forest vegetation. Interpretations of discriminant and ordination analyses were used for this purpose. As regards the discriminant analyses, it is assumed that each of the set of variables discriminating between the vegetation clusters reflects an underlying ecological gradient which can be interpreted from the discriminant function coefficients. In the case of the ordination analyses, the major ordination axes are interpreted indirectly using species scores and previous knowledge (e.g. Kujala 1926a, 1926b, Ellenberg 1974) about the species' preferences and environmental requirements. Both approaches are explanatory rather than confirmatory; in other words, no *a priori* hypotheses were postulated for empirical confirmation (cf. Kuusipalo 1984a, 1984b).

Both approaches provide some support for the concept of ideal unidimensionality implied in the Finnish forest site type system: gradient of "soil fertility" seems to be of major importance. The chemical properties of the soil alone explain the most important discriminant function in Table 6. However, when a "secondary" site factor, canopy coverage, is incorporated as an environmental variable, it constitutes the most important discriminant function without having any close connections with the fertility characteristics (Table 7). Only when additional information provided by the site index is incorporated as a measure of potential productivity, does the "fertility gradient" reflected in site index and some chemical properties of the soil exceed the explanatory value of canopy coverage (Table 8). The apparent independence of canopy coverage of soil fertility is probably partly a result of different tree species composition in the different clusters; the clustering appears to be somewhat bipolar, spruce-dominated stands being confined to clusters 1–3 and pine-dominated stands to clusters 4–6. On the other hand, e.g. stand density seems to increase almost linearly in increasing order of site fertility (see Table 5). Probable additional determinants of pattern in the tree stratum include silvicultural activities which, in commercial forests, may change the natural balance between different vegetation strata. In undisturbed, natural forest stands, a particular type of understorey vegetation may be associated more decisively with a particular tree species composition, both depending upon the same primary site factors (Cajander 1949). In general, a clear series was found in the present study in the nutrient regime of the humus layer from the most fertile to the most infertile cluster (1–6). As regards the light conditions as controlled by canopy closure, the clusters are roughly ranked in the same order, but constitute a somewhat different pattern in comparison with the fertility gradient (Tables 6–8).

It should be noted here that site index is computed from the dominant height and dominant age of the tree stand. It is in fact a tree stand characteristic, but is assumed here to reflect primarily the soil properties and is therefore treated operationally as a measure of site fertility. The most important individual components of the fertility factor are the pH and the total contents of nitrogen and phosphorus in the humus layer (Tables 6 and 8). The pH is an overall variable which is connected with many chemical, physical and biological soil processes (Jansson 1978). It is known from fertilization experiments that nitrogen is a limiting factor for growth in upland forests (Tamm & Carbonnier 1961, Viro 1967, Kukkola & Saramäki 1983). On the other hand, the positive association of the phosphorus content is somewhat surprising since phosphorus has not been found to follow the fertility series of the Finnish forest site types (Valmari 1921, Viro 1951, 1953, Urvas & Erviö 1974). Kukkola & Saramäki (1983), however, have reported that phosphorus added together with nitrogen fertilization improves the growth of spruce stands and that the effect of phosphorus becomes proportionally more important as the fertility of the site increases. It is important to remember that a considerable proportion of the annual nutrient consumption of the stand may be bound by the grass and herb vegetation on fertile soils (Mälkönen 1977). As emphasized by Sepponen (1985), the humus layer is itself a product of the plant community, and it is therefore only natural that its nutrient contents are well adapted to the composition of the plant community.

The thickness and type of humus layer combined with the degree of paludification appear to be the most significant additional environmental gradient. This gradient can be identified from ordinations (Tables 3 and 4, Fig 4) as the second DCA axis and from disriminant analyses (Tables 6 and 8, Figs. 7 and 9). In the ordination analyses, this gradient seems primarily to separate a subset of paludified sample plots from the remaining material confined to genuine upland forest sites. In the discriminant analyses, a gradient ranging from sites characterized by a thin humus layer to those with thick, poorly decomposed deposits of raw humus can be identified. The thickness and type of humus layer depends primarily on the composition of vegetation itself. The microclimatical conditions (moisture and temperature) in spruce stands significantly reduce the degree of decomposition (Aaltonen 1932). The soft leaves of deciduous trees and bushes and the remains of herbs and grasses decompose more readily than coniferous needles and the litter from dwarf-shrubs and mosses (Hesselman 1926, Mikola 1955). In general, the thickness of the humus layer increases on moving from dry to moister clusters. According to Söyrinki & al. (1977) and Sepponen (1985), the humus thickness is greatest on damp site types and decreases on moving to more dry site types. In this study, the calcium content was found to be strongly negatively associated with the thickness of humus layer. However, as can be seen from Table 5, the total amount of calcium follows the pattern of fertility gradient implied in the vegetation clustering. The negative association is a result of the skewed distribution of calcium content in the presented material: lime-rich soils are confined mainly to cluster 1, which represents demanding, rich grass and herb vegetation and is characterized by rapid and efficient litter decomposition and, thus, by a low level of raw humus accumulation. Accordingly, the corresponding discriminant functions are biased by the calcium content and humus thickness distributions of the soils included in this study (cf. Table 5).

Among the properties of mineral soil, the volume percentages of stones (Viro 1947) and fine-textured particles (<0.06 mm) seem to be associated with the fertility gradient (Table 7). The latter textural characteristic of mineral soil is associated primarily with aeration and moisture conditions (Sepponen 1981). In general, it has been concluded that the more fertile sites are to be found on soils with a finer than average texture, and the more infertile ones on the more coarse-textured soils (Ilvessalo 1933, Urvas & Erviö 1974, Sepponen & al. 1982). The results of the present study support these conclusions (see Table 5). It has earlier been demonstrated that stoniness has a considerable effect on tree growth (Viro 1947), and is generally used as an additional attribute in site fertility estimation (Kuusela & Salminen 1969). According to Viro (1953), a small proportion of stones in mineral soil probably increases soil fertility due to its effect on soil aeration and temperature. However, when the relative abundance of stones exceeds 20 %, it starts to reduce soil fertility. This is mainly due to the fact that stones decrease the volume occupied by the small soil particles which constitute the major source of nutrients for plants. In comparison with the fertility characteristics of the humus layer, however, these associations in the present study appear to be weak and statistically less significant.

In previous studies, no apparent relationships has been found between the superficial deposit type and the forest site type (Ilvessalo 1933, Aaltonen 1941, Urvas & Erviö 1974, Sepponen & al. 1982). As emphasized by Sepponen (1985), site properties of sorted soils can only partly be determined on the basis of geological processes, and till soils would presumably be even more difficult to analyze in this respect (see also Saarnisto & Peltoniemi 1984). The present study material is confined majorly to till soils, and the results support the conclusions made in earlier studies: each forest vegetation type can occur on almost any superficial deposit type (Table 5). However, sorted, sandy soils with low percentage of finetextured particles are particularly characteristic of cluster 6, which represents the most xerophilous vegetation in this material. Thickness of the superficial deposits naturally affects the moisture conditions; shallow soils are particularly characteristic of sample plots included in cluster 5, which also represents xerophilous vegetation.

In general, the forest vegetation is governed by many environmental factors simultaneously, the effects of which are only partly independent of each other. According to the results of this study, the nutrient gradient seems to be of major importance. Nutrient status is reflected in the pH and the nitrogen and phosphorus contents of the humus layer and is, of all the factors, most closely connected to site fertility estimated with the help of site index. On the other hand, the nutrient contents for the mineral soil do only partly follow the same pattern and appear to indicate statistically weakly significant associations with the vegetation clustering. Similar results have been reported also by Urvas & Erviö (1974) and Sepponen (1985). There may be many reasons for these results. The soils of different geological genesis differ from each other as regards their structural and textural properties. These properties presumably regulate, in turn, the long-term processes fashioning the ecosystem as follows: there may be no statistically significant differences in chemical properties in different types of mineral soil, but because they differ from each other in terms of physical properties, chemical differences in the humus layer develop during the development of different types of site (Sepponen 1985). There are also minerological differences in the parent material of the soils in different areas. This is presumably especially apparent as regard the differences in calcium content between the sites included into cluster 1 and the remaining ones. As the physical and other differences are derived from geological patterns and processes, these are in the end also the causal agents for the differences in the chemical properties of the humus layer. The nutrient status is obviously also connected to the moisture regime, since the vegetation cannot utilize nutrients unless they are in a soluble form. In addition to the structural and textural properties of the mineral soil, moisture regime is also governed by many topogenic factors. On mesic sites, a shortage of water seldom plays an important role in controlling the nutrient availability. On the other hand, the moisture regime clearly separates xeric sites from mesic ones. This dichotomy appears to correspond to the major division of the vegetation data set as presented in Fig. 6.

5.7. Ecological site classification

In the following, the ecological conditions typical of each of the six clusters defined by vegetation classification are described in general terms. The vegetation clusters are thus described as ecological habitat types. The term "habitat type" is used here to characterize a group of sites which show similarities in tree stand properties, vegetation composition and soil conditions simultaneously. The concept of "site type" is used in the strict sense of productive capacity level (Keltikangas 1959). Neither of the terms is comparable with plant community type or any other phytosociological unit. The habitat types described in this chapter are operational units; no attempt is made to define new forest site types *sensu* Cajander (1949). The relationships between these operational units and the Finnish forest site types are, however, briefly discussed. The major aim is to determine the most apparent environmental discontinuities (if any), which underly the vegetation classification produced using TWINSPAN. An additional aim is to constitute a hierarchical scheme for distribution of the forest vegetation under consideration.

First, ecological descriptions of the six major clusters are briefly summarized. The descriptions are mainly based on the vegetation table in the Appendix, Tables 5–10 and Figs. 3–9. One important thing to remember is that there is a considerable amount of between-cluster overlap in the soil and other ecological characteristics due to the random sampling procedure and inclusion of the complete data set into the vegetation classification. In addition, each cluster can be distinguished into several different subtypes of forest habitats.

Cluster 1 is generally characterized by a rich herb and grass vegetation, which includes many demanding nemoral forest plants. The average number of species is large, and although ericous dwarf-shrubs and forest mosses are common, they are less abundant and occur rather sparsely. This cluster is phytosociologically relatively heterogeneous, consisting of several more or less fragmentary habitat types, e.g. nemoral habitats on brown soils and on fine-textured aeolian deposits, herb-rich paludified habitats, etc. However, major part of the sample plots included in cluster 1 is confined to relatively fine-textured and stone-free till soils and is characterized by a spruce-dominated tree stand with a dense canopy. Mull and moder are the prevailing types of humus instead of mor (for terms, see Jones & al. 1983, p. 50). The calcium content of the soil is high, and there is a plentiful supply of other nutrients, too. In terms of the Finnish forest site type system, this cluster covers the range from nemoral forest types to site types probably more fertile than the *Oxalis-Myrtillus* type in average.

Cluster 2 is characterized by a moderately rich herb and grass vegetation combined with an abundance of *Vaccinium myrtillus*. The moss cover is more continuous than in the preceding cluster. Cluster 2 includes habitats characterized by a considerably high degree of paludification. The major habitat type in this cluster, however, is not paludified to a high degree, although there are indications of a considerable amount of moisture. Dense spruce stands are typical to the sample plots included in this cluster. Instead of mull and moder, mor is the typical form of thick humus layer characteristic of cluster 2. This type occurs most often on rather fine-textured but relatively stony till soils, although it is also quite common on deposits of silt and finer sand. The total amounts of nitrogen and calcium in the humus layer are considerably high, but the average pH is much lower than in the preceding cluster, presumably due to the larger amount of humic acids in the raw humus layer. In the Finnish forest site type system, this cluster would approximately represent the *Oxalis-Myrtillus* site type.

Cluster 3 constitutes the most homogeneous habitat type of all the clusters, and does not include many paludified or markedly dry sites. The general character of vegetation within this cluster approaches that of the spruce-dominated *Myrtillus* site type forests described in forestry textbooks. The vegetation is clearly of mesic character, but demanding forest plants seldom occur and the number of species is lower than in the preceding clusters. Ericous dwarf-shrubs, particularly *Vaccinium myrtillus*, predominate in the field layer, while a more or less continuous cover of *Pleurozium schreberi, Hylocomium splendens, Dicranum majus* and *D. polysetum* dominates the bottom layer. Sites included in this cluster are confined mainly to relatively coarse-textured till soils, although they often also occur on sandy soils. Thickness and acidity of the humus layer approach that of cluster 2, and mor is the typical form of humus. The total amount of nitrogen is lower and the total amount of calcium much lower than in the preceding cluster. The stands are dense and mostly spruce-dominated, although pine-dominated stands are also common.

Cluster 4 is generally characterized by vegetation of a relatively mesophilous character, which manifests in an abundance of many relatively moisture-demanding herbs and other plants. However, an abundance of ligh-demanding, relatively xerophilous dwarf-shrubs (*Vaccinium vitis-idaea* and *Calluna vulgaris*) and forest mosses (*Pleurozium schreberi* and *Dicranum polysetum)* are the characteristic features of the vegetation. This cluster is markedly heterogeneous, consisting of many fragmentary habitats: it includes e.g. genuine subdry sites, relatively fertile sites on dry esker slopes, heterogeneous habitats on shallow soils with both extremely dry lichen-rich patches and even paludified patches in depressions and crevices, etc. A considerable proportion of the sites in cluster 4 is confined to sandy soils, indicating affinities with the esker slope vegetation, but the major part to relatively coarse-textured and stony till soils. One third of the sample plots are located on shallow soils in the vicinity of exposed bedrock. However, the sites included in cluster 4 indicate obvious similarities not only in vegetation characteristics but also in ecological terms. The average pH equals to that of the preceding cluster, but the total amounts of nitrogen and calcium are somewhat lower, probably due to a thinner layer of raw humus. Pine is dominant and the stand densities are comparatively low. Microclimatical and light conditions therefore differ considerably from those characterizing the preceding cluster, largely explaining the apparent differences in vegetation composition and character of humus layer. In the Finnish forest site type system, this cluster would approximately represent the pine-dominated *Myrtillus* site type.

The xeric sites included in cluster 5 indicate somewhat moister conditions than those in the subsequent cluster, as reflected in the greater abundance of certain grass and herb species (e.g. *Deschampsia flexuosa, Calamagrostis arundinacea* and *Luzula pilosa)*. Terricolous lichens are common, but *Pleurozium schreberi* and *Dicranum polysetum* predominate in the bottom layer. *Calluna vulgaris, Vaccinium vitis-idaea* and *Vaccinium myrtillus* dominate the field layer. The sites of this cluster are confined to coarse-textured till soils, but more than half of them are located on shallow soils in the vicinity of exposed bedrock. The last-mentioned habitats are markedly heterogeneous and may include patches in depressions and crevices, which vegetationally resemble quite closely the genuine mesic sites, and patches on which lichen-dominated rock outcrop communities occur. Pine is dominant and the stand densities are low. The characteristics of soil indicate markedly lower fertility than that of the preceding cluster and, according to the site index values, cluster 5 would be placed between the *Vaccinium* and *Calluna* site types.

The sites included in cluster 6 indicate extremely dry conditions. The number of species is low; xerophilous plants such as terricolous lichens predominate, and grasses and herbs are infrequent. Pine is dominant and the stand densities are very low. Although the sites included in this cluster are confined largely to sandy soils, presumably on coarse-textured glaciofluvial formations, they do also occur on coarse-textured till soils characterized by a considerable stoniness. The characteristics of soil indicate lower fertility than that of cluster 5. In the Finnish forest site type system, this cluster would represent the *Calluna* site type. Since many of the sample plots included in cluster 6 occur on similar soils than sites included in cluster 5, it is possible that vegetational differences between these two clusters are partly topogenic. The xeric sites in cluster 6 may thus include lichen-dominated habitats of southern aspects and upper slopes on coarse-textured till soils, while the xeric sites within cluster 5 may respectively include more mesic, lichen-rich but moss-dominated habitats of northern aspects and lower slopes on corresponding soils (see Oksanen 1983).

The major division in the forest vegetation of southern Finland lies, according to the present material, between mesophilous and xerophilous vegetation (Fig. 6). The most unambiguous criteria used in distinguishing between these two major types of vegetation are a frequent occurrence of *Maianthemum bifolium, Melampyrum sylvaticum* and other forest herbs and grasses on mesic sites, and an abundance of *Vaccinium vitis-idaea* and *Calluna vulgaris* and frequent occurrence of *Cladina* lichens on xeric sites. The variation in the tree species composition may, however, cause confusion in distinguishing between these major ecological habitat types: a predominance of pine reinforces the xerophilous character of the vegetation. Instead of ericous dwarf-shrubs and light-demanding mosses (e.g. *Dicranum polysetum*), one ought to pay attention to the herb and grass vegetation, as well as to the total number of species, when allocating pine-dominated stands into either the mesic or xeric site categories (cf. Appendix).

This major division of the vegetation classification is reflected in most of the axes produced by the discriminant analyses. If the division is compared simultaneously with all of the discriminant functions, we gain the impression that the underlying environmental discontinuity is connected to the moisture regime. Owing to the differences in tree growth (Tables 9–10), this division by vegetation characteristics also represents an important threshold: mesic sites (clusters 1–4) approximately cover the fertility range where spruce occurs as a forest-forming tree. There are obviously many causes for the lower moisture content of the xeric sites. Vegetation of xerophilous character very often occurs on sorted, sandy soils, but also on coarse-textured till soils. In addition to the textural properties of the soil, topogenic factors evidently affect the moisture regime. However, no apparent underlying environmental discontinuities were found on the basis of the present material. Vegetation growing on shallow soil often constitutes a mosaic pattern of patches characterized by considerably different plant communities. As can be concluded from the above, it is very difficult to use soil and other environmental characteristics as the sole criteria in distinguishing between mesic and xeric sites. On the other hand, the plant cover appears to be a very useful basis for classification in this respect.

In the further division of mesic sites (clusters 1–4) the vegetation composition changes gradually in accordance with increasing fertility. The number of demanding herb, grass and moss species increases, while the dominance of ericous dwarf-shrubs and common forest mosses (*Pleurozium schreberi, Hylocomium splendens* and *Dicranum* spp.) weakens. It would appear that the mesic habitat types distinguished with the help of the TWINSPAN classification can be divided into at least three fertility classes on the basis of rather unambiguous vegetation criteria. Hierarchically speaking, mesic sites can first be divided into rich sites (clusters 1–2) and damp sites (clusters 3–4). These two types of habitats can be distinguished from each other on the basis of the diversity, occurrence and abundance of forest herbs and ferns, of which the most indicative ones are *Dryopteris carthusiana, Oxalis acetosella* and *Maianthemum bifolium* (when abundant) (see Appendix). Clusters 1 and 2 appear to constitute different fertility classes, whereas clusters 3 and 4 have almost equal fertility but a different tree species composition.

Identification criteria for the habitats representing the most fertile sites (cluster 1) are an abundance of *Oxalis acetosella* combined with a plentiful occurrence of demanding herbs such as *Carex digitata, Viola riviniana, Melica nutans* and *Fragaria vesca*. However, under a very dense canopy a plentiful abundance of *Oxalis acetosella* alone can be used as an identification criterion, since less shade-tolerant species may be totally absent. Moderately fertile sites (cluster 2) are characterized by a greater abundancy of ericous dwarf-shrubs (particularly *Vaccinium myrtillus*) and by a more continuous moss cover. *Vaccinium myrtillus, Pleurozium schreberi, Hylocomium splendens* and other common, relatively indifferent forest plants seem to prefer soils with a thick raw humus layer, whereas herbs and grasses in general usually prefer fertile soils with a less acidic humus layer.

Clusters 3 and 4 apparently represent the *Myrtillus* site type forests; these two clusters also form a fertility class in which both pine and spruce generally occur as forest-forming trees. It is therefore important to distinguish between the vegetational features which discriminate between pine and spruce-dominated mesic sites and, on the other hand, between mesic and xeric sites dominated by pine.

The major division within xeric sites passes between moss-rich (cluster 5) and lichen-rich (cluster 6) habitat types. In general, the differences in nutrient regime between these two clusters seem to be weakly associated with differences in potential stand productivity (see Tables 9–10), probably because the shortage of water, instead of the nutrient level, is the main limiting factor for growth.

Generally speaking, the clusters seem to form three distinct groups in terms of stand productivity and nutrient regime: the least productive, nutrient-poor and dry sites represented by clusters 5–6, the intermediate sites represented by clusters 3–4, and the most productive, nutrient-rich sites represented by clusters 1–2. This division is rather consistent with the division of forest sites into major site classes in the Finnish forest type system: dry (and subdry) sites, damp sites and rich sites (Kuusela & Salminen 1969). The results show that the main direction of variation in the forest vegetation pattern can be explained by an underlying gradient that mainly reflects nutrient availability. In addition, there evidently exists more or less sharp discontinuities in the vegetation continuum. On the basis of the present material it was not possible to recognize unambiguously any environmental discontinuities underlying the apparent discontinuities in the vegetation pattern. However, the most apparent one is presumably connected to the fundamental difference in the moisture regime between the mesic and xeric sites.

6. DISCUSSION

6.1. Methodological appraisal

Selection of the method to be used in vegetation analysis is connected to the user's concept of plant community (Mueller-Dombois & Ellenberg 1974, pp. 22–30) and to the intended use of the results (Goodall 1978a, pp. 276–279). Both discrete and continuous multivariate techniques are applied to a community data matrix with scores for species in a set of samples in order to describe and interpret an underlying structure that is implicit in the data but not easily recognized in the matrix (for terms, see Noy-Meir & Whittaker 1978). Most classification techniques assign samples and species to units which are assumed to be discrete or discontinuous with one another. In contrast, ordination techniques arrange samples and species in relation to several continuous, latent variables and express the compositional similarities of samples and species in a simplified and condensed form.

Agglomerative clustering methods (Goodall 1978a, Gauch 1982), which are mostly based on measures of similarity and dissimilarity between samples (Goodall 1978b), are often applied in vegetation classification. These techniques, however, cannot solve some of the fundamental problems involved in classifying continuosly intergrading communities (see Whittaker 1962). They begin by examining close pairs of individual samples and the small differences in distances between samples. This implies one important limitation: attention is focused on the aspect of data which is primarily either noise, or consequent on sample density (Gauch & Whittaker 1981). As emphasized by Lambert & al. (1973), the topmost divisions are critical in hierarchical classifications and all the available information should be used to make them. In agglomerative techniques, however, the amount of information declines as the clustering process progresses because once an individual sample is incorporated in a certain group it is no longer compared to samples included in other groups. According to Gauch & Whittaker (1981), placing the emphasis on the comparison of individual samples would be more justified if data structures were naturally clustered, i.e. forming distinct clouds in dissimilarity space. However, the community data are usually relatively continuous, and consequently the clustering is imposed.

Ordination methods characteristically belong to the continuum approach to vegetation analysis (Whittaker & Gauch 1978, Gauch 1982). The fundamental question in the ecological interpretation of vegetation analysis is how to relate community variation to environmental measurements. Often the interpretation is made intuitively, using none or only a few environmental characteristics to support more or less circular conclusions primarily based on common sense and ecological experience, e.g. in those cases where ordination axes are interpreted on the basis of the known ecology of species at the poles of the axes (Whittaker 1973, Dale 1975, Persson 1981, see also Chapter 5.1. in this study). The ordination axes are often orthogonal by definition, whereas the effects of environmental factors are seldom independent (however, see Oksanen 1985). Furthermore, the abundances of species are known to be primarily related to environmental gradients through nonlinear functions (Orlóci 1978, Green 1979). Attempts to relate ordination axes directly to environmental gradients are therefore bound to fail in many ecological situations (Green 1979, pp. 205–217). The most convenient way of exploring the relationships between vegetation and the environment is by classification of the samples and subsequent identification of the set of environmental conditions that prevails in each class (Green & Hobson 1970, Green & Vascotto 1978).

Ordination methods are often applied in sample classification using a visual procedure consisting of the following steps: stand ordination and graphical presentation of the sample points in ordination space, looking for distinct clouds of points (if any), and checking their discreteness according to floristic composition. Two- or three-dimensional solutions are most often used. According to Kruskal (1977), visual dissection of an ordination space is not a good approach to classification because distances in ordination space do not correspond to actual ecological distances between samples. Furthermore, if the vegetation data consists (for instance) of two discrete clusters, the first ordination axis would separate them, but on subsequent axes the main directions of variation (presumably different) would be confounded with each other (Noy-Meir & Whittaker 1978). An additional disadvantage in the operational grouping by ordination is the general problem of defining unambiguous and practical criteria for allocating individual samples into the groups. Oksanen (1985), however, reports some promising recent developments in the cluster-seeking ordination.

In the present study, the vegetation types are seen as arbitrary segments of community gradients; these segments of the gradients are used as operational groups in approaching ecological site classification. The groupings should therefore be ecologically meaningful when tested by appeal of the external information provided by environmental measurements. Furthermore, to be practical the groups must also be identifiable in the field, not only in an unique data set. The groupings should therefore contain unambiguous criteria for reliable allocation of individual stands into the groups. Since the groups are derived from vegetation continua, i.e. they are imposed by the clustering technique but are not necessarily intrinsic in the data, the allocation process is essentially probabilistic rather than deterministic. However, it is assumed that although the samples are relatively evenly spread out through the species space, in some regions the clouds of sample points are relatively dense and in others relatively sparse. The boundaries between clusters must therefore be drawn through the sparsest regions. Hence it follows that the groupings should compose a hierarchical system: the probability for misclassification is smaller at the topmost levels of classification, and increases on moving towards the more detailed classification (Gauch & Whittaker 1981). Furthermore, hierarchical clustering techniques define the relationships among the clusters, too. In addition, dendrogrammes always imply high-dimensional configurations; consequently, hierarchies are intrinsically appropriate for high-dimensional data structures underlying most of the real community data (Holman 1972).

The method which best fulfills the requirements for the method to be used in this study is TWINSPAN. This method reconciles the practical need to form vegetation classes for operational purposes with the reality of vegetation continua by using ordination to classify both samples and species into clusters which are ordered hierarchically. In comparison with agglomerative clustering techniques, TWINSPAN is robust since it is only mildly affected by sample error or noise and the removal or addition of samples. The usually better results and greater robustness of TWINSPAN are due mainly to its emphasis to use ordination for an overall view of the data structure rather than preoccupation with details; all the available information is used to make the critical topmost divisions. In this study, TWINSPAN produced roughly similar topmost divisions in all of the three separate classifications (Figs. 3, 5, 6, also Kuusipalo 1983b) although the sample size varied considerably. As listed by Gauch & Whittaker (1981), advantages of TWINSPAN are: (a) it uses the original vegetation data rather than a secondary resemblance matrix, (b) it clusters species as well, and (c) it produces a re-ordered data matrix. Further advantage of TWINSPAN is that it also provides a tool to develop a successive key for definition of operational vegetation units; in this respect, TWINSPAN has been used very succesfully in forest ecosystem classification studies in Canada (Jeglum & al. 1982, Jones & al. 1982).

TWINSPAN evidently has some drawbacks which have restricted its use among ecologists. First, divisive classification is not necessarily the "natural" classification of objects and attributes. The first ordination axis should perhaps be divided into three equally important clusters instead of the two produced by divisive clustering. Secondly, TWINSPAN is seen to be relatively sensitive to changes in programme parameters, particularly to the alternations of the pseudospecies cut levels. However, it is not necessary to use any technique mechanically. As in the present study, one can divide the data set initially into subsets and then reclassify each or some of them separately. Definition of the programme parameters is a question of the phytosociologist's choice of the characteristics he uses to derive clusters from continuous data. As in any "objective" numerical method, some subjectivity is needed in defining the programme parameters as well as in the final compilation of the results. The optimal level of classification, the number of clusters and details affecting desirable locations of boundaries are then controlled by the ecologist. As stressed by Oksanen (1984), the ecologist cannot hide behind "objective" numerical methods since he must be responsible for his results.

It is generally known that if the sampling is stratified according to previously defined vegetation or site types, the within-type variation in vegetation composition, as well as in environmental characteristics, is essentially smaller than in the case when a random sampling procedure is used (Brenner 1921, Dahl & al. 1967, Green 1979). It is obvious that this strengthens the belief in distinct plant communities. Stratified sampling is also often biased in favour of some factor, which is presumably dominant and therefore also appears to be dominant. Due to the fact that a random sampling procedure was used, all the intermediate variants between the forest types are represented in the present material, and no *a priori* hypotheses about presumable gradients were postulated. In spite of this, the divisions at the first levels of classification indicate surprisingly clear vegetational differences and reflect a clear dominant environmental factor underlying the vegetation distribution. In general, an overall view of the data set suggests that although the forest vegetation intergrades continuously, there are evidently rather steep discontinuities which distinguish between essentially different habitat types.

A hierarchical classification system seems to permit more precise definition of the environmental conditions underlying the vegetation distribution than does nonhierarchical classification by site types. It also avoids the drawbacks of the fundamental unidimensionality of the Finnish forest site type system since it has the capability to consider different ecological gradients at different levels of classification. For example, stands can be first allocated into fertility classes by their moisture regime, secondly by their nutrient conditions, and at last according to their dominant tree species. In other words, clustering hierarchy implies a multidimensional data structure. The divisive method of hierarchical classification also permits the reduction of species to be taken into account simultaneously, because the classification proceeds successively from the main division to the subsequent levels. However, such a successive division soon leads to subtle and obsure clusterings which can neither be interpreted ecologically nor identified in the field. Since one of the major aims of the present study is to develop an applicable key for allocating stands into operational groups representing different site conditions, these finer features are unimportant in relation to the topmost divisions. The overall pattern of major differences in vegetation composition that are significantly related to differences in the environmental gradients is just what the forest site type classification seeks to express.

Any model that assumes a linear relationship between species' success and environmental variables is inappropriate for methods relating the biological data to the environmental data (Green 1979). Such a relationship is also assumed by multivariate methods such as canonical correlation, principal component and factor analyses when both biotic and abiotic variables are included in the same analysis. However, linear structural modelling such as in LISREL (Jöreskog & Sörbom 1981) seems to provide an effective tool to handle both biotic and abiotic factors simultaneously in a causal context (Kuusipalo 1984b). In the present study the first stage of the analysis was the efficient reduction of species abundance data by means of divisive clustering. The resulting clusters are characterized by relatively homogeneous species-assemblages that ought to be related in some manner to the environmental variables. A very simple approach is to carry out a one-way analysis of variance for each environmental variable (Table 10, see also Green & Hobson 1970), or for linear combinations of the environmental variables (Kuusipalo 1983b), in order to determine whether the clusters differ significantly from each other in their mean values on these measured or latent variables.

Evaluation of the significance of cluster separation and interpretation of this separation was done in the present study using canonical discriminant analysis. There are, say, two clusters of samples, A and B, each presumably with a different species composition, and a set of environmental variables, say, x_1 and x_2. In such a simple case, the discriminant function is the linear combination $b_1x_1 + b_2x_2=0$, with the b_j such that the separation of the clusters is maximized. If, say, $b_2>b_1$, the conclusion is that the environmental variable x_2 contributes more to the separation. Thus the assumed linear relationship is among the environmental variables, but not among the biotic variables nor between the biotic and environmental variables. The distribution of the biotic variables (the species-assemblage sample clusters) on the environmental variables is assumed to be roughly multivariate normal. However, if no formal tests of significance are made, even this assumption is unimportant (Morrison 1969). In the present study, a stepwise variable selection procedure was used (see Chapter 4.2.). It should be noted, however, that the method used in variable selection not necessarily involves any correct ranking with correlated variables (Green 1979, p. 117).

The relationship between vegetation clusters and the environmental conditions they characterize can now be studied by plotting the clusters in the reduced discriminant space. Usually the individual samples belonging to different clusters are plotted and the configuration is examined in order to see whether and how well the functions discriminate between the clusters of samples. In the present study, however, the material and the clusters into which the samples were assigned were so large that a visual display of all the samples plotted against discriminant axes would be confusing rather than informative. For this reason, only the cluster centroids were plotted. This is not a statistically satisfactory procedure, because the between-cluster overlap is not shown and significance can not be evaluated by visual display nor by formal tests. Thus the display is of explanatory value only (cf. Bradfield & Scagel 1984).

The confounding of variables is often characteristic of spatial relationships between biotic and environmental variables. This usually arises as a result of strong intercorrelations of environmental variables (Eisenbeis & al. 1973, Green 1979). Descriptive field sampling alone cannot show whether a statistical relationship between a species distribution and, say, soil texture has a direct causal basis (Grime 1965, cf. Sepponen 1985). Distributions of species on environmental gradients may not be solely explained in terms of the environmental variables, even if all the relevant ones are considered. The effect of competition or other intrinsic biological variation can easily be missattributed to environmental variation in a descriptive study (Leonard 1970, Harper 1977). The difficulty in actually separating social and environmental causes of species associations is emphasized by Cole (1957). Finally, frequent zero-abundances of species can pose serious interpretation problems. If a species is present, one knows that it can live in that location, but the absence of that species from two samples need not indicate environmental similarity of the samples.

Fortunately, the environmental requirements of forest plants are rather well known (e.g. Kujala 1926a, 1926b, Ellenberg 1974, Persson 1981) and, as emphasized by Cajander (1949), the understorey vegetation of forest stands in Finland usually consists of enough species for definition of the vegetation type. The type of understorey vegetation can thereafter be related to certain environmental conditions rather reliably. This can be seen from the results of this study, too. Each of the clusters cover a certain range of the major gradient of vegetation variation. Although misclassifications evidently exist, these can be included in the random error variance which must be accepted. Environmental correlations of clusters need not be related to individual site characteristics, but merely to the underlying, latent causes of species assemblage. Canonical discriminant analysis seems to provide an effective tool for this, giving an overall view and revealing the relative importance of the factors underlying the environmental control of the spatial pattern of vegetation. An alternative approach, DISCRIM (ter Braak 1982) is less effective and informative, and should be used only in cases where only descriptive, binary or rough ordinal-scale data on environmental conditions are available.

In conclusion, it seems that many advantages are gained by applying ordination-based hierarchical classification instead of direct classification such as the traditional Cajanderian one. Combined with arranged tabulation of vegetation (Appendix), divisive hierarchical clustering allows detection of the maximum number of clusters which can be recognized reliably and reduction of the number of indicators which must be taken in account at each step. Estimation of the optimal level of classification can be done by employing external criteria such as site index, nutrient status or any other characteristics which are related to the purpose of classification. One disadvantage of all classification methods is that they can only be used to assign an individual forest stand to one of the few rough categories of vegetation response to environmental gradients. It is not possible to define the actual location of an individual stand along a gradient. For instance, the nutrient status of a site assigned, say, to cluster 2 may be close to either that of the sites included in cluster 1 or to that of the sites included in cluster 3.

The overlapping clustering methods (Noy-Meir 1973, Carleton 1979, Carleton & Maycock 1980) can provide more flexible characterization of vegetation noda through their ability to produce continuous scale affinities for samples and species to different noda (Noy-Meir & Whittaker 1978). When combined with environmental measurements e.g. by linear structural modelling, such nodal component analysis could provide a more exact characterization of environmental conditions by vegetation criteria. Since each axis can be interpreted (and named) independently, any number of axis can be used and interpreted, and the relationships between them, and between them and environmental characteristics, can the be examined. However, a classification system based on such an analysis would be difficult to create because the noda tend to overlap and are not sharply bounded. The application of such a classification system in the field would be laborious and difficult. The required information could certainly first be collected in the field and the affinities of the stand to different noda computed afterwards using a computer programme designed for this purpose.

6.2. Theoretical implications

6.2.1. Plants as site indicators

The main sources of environmental control of vegetation can be summarized as follows: (a) climatic control, (b) edaphic control and (c) disturbance (including historical and cultural factors) and the subsequent succession.

The climatic control of vegetation has received considerable attention in Finland (e.g. Kujala 1938, Kalela 1961, Ahti & al. 1968). No evidence of differences caused by climatic gradients could be found in the present study material. This supports one of the basic presumptions of the study approach, i.e. that climatic control is of minor importance within the macroclimatical region under consideration. Since the present material was confined to closed, relatively mature forest stands only, no differences induced by successional stage or any genuine disturbance (clear-cutting, forest fires) were found in the vegetation analysis. However, it is possible that part of the variation within the vegetation growing on mesic sites is affected by earlier land use. In eastern Finland, especially, these sites have quite recently been subjected to slash-and-burn cultivation. The sites which were unsuitable for cultivation have been left untouched, while on suitable sites the area was burnt over, the soil receiving an ash fertilization which still may affect the vegetation composition. Forest vegetation has also been affected by the intensive use of woodlands for pasture (Lampimäki 1939). Although a minor part of the variation in vegetation composition may also result from the absence of certain species for historical biogeographic reasons (Kalliola 1973 and references therein), the site factors evidently play the decisive role. The variation between the different study areas (Fig. 1) can be explained almost completely by the differences in soil characteristics such as the distribution of superficial deposits and the origin of the parent material.

It thus appears that the plants do serve as good indicators of soil-site qualities. However, only a relatively rough classification can be performed on the basis of vegetation characteristics due to the limited predictability of the occurrence and abundance of forest plants. This limitation arises mainly from intrinsic biological variation caused e.g. by dispersal processes (Oinonen 1967a, 1968, 1969, 1971, Harper 1977), by continual, small-scale disturbances which prevent competitive displacement (Drury & Nisbet 1973, Connell 1978, Huston 1979), and from the more or less patchy distribution of environmental resources (Troedsson & Tamm 1969, Hanawalt & Whittaker 1976, Tilman 1982).

As discussed e.g. by Werger & Maarel (1978), species are more specific environmental indicators near to the margins of their distribution area. Near to the centre of a species' distribution area, the plant is well adapted to the environmental conditions and is thus strongly competitive to other species. Towards the margins, the environmental factors gradually change and the tolerance limits of the species for these factors are reached one by one, until one factor becomes critical and determines the occurrence or absence of a species. Species therefore characterize the site more distinctly near to the margins of their distribution area (Vinogradov 1965, Werger & van Gils 1975, Holzner 1978, Willems 1978).

Plant species tend to form ecological groups characterized by rather similar resource requirements and tolerance limits (Ellenberg 1977, Grime 1977, Tilman 1982). At a certain threshold level of e.g. nutrient availability, a whole group of species with more or less similar nutrient requirements begins to succeed at a time. Discontinuities encountered in vegetation gradients thus do not necessarily correspond to environmental discontinuities, but rather to the tolerance limits of groups of species with quite similar requirements for some critical limiting resources governing their competitive ability (Tilman 1982, 1985).

In a larger context, the present material represents only a narrow sequence of the northern temperate forests. The two types of the northern temperate forests, boreal coniferous and nemoral deciduous forests, are ecologically and floristically strongly contrasted, having separate origins and different evolutionary histories (Pielou 1979). Most of the species which appear to be ecologically rather indifferent in the present material have their central distribution area within the boreal coniferous forests, and they tend to dominate or at least stably co-occur with the dominants in all but somewhat marginal habitats. These species are regionally common, locally abundant, and evidently well spaced-out in niche space (*sensu* Hutchinson 1957). According to Hanski (1982), this kind of species should be called a core species. In the present material, the typical core species are e.g. *Vaccinium myrtillus, V. vitis-idaea, Deschampsia flexuosa, Calamagrostis arundinacea, Luzula pilosa, Trientalis europaea, Pleurozium schreberi, Hylocomium splendens, Dicranum polysetum* and *D. majus*. It should be noted that the tolerance limits and optimal resource supply ratios (*sensu* Tilman 1982) of these species do not coincide but are relatively near to each other. For instance, *Vaccinium vitis-idaea* reaches its maximum abundance in somewhat better light conditions than *V. myrtillus*, but requires at the same time less nutrients to reach its maximum growth rate (Ingestad 1973). If the optimal resource ratios of two species coincide completely, one of them will competitively displace the other, depending upon the initial situation (Tilman 1982).

Demanding soft-leaved herbs which best indicate nutrient-rich sites in the present material have their central distribution area and reach their maximum abundances in the southern nemoral forests, whereas boreal coniferous forests can be regarded as their marginal distribution area (cf. Hultén 1971, Ellenberg 1974). Compared to the above core species, they generally have higher nutrient requirements, but are at the same time more shade-tolerant (Kujala 1926a). In the present material, this kind of species are e.g. *Oxalis acetosella, Viola riviniana, Carex digitata, Melica nutans, Veronica officinalis* and *Anemone nemorosa*. In addition, most ferns (e.g. *Dryopteris carthusiana*) indicate the sort of humid microclimatical conditions which are encountered in the dense spruce-dominated forests growing on moist, fertile soils (cf. Sissingh 1982).

Our forests show the same kind of species-resemblance connections to other major types of ecosystems, too. In the present material, species indicative of very moist conditions have their optimal resource supply relations within mire ecosystems, which differ fundamentally from the upland forests in their edaphic conditions. Indicator species for paludification are e.g. *Sphagnum* spp., *Polytrichum commune* and *Carex globularis* (see Eurola & Kaakinen 1978). Species indicative of the very driest sites in the present material, e.g. terricolous lichens such as *Cladina* spp. and *Cetraria islandica*, and dwarf-shrubs such as *Calluna vulgaris* and *Arctostaphylos uva-ursi*, have their optimal conditions within well-lit and physiologically dry, usually open habitats (Gimingham 1960, 1978, Oksanen & Ahti 1982, Oksanen 1984).

In conclusion, several ecological groups of species can be distinguished in the vegetation growing in upland forests of southern Finland. In addition to the core species of these coniferous, boreal forest habitats, there are groups of species which indicate some kind of marginal, i.e. extraordinary fertile, moist or dry conditions. The resource supply ratio (for terms, see Tilman 1982) of these marginal forest habitats fits well to the equilibrial requirements of species which have their evolutionary origin in ecologically fairly similar habitat or ecosystem complexes (i.e., deciduous nemoral forests, mire ecosystems, or habitats such as treeless heaths, sand dunes or rock outcrops). In other words, these species have colonized "islands" within an environment that is in most places unsuitable for them. I would term such species "marginal species" in contrast to core species; "satellite species" (Hanski 1982) is not a valid term, because it refers to non-equilibrium species, whereas I consider marginal species to have arrived at a state of equilibrium in the habitat "island" they have colonized. These terms are, of course, of operational and descriptive value only; other ecological groupings of species could be theoretically justified as well (see e.g. various descriptive methods referred by Shimwell 1971).

In comparison with marginal species, core species are relatively unreliable indicators of site quality. Many of them are completely constant, fairly abundant and often dominant species over a wide range of variation in site conditions. Since many of them are limited by light rather than soil resources, even considerable differences in their abundance relationships may be misleading as far as soil properties are concerned (e.g. differences between clusters 3 and 4 in the present study). In contrast, marginal species are plausible indicators of site qualities, because their occurrence and abundance is often limited by a single soil resource. For instance, many demanding herbaceous plants occur only on lime-rich habitats. The occurrence of mire plants in upland forests is strictly limited by soil moisture. *Cladina* lichens are confined to dry habitats, because they are heavily suppressed by mosses in more moist habitats (Oksanen 1983). Hanski's (1982) non-equilibrium satellite species, e.g. the weeds from cultivated land that often occur in forests near fields and settled areas, are the worst indicator species since their occurrences and abundances are governed by random processes rather than by site qualities.

According to the theory of island biogeography (MacArthur & Wilson 1967), the number of marginal species should be greater in large than in small distinct marginal habitats within upland forests, and the number of marginal species should decrease with increasing isolation of the habitat from the species' core habitats. Hanski (1982) further suggests that the probability of local extinction is a decreasing function of distribution. In addition to the site conditions, the presence and absence of a marginal species is thus dependent upon the size of the habitat, the distance from other suitable habitats, the geographical distribution of the species, and the efficiency of the species' dispersal.

To be applicable to forest site evaluation, an indicator species must satisfy two important requirements: it should reflect site conditions reliably, without being too highly affected by any random variable, and it should be sufficiently constant on sites suitable for it within the region where it is to be applied as an indicator. The size of a forest site, as well as its state of isolation from other sites of corresponding quality, are random variables which evidently affect the constancy of an indicator species. Thus it may be absent or extinct on sites where it should be present judging by the site conditions. Inside the geographical distribution limits of an indicator species, local interactions should largely determine its occurrence and abundance, but towards the margins regional distribution becomes a variable factor and may influence local abundances.

6.2.2. Resource competition in forest environments

According to Tilman's (1982) equilibrium theory of resource competition, each plant species is a superior competitor for a particular proportion of the limiting resources. Each plant species has its optimal resource ratio which enables the species to dominate on those sites where the resource supply ratio corresponds to that of the species. Therefore, community composition should differ between sites whenever the relative availability of two or more limiting resources differ. As emphasized by Harper (1977), competition can occur only between neighbouring individuals. It is very unlikely that each plant of a given habitat will gain the same rate of supply for each resource. For terrestrial plants, small-scale variation in soil type, moisture and topography should cause individual plants in a habitat to experience different average rates of resource supply. Solar radiation tends to reach the forest understorey unevenly, patches that receive different amounts of light constituting an additional mosaic pattern. This means that a large number of species can coexist in a spatially heterogeneous environment such as a forest habitat. For a given level of resource richness, increased spatial heterogeneity should thus lead to increased species richness.

Each plant species has its intrinsic equilibrial requirements for the essential resources the species consume. These requirements determine the availabilities of essential resources for which the reproductive rate of a species equals its mortality rate. The growth rate of a species is determined by the one resource in shortest supply relative to need. Consider a species which require two essential resources, say, R_1 and R_2. In the absence of competition, the species is capable of increasing its population density in the resource availabilities that fall inside the region in the two-dimensional resource space limited by the species' equilibrial requirements for these two resources. At any point within this region, i.e. in any habitat suitable for the species, the species would equilibrate at the population density for which its consumption of the limiting resources just balanced supply. At a given level of resource richness, the species reaches its peak population density at the point where the species is equally limited by availabilities of R_1 and R_2, i.e. when the ratio R_1/R_2 equals to the species' optimal resource ratio (for further details, see Tilman 1982, 1985).

In the presence of competition, the population density distribution of a species is truncated by the competitive displacement of the species which are superior competitors over a certain range of resource supply ratio. Consider two species, A and B, competing for two essential resources, R_1 and R_2, species A having the lower equilibrial requirement for R_1 and species B having the lower equilibrial requirement for R_2 (see Tilman 1985, p. 829). It is now possible to define three states of equilibrium prevailing at different points of the resource supply ratio R_1/R_2: (1) Habitats with low supply rates of R_1 but high supply rates of R_2 would be dominated by species A, with species B extinct because species A would reduce R_1 to a level insufficient for the survival of species B. (2) Habitats with low supply rates of R_2 but high supply rates of R_1 would be dominated by species B, with species A extinct because species B would reduce R_2 to a level insufficient for the survival of species A. (3) Habitats with intermediate R_1/R_2 ratios would have the two species stably coexisting, because both species are limited by a different resource, species A by a low supply of R_1 and species B by a low supply of R_2. The coexistence is stable because each species consumes relatively more of the resource that limits it at this two-species equilibrium point (for experimental evidence of the theory, see Tilman 1982).

In plant communities growing on relatively fertile soils, many studies have suggested that light, especially that available at the soil surface for seedlings and shoots, is an important limiting resource (Anderson 1964, Grime & Jeffrey 1964, Horn 1971, 1975). In forests, competitive ability for light, often referred to as the degree of shade tolerance, is frequently cited as a determinant of species replacement (Kujala 1926a, 1926b, Decker 1952, Horn 1971, Ellenberg 1974). Since light is a directional resource, taller plants intercept more light. Givnish (1982) reported that forest understorey plants followed a pattern in which taller species are dominant on fertile soils and plants of low stature on poorer soils. Tall trees are of exceptional importance as community dominants: they strongly affect the light climate below the canopy but are never suppressed by lower vegetation strata (except at their seedling stage in naturally regenerating stands). Therefore, shade-tolerant species dominate the understorey vegetation under severe shading by the dense tree canopy which often develops on fertile soils. According to Horn (1971), species with a multi-layered leaf distribution are superior competitors to species with a mono-layered leaf distribution at high light intensities, but inferior competitors at low light intensities. The soft and large leaves of shade-tolerant forest herbs are usually densely packed in a single uniform layer and do not overlap considerably. In contrast, the foliage of many dwarf-shrubs is more or less multi-layered with small and often drought-resistant leaves loosely scattered among several layers (Horn 1971).

To acquire more of soil resources, a plant must allocate a large proportion of its potential growth to developing its belowground structure for nutrient uptake. A plant with effective nutrient uptake owing to an extensive root system and mycorrhizal association would be favoured over a plant that allocated more to its aboveground photosynthetic structures because the former would acquire more of the limiting soil resource and thus reproduce more rapidly on poorer soils (Orians & Solbrig 1977, Chapin 1980, Persson & al. 1980, Raudaskoski 1984). On very poor soils, species characterized by a low intrinsic growth rate would be favoured over species with a high intrinsic growth rate, because the latter require more nutrients. Dwarf-shrubs are perennial chamaephytes with small and often perennial leaves. Hence they grow slowly and use the available nutrients economically (Bormann & Likens 1979). Forest herbs are mostly either geophytes or hemicryptophytes with annual shoot and foliage. Therefore, in plants with such a growth form more nutrients must be allocated to maintain the fast growth rate in the above-ground biomass. For instance, in rich, well-lit birch stands, about 20 % of the total annual nitrogen consumption of the stand is bound by the grass and herb vegetation (Mälkönen 1977). It should be noted that the annual consumption of such a rich stand is almost equal to the amount of nitrogen available in the soil (Nömmik 1968, Viro 1969, Mälkönen 1977, Havas 1980, Mikola 1980).

Nitrogen is evidently the major limiting soil resource in the upland forests of Finland (Viro 1967, 1969). Nitrogen fertilization increases tree growth even in forests on relatively fertile soils (Albrektson & al. 1977, Kukkola & Saramäki 1983). In addition to nitrogen, water is evidently an important soil resource. However, since the water-holding capacity, total nitrogen, and the nitrogen mineralization rate of the soil are highly correlated, the relative importance of nitrogen and water limitations is difficult to determine (e.g. Robertson & Vitousek 1981). In forest habitats there is a considerable mosaic pattern in the total nitrogen content as a result of different small-scale variations in soil properties and processes (Mikola 1955, Troedsson & Tamm 1969, Tilman 1982). However, only a minor part of the total soil nitrogen is in an available form (Nömmik 1968). In forest soils, nitrogen availability is mainly dependent on the rate of release of ammonium ions from organic compounds in the soil (Tamm & Petterson 1969). On poor soils, drought and other factors affecting the mineralization of the organic material greatly slow down the rate of release of ammonium ions and may even reduce the nitrogen availability from its initial level (Aura 1984).

As far as the mineral nutrition of the cryptogams (terricolous mosses and lichens) is concerned, it is a commonly held view that the atmosphere is the sole source of nutrients (Tamm 1953, Brown 1982). Nutrients may also be supplied from the upper soil layers through ectohydric mechanisms (Buch 1945, 1947). However, the cryptogams are considered to compete for light and space mainly, both with other cryptogams and with vascular plants (Kujala 1926b). Cryptogams are generally more abundant on poor soils where they are not suppressed by higher plants. On poor soils, the competition between cryptogams (especially between mosses and lichens) for light and space largely modifies the general character of the understorey vegetation (Oksanen 1983).

In conclusion, the major limiting resources for upland forest habitats are often a soil resource (especially nitrogen), and light. Furthermore, these resources are usually naturally inversely related, the habitats with poor soil having high light availability and the habitats with fertile soil having low light availability (Tilman 1985). This inverse relationship appears to be evident according to the results of the present study, too (Tables 7 and 8, Figs. 8 and 9). The negative correlation between these two essential resources arises as a result of the fact that total plant biomass increases along with a rise in the availability of nitrogen, and that light becomes increasingly limiting at the soil surface. On poor soils, plant biomass (in forests, particularly that of the tree stand) would be low, causing little attenuation of light. Under such conditions, competition should primarily be that for the limiting soil resource. On fertile soils, competition for light tends to be more important. For historical biogeographic reasons and as a result of silvicultural activities, there are practically only two important forest-forming tree species in southern Finland, pine and spruce, both capable of dominating in a wide variety of sites with different understorey associates. Competition and niche diversification among the tree species does not take place to the extent than it does e.g. in North America, where there are more of forest-forming tree species (cf. Horn 1971, Heinselman 1981, McCune & Allen 1985).

In the present study, the tree stand is treated essentially as an environmental factor, not as a part of the plant community. However, the effects of the tree stand on understorey vegetation can be understood as an outcome of competition controlled by the soil resource/light ratio. Light becomes increasingly limiting through the increment of stand density on moving from poor to fertile soils. The foliages of pine and spruce differ markedly from each other in their optical properties. At a given stand density, the illumination level under a spruce canopy is much lower than that under a pince canopy (Kuusipalo 1985). Spruce cannot form stands on poor soils as pine can, but when the availability of soil resource limiting its growth increases, spruce rapidly begins to predominate over pine owing to its higher competitive ability. Consequently, the change in light conditions along a nutrient supply gradient appears to be fastest at a certain point equivalent to a moderate supply of nutrients where spruce takes over. In addition, spatial heterogeneity increases considerably because moderately shaded stands are more diverse in differently illuminated patches than more open stands (Kuusipalo 1985).

6.2.3. Forest habitat type as an outcome of resource competition

In the following, it is suggested that (1) the major limiting resources for forest habitats in southern Finland are nitrogen and light, and (2) these resources are naturally inversely related, as presented above. Furthermore, it is assumed that the forest plant species are not evenly distributed in the two-dimensional resource space, but tend to form ecological groups according to their equilibrial requirements and optimal resource ratios for light and nitrogen availabilities. The groups can be summarized as follows (note that marginal species indicating paludified forest sites are not considered here):

(A) Core species of forests on mineral soil in southern Finland. These are relatively mesophilous plants with moderate or low nutrient requirements, and are ecologically indifferent over a wide range of site conditions. Characteristic core species are e.g. *Vaccinium myrtillus, V. vitis-idaea, Deschampsia flexuosa, Calamagrostis arundinacea, Luzula pilosa, Trientalis europaea, Melampyrum pratense, Pleurozium schreberi, Hylocomium splendens* and *Dicranum polysetum.*

(B) Marginal species of fertile upland forest sites. These are mesophilous, shade-tolerant species with relatively high nutrient requirements and are strictly confined to fairly nutrient-rich soils. Some of these species do not actually have very high nutrient requirements but require the sort of humid microclimate which is encountered in mesic sites under severe shading by the tree canopy. Species characteristic of this group are e.g. *Oxalis acetosella, Dryopteris carthusiana, Carex digitata, Viola riviniana, Melica nutans* and *Veronica officinalis.*

(C) Marginal species of poor upland forest sites. These are xerophilous, light-demanding species with very low nutrient requirements and are confined to nutrient-poor, dry soils with a relatively open or sparse tree canopy. Species characteristic of this group are terricolous lichens such as *Cladina stellaris, C. rangiferina, C. arbuscula* and *Cetraria islandica,* and dwarf-shrubs such as *Calluna vulgaris* and *Arctostaphylos uva-ursi.*

Hypothetical, schematic model of the formation of forest habitat types as an outcome of competition for two essential resources is presented in Fig. 10. The total nitrogen content in the humus layer is the abscissa (N), and the canopy coverage, which determines the light availability, is the ordinate (L). The group means for the total nitrogen content and canopy closure of sample clusters 1–6 are used as the coordinates (N, L), respectively, when plotting the clusters against the two-dimensional resource space. The clusters are combined pairwise into major habitat types as follows: (I) Fertile sites included in clusters 1 and 2, approximately representing the *Oxalis-Myrtillus* site type forests; (II) Intermediate sites included in clusters 3 and 4, representing both spruce and pine-dominated forests of the *Myrtillus* site type; (III) Poor sites included in clusters 5 and 6, representing approximately the *Vaccinium* site type and the still poorer forest site types. Because each cluster represents a heterogeneous group of forest habitats with different ratios of nitrogen and light availabilities, the major habitat types (I–III) are indicated by interpolated regions with a diameter determined by the standard deviation of each cluster mean for canopy coverage and nitrogen content. Accordingly, each region indicates a heterogeneous habitat type and should be understood as a cloud of resource supply points, or microsites *sensu* Tilman (1982).

Following the conceptual framework of Tilman (1982), each species capable of occupying microsites within the two-dimensional resource space defined in Fig. 10 should have different equilibrial requirements for the two limiting resources. The species thus have a trade-off in their resource requirements, such that the superior competitor for one resource is an inferior competitor for the other, and all the competing species have trade-offs such that the species are inversely ranked in their requirements for the two limiting resources. Consumption vectors determined by the amounts of the resources consumed by each species per unit time define the types of habitats in which one species competitively displaces the other ones, and in which two ecologically adjacent species stably coexist at equilibrium. In all cases, an equilibrium will occur only if resource consumption equals resource supply and if the reproductive rate of each species equals its mortality rate.

The broken lines in Fig. 10 define the approximate regions of the resource space in which individual species assigned to ecological groups A, B and C are able to exist. Within the regions indicated by C, A and B, respectively, species assigned to the corresponding ecological groups tend to dominate. Within the intermediate regions, species belonging to either of the two ecologically adjacent groups are able to coexist stably (A+B or A+C, but not B+C). In high light intensities but low availabilities of nitrogen, marginal species of poor sites (group C) dominate. In high availabilities of nitrogen and low light intensities, marginal species of fertile sites (group B) dominate. Core species (group A) dominate on sites characterized by intermediate availabilities of both light and nitrogen, co-occur with marginal species of group B on moderately fertile but markedly shaded sites, and co-occur with marginal species of group C on considerably poor and well-lit sites.

The cluster centroids (6–1) are linked by a solid line that constitutes the approximative resource supply gradient ranging from poor soils to fertile soils. Within habitat type II (clusters 3 and 4), there is a downward turn in the resource supply gradient indicating that at a certain threshold level in nutrient availability, spruce takes over as a dominating tree species and there is a consequent steep decline in light availability. It should be noted that the variation range in light availability is very large within habitat type II, which includes both spruce and pine-dominated stands. However, the variation amplitude in nitrogen availability is relatively narrow. This means that the considerable internal heterogeneity of habitat type II is mainly a result of variation in the light regime. The variation ranges in both the light and nitrogen availabilities is markedly large within the pine-dominated, poor sites included in habitat type III. On the contrary, habitat type I covers a wide range of variation in nitrogen availabilities, but is relatively homogeneous as far as the light regime is concerned. Both habitat type I and habitat type III overlap considerably with habitat type II in the presented two-dimensional resource space.

Habitat type III represents pine-dominated stands on poor, largely sandy or shallow soils (cf. Table 5) and is generally characterized by a high light intensity and a low nitrogen availability. The light climate varies

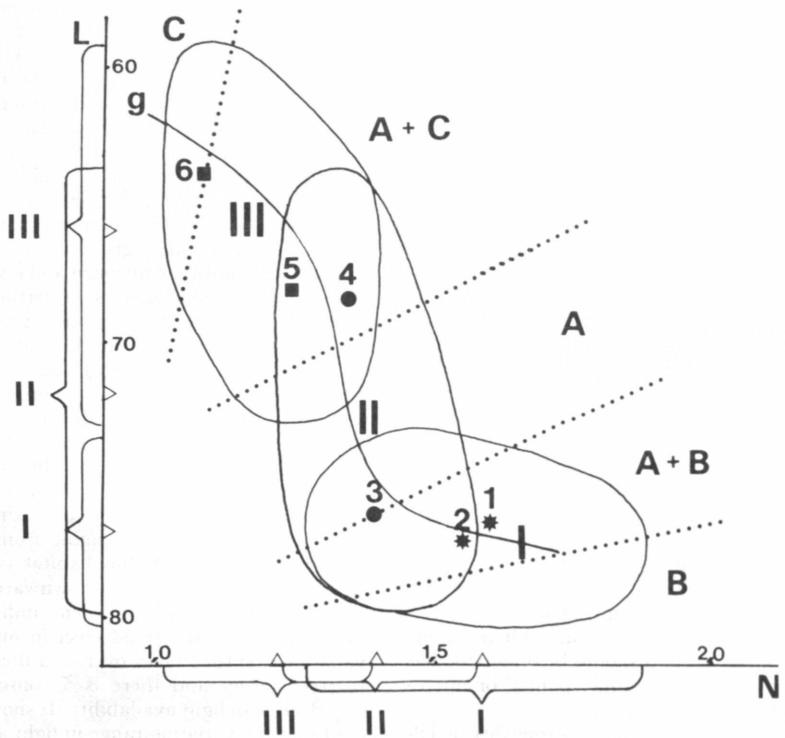


Fig 10. Hypothetical model of the formation of forest habitat types as an outcome of competition for two limiting resources. Habitat types I (clusters 1–2), II (clusters 3–4) and III (clusters 5–6) are presented in a two-dimensional resource space determined by the cluster means and the standard deviations for light (L) and nitrogen (N) availabilities. The dimension of the L axis is percentual canopy coverage, and the dimension of the N axis is total percentage of nitrogen in air-dry humus. The habitat type means and standard deviations are indicated on both resource axis. The broken lines define the approximate regions of the resource space in which individual plant species assigned to different ecological species groups are able to exist at equilibrium. C denotes the predominance of marginal species of poor forest sites, A denotes the predominance of the core species, and B denotes the predominance of marginal species of fertile forest sites. A+B and A+C denote stable coexistence of the corresponding species groups, respectively. Gradient G indicates the approximate interrelationship between light and nitrogen availabilities in the present material; the downward turn within habitat type II is a result of change in tree species composition. The densicy distributions of individual species assigned to different ecological groups are assumed to follow a trade-off pattern along the gradient G, which determines the supply ratio of light and nitrogen.

considerably from sparse stands of the extremely poor sites to denser stands of the slightly more nitrogen-rich sites. The sites of this habitat type assigned to cluster 6 are predominated by plants of species group C (lichens and other xerophilous plants), while those sites assigned to cluster 5 have xerophilous plants dominating on well-lit microsites, and coexisting together with core species of group A on more shaded microsites. It should be noted that although habitat type III covers a relatively large area of the presented resource space, thus including a great number of microsites, the total number of species is low and the vegetation consequently relatively monotonous. This is a result of the fact that the total nitrogen content does not reflect the nitrogen availability limited by low average moisture content of the soil within this habitat type.

Site conditions within habitat type I are inversely related to those within habitat type III: a high nitrogen availability associated with a low light intensity is characteristic of this habitat type. The light climate is relatively uniform: well-lit microsites are infrequent due to the predominance of spruce on most sites included in this type. The major direction of variation reflects the level of nitrogen availability. Demanding herbaceous plants tend to predominate on the most nitrogen-rich sites of this type since they have a competitive advantage in their low light requirements. However, on most microsites core species of group A coexist with plants of species group B. In contrast to habitat type III, habitat type I is vegetationally very heterogeneous, although it covers smaller area of the presented resource space and clusters 1 and 2 appear to be close to eachother as far as the availabilities of light and nitrogen are considered. This is the result of the fact that nitrogen is not the only one of the limiting resources constituting habitat heterogeneity: as can be seen e.g. from Fig. 9, clusters 1 and 2 differ from each other markedly in their average calcium content and the amount of raw humus in the uppermost soil layer.

The theory of resource competition in a heterogeneous environment applied in this chapter makes several implications which can be used in the description and interpretation of the forest vegetation and its ecological control. Although the model presented in Fig. 10 is strongly deductive and simplified, referring only to two essential resources and three assumed species groups, it provides a basis for deriving some major generalizations concerning the formation of forest understorey vegetation.

(1) The major limiting resources for forest vegetation are the availabilities of nutrients and light. These are naturally inversely related to each other so that the supply ratio of light and nutrients is governed majorly by the changes in tree species composition and stand density. Stand biomass gets larger and light becomes increasingly limiting along with an increase in the nutrient supply. At the same time, the number of resource supply points (spatial heterogeneity) and the number of species potentially capable of occupying forest habitats increases.

(2) The core species group includes plants that are well adapted to the conditions prevailing in northern boreal forests and well spaced-out in niche space. Most of the core species are capable of developing different phenotypes to meet various ecological conditions within boreal forest habitats, and are consequently ecologically indifferent and strongly competitive to the marginal species. Marginal species have their optimal conditions within habitats other than the types of forest in question, and their phenotypical amplitude is primarily focused to meet a different range of variation in ecological conditions.

(3) As a consequence of the above phenomena, competitive displacement modifies the community composition gradient to so as give a series of apparent discontinuities. Changes in community composition on nutrient-poor sites are primarily reflected in the abundance relationships between only a few species. On moving to more nutrient-rich sites, the changes in community gradient are reflected more and more in the species composition. This is because a restricted availability of nutrients allow only a few species to survive on dry-and-poor soils, and the community composition is governed majorly by the tolerance limits of the species. In contrast, numerous species can survive on mesic, fertile soils, and the community composition is governed majorly by competitive displacement.

(4) A slight change in the availability of a limiting soil resource can cause a complete change in the community composition, the effect being most marked within intermediately fertile sites, where the change in the soil resource is often associated with a change in tree species composition and consequent abrupt change in the resource supply ratio. Hence it follows that all site classification systems based on the identification of plant communities would be relatively rough. Species characterized by high light but low nutrient requirements are capable of occupying much more fertile sites at high light availabilities than at low light availabilities. On the other hand, species with low light but high nutrient requirements are able to dominate on poorer soils at low light availabilities often associated with more humid microclimatical conditions.

6.3. Ecological appraisal of forest site classification

The Finnish forest site type system consists of an assumed normal series with typical site types, the untypical stands being considered as minor deviants from the typical types. As such, the system appears to constitute an unidimensional series of equally important types of forest stands with a gradually increasing productive capacity that reflects an increase in the moisture and nutrient availabilities. In practice, the system as a whole is used as a single categorical variable measuring site fertility. Between-type differences in site characteristics are expressed *ad hoc* for the normal stands of each site type, i.e. on the basis of samples collected from selected stands that bear close resemblance to the previously described vegetation types (see Keltikangas 1959 and references therein). This kind of approach almost always leads to the situation where statistical comparisons concerning continuous variables designed to measure site fertility indicate that each site type differs significantly from the adjacent types. As emphasized by Green (1979), independence of errors is an assumption whose violation is both serious and impossible to cure after the data have been collected, and only truly random sampling will prevent that violation; putting samples in "representative" or "typical" places is not random sampling. Furthermore, although additional attributes such as stoniness and degree of paludification are used to characterize the ecological conditions more precisely, the Finnish forest site type system cannot be regarded as a proper ecosystem classification since it only considers economically important, "typical" types of productive forest. Neither can the system be incorporated in or compared with any phytosociological classification system (Keltikangas 1959, Oksanen 1984).

The present study material comprises an essentially random sample of relatively mature forest stands distributed in different parts of southern Finland. As a whole, the sample is representative owing to the mesic forest sites, but less representative owing to the xeric forest sites; this is because the sample is distributed approximately by the same way than the types of forests in the study areas in question. To get the sample more representative, it should be enlargened; stratification before sampling should be inconvenient, because there is no unambiguous way to distinguish between mesic and xeric sites beforehand. An additional fact is that the sample has a limited geographical representativity.

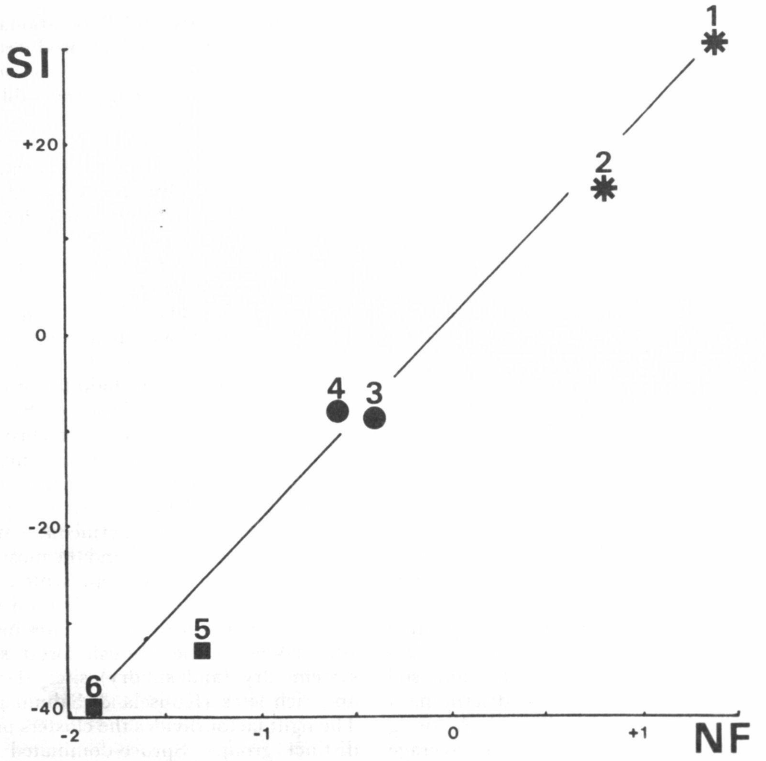
However, the random sampling procedure allows for valid use of multivariate numerical methods; different outliers, intermediate types and "variant" or "vicariant" forest types are all included in the material. The "null hypothesis" determined in the present study is that the vegetation composition is not dependent on the edaphic variation. The alternative hypothesis may seem obvious but, as emphasized by Green (1979), it is a recommendable precaution to reject the null hypothesis first, before proceeding to carry out multivariate descriptive analyses which can yield results that give the appearance of things going on even when applied to data simulated to be completely random. An additional null hypothesis for the classification study should be that the data structure is continuous rather than discontinuous, contrasted with an alternative hypothesis that there are natural clusters of the *n* samples defined by the *p* variables. The decisions were made by checking whether there is any edaphically interpretable variation in the vegetation gradient that is superimposed by logic internal to the numerical method used, and whether the discontinuities revealed by the method reflect any underlying differences in site conditions.

The results show that the main direction of variation in the forest vegetation pattern can be explained by an underlying gradient that majorly reflects nutrient regime. Different analyses lead to fairly similar results, despite their different sample sizes and different combinations of variables. The discontinuities revealed from the vegetation gradient reflect clear differences in site conditions; this was rendered statistically using site index as an external criterion variable. In spite of limitations as regards its applicability, site index provides an effective tool for relating stand productivity to site fertility. In conclusion, the first one of the above vaguely defined null hypotheses can be rejected, as far as it is possible when carrying out exploratory analyses on multivariate ecological data sets (see Green 1979, pp. 12–15). The second one, questioning whether there are natural clusters, requires further consideration.

The relationships between the vegetation clusters, stand productivity (site index) (Table 9, adjusted cluster means) and soil nutrient regime (Table 6, first discriminant function) are illustrated in Fig. 11. A strong linear relationship indicates that the average productive capacity of a mature stand is highly dependent upon the nutrient level, particularly nitrogen availability, and that the vegetation gradient produced reflects productive capacity and nutrient level very well. In addition, nutrient regime/productive capacity centroids of the vegetation clusters are relatively evenly distributed along the corresponding gradient, indicating that discontinuities in the vegetation gradient do in fact discriminate between significantly different fertility classes. However, clusters 3 and 4 indicate equal fertility and nutrient availability. This suggests the already presented implication that these two vegetation clusters represent spruce and pine-dominated stands of the same site type. It should be noted that the concept of site type is used in the strict sense of productive capacity level (Keltikangas 1959), whereas the term habitat type is used here to characterize a group of sites which show similarities in tree stand properties, vegetation composition and soil conditions simultaneously (cf. "operational group" *sensu* Jones & al. 1983). The produced vegetation clusters thus represent one or several habitat types, but do not presumably correspond to the site types.

The second important axis discriminating between vegetation clusters is connected to the light availability as governed by tree species composition and stand density (see Tables 7 and 8). The columns in Fig. 12 represent average productive capacities for habitat types represented by the vegetation clusters (cf. Fig. 11). The position of vegetation cluster centroids in a two-dimensional resource space constituted by the nutrient factor (Table 6) and the light factor (Table 7) are indicated by the base of the columns representing each cluster. The clusters seem to form three distinct groups in terms of stand productivity and nutrient regime: the least productive, nutrient-poor sites represented by clusters 5–6, the intermediate sites represented by clusters 3–4 and the most productive, nutrient-rich sites represented by clusters 1–2 (cf. Fig. 10). This division is rather consistent with the division of sites into major site classes in the Finnish forest site type system: dry (and subdry) sites, damp sites and rich sites (Kuusela & Salminen 1969). The light factor divides the clusters into three distinct groups. Spruce-dominated clusters 1–3 are characterized by a low light availability at the understorey level. These clusters differ slightly from each other in that the stand density increases with increasing productivity (cf. Table 5). Pine-dominated clusters 4–5 indicate a much higher light availability. Pine-dominated cluster 6 clearly indicates the highest light availability; the pine stands within this cluster are much less dense than the pine stands within clusters 4–5. Thus the light factor apparently follow the fertility pattern, except a change in the dominant tree species causes an abrupt change in light availability (cf. Fig. 10).

One other important axis revealed by the discriminant analyses requires further consideration. This is the thickness of humus layer, which decreases along with the nutrient availability on moving from cluster 2 to cluster 6; the total amount of nitrogen is also clearly dependent upon the thickness of humus layer (Table 5). Cluster 1 forms an apparent exception to this rule, because the



NF = Discriminant function F1 (Table 6, Fig. 7), evaluated at cluster means.
SI = Site index (adjusted for the effect of tree species) deviation of the cluster mean from the total mean (0) (Table 9).

Fig. 11. Ordination of the cluster centroids according to their average nutrient level (NF) and stand productivity (SI).

humus material on sites assigned to this cluster is well mixed with the mineral soil, and mull and moder are habitual humus types instead of mor (Table 5). Clusters 1 and 2 both represent productive sites on fertile soils, but they differ considerably from each other as regards the properties of the humus layer. Since the development of the humus layer is closely connected to the species composition and other properties of the vegetation, including the tree stand, one fundamental question is whether the type of humus is a consequence of vegetation composition or vice versa, and to what extent the properties of mineral soil determine the concurrent development of the types of humus and vegetation (cf. Mikola 1955, Sepponen 1985).

One important thing to remember is that although sites included in clusters 1 and 2 occur on fairly similar soils (Table 5), the content of calcium in humus layer is higher on sites assigned to the former cluster. This implies that the calcium content in the parent material should presumably be the causal agent for differences in the types of humus and vegetation between these two clusters.

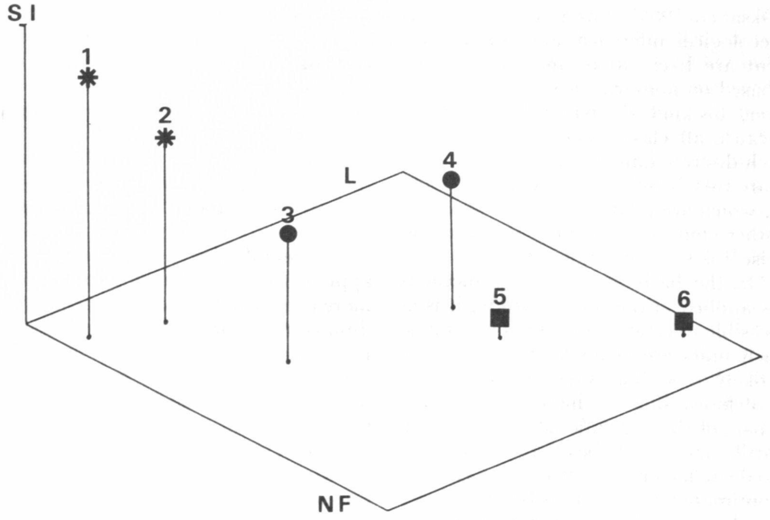


Fig 12. Ordination of the cluster centroids according to their average nutrient level (NF), light availability (L) (canopy closure, Table 7) and stand productivity (SI).

Minerological differences are evident when the study areas I and II (Fig. 1) are compared geologically: soils of a rapakivi granite origin (study area II) are much less fertile than soils of a granodiorite origin (study area I), especially when the effect of the lime factor is considered (Kalliola 1973, pp. 75–77). However, minerological differences could not be rexognized on the basis of the present material, because there are great differences in superficial deposit types between these two areas, and textural properties affect the measured chemical properties of mineral soil to a great extent (cf. Sepponen 1985).

According to e.g. Matthews (1979) and McCune & Allen (1985), it is possible that on similar sites, considerably different types of forest may develop, mostly as a result of successional divergence caused by some historical events. In both of the above-mentioned studies, the evidences are largely based on a considerable within-type variability which occurs when individual sample plots each having a known status in some vegetation-based classification system are ordinated in an environmental space using multiple discriminant analysis with measured environmental characteristics. Corresponding overlap between clusters is also evident in the results of the discriminant analyses carried out in the present study. However, the unexplainable variance implied by broad overlap does not judge one to argue that site conditions are of minor importance as causal agents in the formation of plant communities. As far as the environmental conditions are considered, a site as an unit where a certain type of vegetation should occur is a "black box", of which only indirect and incomplete information can be obtained by measuring measurable environmental variables. Hence it follows that the unexplainable "error variance" is primarily a result of imprecise measurement and suboptimal mathematical models and cannot be used as an argument against the utility of vegetation-based classification systems in estimating site conditions.

As emphasized by Matthews (1979), considerable debate has occurred on the status of plant assemblage-types (i.e. vegetation noda *sensu* Oksanen 1984); this is important, because ecological inference, analysis and experiment are likely to be most meaningful when based on non-arbitrary, discrete units. However, this kind of debate is less meaningful, because all classifications are arbitrary and such discrete units do not actually exist. There are two "black boxes", vegetation and its site, which are related in some manner to each other, but we gain only indirect and imprecise information about these relationships. On the basis of descriptive methods such as applied in the present study, it is at least possible to create units of known status, and such units are of an operational value that is likely to be what is required in classification of forest sites, or habitats. If only a minor part of the vegetational variation can statistically be shown to be attributable to the measured site factors, this at least reveals the major outlines of relationships between vegetation and its site. The clusters described in the present study represent more or less heterogeneous types of forest, each consisting of at least a few different habitat types. One of the major aims of the present study was to approach a kind of "optimal" classification of forest habitat types, and to relate these types to the forest site types. There are two requirements for such an optimal classification: (a) the classes should be relatively unambiguously recognizeable in the field, and (b) the classes should reflect significant differences in site conditions.

Owing to the fact that a random sampling procedure was used, the presented data contain a lot of noise caused by both vegetational and environmental characteristics. This makes the classification and ecological interpretations difficult, but provides an objective view of how the vegetation is distributed within the wide range of site conditions prevailing in the present-day forests in southern Finland. Because one aim of this study was to develop an easily applicable and unambiguous key for allocating all kinds of site, be they "typical" or not, into operational groups related to the site fertility, the whole spectrum of variation met in forest vegetation and site conditions in southern Finland has to be taken into account. The presented material is far from being satisfactorily representative, but it does provide a basis for drawing some general outlines for future development of the forest site classification. As far as the requirements of an optimal classification are concerned, it seems likely that only a relatively rough classification of forest site types can be established on the basis of vegetation characteristics. This is a result of the fact that only incomplete information is obtainable about the relationships between the two "black boxes" discussed above, i.e. vegetation and its site.

In general, the hierarchical classification approach presented in this study allows for a more precise definition of environmental conditions than does simple classification by plant communities. As an approach, it also avoids the drawbacks of the fundamental unidimensionality of the Finnish forest site type system through its ability to consider different ecological gradients at different levels of classification. In actual fact, Cajander (1926) presented a kind of hierarchical system: forest sites are primarily divided into three major classes. These are: (1) The Dry Moss- (and Lichen) Forest Class, (2) The Moist Moss-Forest Class and (3) The Grass-Herb Forest Class. The ecological differences between the major classes are greater than the more subtle differences between individual site types within each class. For instance, the *Vaccinium* site type, belonging to the dry forest class, differs in many ecological respects from the *Myrtillus* site type that belongs to the moist forest class together with the *Oxalis-Myrtillus* site type, the latter being regarded as a more fertile deviant of the *Myrtillus* site type. In subsequent developments of the site type system, the original hierarchical approach has largely been forgotten. However, a hierarchical system would provide an easily applicable key for allocating even untypical stands successively into site types (cf. Jones & al. 1983).

The hierarchical classification presented in this study shows considerable correspondence to the Finnish forest site type system as originally presented by Cajander (1926). A rough outline of the relationships between the produced clusters and the forest site types are presented in Fig. 13. The dendrogramme also shows the approximative vegetational and ecological similarities between the forest site types. "Mesic sites" in Fig. 13 are roughly consistent to the Moist Moss Forest Class of Cajander, whereas "xeric sites" represent a part of the Dry Moss- (and Lichen) Forest

Class. Furthermore, these two major classes can be divided into individual site types. The dendrogramme also presents a key, based on a few plant species of considerable indicator value, for allocating stands successively into operational groups which approach the final site definition. The key, however, is not ready for practical use, but is presented as a generalized scheme of such a practical application not only in site fertility estimation needed in forestry, but also in forest ecosystem classification which is required as a framework in biological studies concerning different components of forest ecosystem.

The applicability of such a successive key depends largely upon the constancy of the species involved as indicators (cf. Pakarinen 1982). TWINSPAN usually considers more than one species (or pseudospecies) as indicators, hence reducing the probability for misclassification. It can be seen from the Appendix that indicator species are seldom completely constant on sites suitable for them. Under certain circumstances it is even possible that all of the potential indicators will be absent at the same time due to the effect of some secondary factor, or a random event, e.g. extremely low light availability in very dense forest stands, or some occasional disturbance. In such cases, it should be possible to find patches where there are traces of the initial understorey vegetation, or to use identification criteria derived from ecosystem components other than the understorey vegetation.

The key (Fig. 13) begins with deciding, whether the stand belongs to the mesic site class or to the xeric one. In this step, particular attention has to be paid to the abundance of herbs and grasses characteristic of the mesic sites, and also to the occurrence of lichens characteristic of xeric sites. It is important to distinguish between pine-dominated mesic sites (cluster 4) and the genuine subdry sites which show similarities in vegetation composition, particularly the frequent occurrence of light-demanding plant species. If the stand is allocated to the mesic site class, the second step is to look for some herb, grass and moss species indicative of nutrient-rich conditions. If these species are present at a sufficient frequency or abundancy, then the decision has to be made whether the stand belongs to the "*Oxalis-Myrtillus*" site type or to the somewhat less fertile transitional class, here termed as MT+ (rich *Myrtillus* type). It should be noted that many highly indicative species are far from being being completely constant and, on the other hand, many constant indicator species may occur over a wide range of sites in suitable microhabitats. Therefore the occurrence of *Oxalis acetosella*, for instance, is an inadequate criterion for allocating a stand to *Oxalis-Myrtillus* site type; only when *Oxalis* is accompanied by other demanding plants such as *Carex digitata*, *Viola riviniana*, etc., or is strikingly abundant, can a site be assigned to that type. However, even a low occurrence of *Oxalis* accompanied by an abundance of e.g. *Dryopteris carthusiana* seem to indicate that a site is significantly better than the genuine *Myrtillus* site type. According to Sissingh (1982), ferns such as *Dryopteris carthusiana* require humid microclimatical conditions which are found in dense spruce stands most frequent on fertile sites. As regards the vegetational differences between spruce and pine-dominated stands of the *Myrtillus* site type, the division is clearly less significant than the preceding divisions. The results thus support Ilvessalo's (1922) opinion that the vegetational differences between pine and spruce stands of the *Myrtillus* type are smaller than those between the *Myrtillus* type and the adjacent forest site types. However, in order to avoid misclassifications of pine-dominated *Myrtillus* site type stands into the xeric site class, the pine and spruce-dominated types should be described separately.

Within the xeric site class, the occurrence and abundance of certain lichens discriminate between clusters 5 and 6, which are here related to the *Vaccinium* site type and the *Calluna* site type, respectively. The latter involves stands which may be related to the *Cladina* site type, while, the former incorporates a lot of stands on shallow soils. However, the material is not sufficiently representative as regards the xeric sites. Since the xeric clusters contains only pine-dominated stands, the study sheds no light on the question of spruce-dominated dry sites discussed e.g. by Keltikangas (1959). Nor were any "feathermoss type" sites, located between the *Myrtillus* and *Vaccinium* site types, recognized from the present material. In southern Finland, this type should occur rather frequently

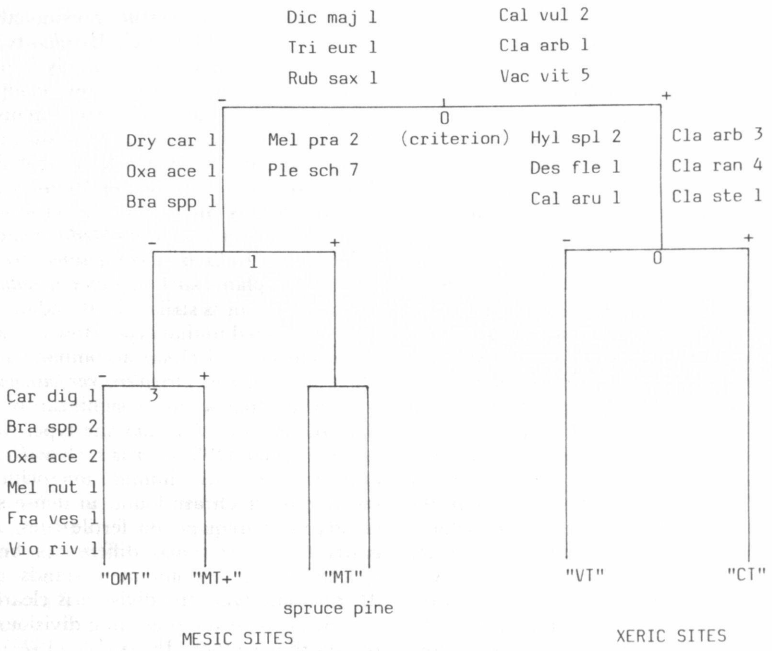


Fig 13. An example of a key to allocate forest stands to operational clusters, here related to the Finnish forest site types as follows: "OMT" = cluster 1, "MT=" (or "OMT–") = cluster 2, "MT" = clusters 3–4, "VT" = cluster 5 and "CT" = cluster 6. The key can be used e.g. by the following scheme:

1. *In a 10×10 m plot centered at the sampling point, determine the presence/absence and the rough abundance class of the appropriate indicator species as you proceed through each successive division of the key. Abundance classes are: 0 = absent 1 = present here and there occasionally 2 = present more than occasionally, but with less than 1 % (1 m^2) total coverage 3 = present with 1–5 % (1–5 m^2) total coverage 5–10 % 5 = total coverage 10–16 % 6 = total coverage 16–25 % 7 = total coverage 4 = total coverage 25–50 % 8 = total coverage more than 50 %.*
2. *Score –1 for each "negative" (left) indicator species and +1 for each "positive" (right) indicator species. Add –1 or +1 for each indicator species if it is one class more abundant than required in the key, –2 or +2 if it is two classes more abundant, a.s.o. Then calculate the sum of scores.*
3. *Compare the sum to the allocation criterion number (0 . . . 3). If the sum is greater than the criterion, proceed to the right; if the sum is less than the criterion, proceed to the left. If the sum equals to the criterion, select another random sampling point from near by the first one.*
4. *Proceed through successive divisions to determine the site type. Note that in some divisions one indicator species is enough, in other cases not.*

along the large watershed of Suomenselkä far to the south (Keltikangas 1959).

According to Keltikangas (1959, pp. 191–192), the Cajanderian forest site type classification is theoretically and systematically complete and requires only adjustments regarding regional parallel types and successional series of stands. Furthermore, Keltikangas summarizes his view of the future development of the forest site type theory as follows: "Many attempts have been made to amend some part of this fifty-year-old theory, but one after another have been frustrated by the brilliance of its basic design . . . Our system of classification hardly requires any essentially new forest site types or new interpretation of types."

The Finnish forest site type system as derived from Cajander's theory is evidently highly applicable in site quality evaluation at least in relatively undisturbed northern forests where the number of different tree species is few and plants generally have very superficial root system (Husch & al. 1982). However, the applicability of the classification system in forestry does not verify the theory upon which the system has been based. In actual fact, the forest site type theory (Cajander 1909a, 1921, 1926, 1949) consists of hypotheses invoking certain structuring and organizing forces in the plant community, but these hypotheses are not verified correctly. Accordingly, there are no theoretically justified obstacles to prevent new interpretations or descriptions of the site types.

The forest site type theory incorporates a basic assumption that plant communities are distinct entities that have developed and arranged in accordance with definite biological laws; such communities are considered as well differentiated and constant for the same site (Cajander 1926). Plant communities of mature, naturally developed and undisturbed forests are used as standards for comparisons: standards for comparing sites on both local and regional scales, and standards of relative stability of community dynamics, including the development of the tree stand. Such use of the plant community concept requires a stable and faithful expression of primary site factors by undisturbed vegetation. Furthermore, competitive replacement should be rapid enough in structuring these communities into a recognizable stage during the short period from clearcutting and stand regeneration to the closure of the tree stand. According to the results of the present study, pronounced differences in the abundance relationships of the dominant plant species are only relatively slightly related to the site differences. However, even scanty occurrences of certain indicator plant species seem to reflect site conditions rather reliably, and these occurrences presumably make their appearance on suitable sites long before the initial community composition is re-established after disturbance (cf. Kujala 1979).

The forest site type theory considers the edaphic gradient as a primary site factor, but the tree stand essentially as an accidental, secondary site factor (Cajander 1926, p. 27). In contrast, in the present study the community composition is not seen to alter along with the gradient of nutrient availability, but according to the gradient of the supply ratio of a limiting soil resource and light. The tree stand is of major importance in governing the change in light availability along the nutrient gradient and changes in tree species composition should consequently affect the composition of the understorey vegetation considerably, both by changing the ratio of available light and nutrients, and by altering spatial heterogeneity. Due to the tendency for spruce to predominate on fertile soils and pine on poorer soils, the relationship between nutrient regime and light availability appears to be nonlinear from an individual understorey plant's point of view (Figs. 10 and 12).

It therefore seems likely that forest site evaluation in the present intensively managed forest stands, most of which are relatively young, should theoretically be based on the indicator values of different, individual plant species rather than on distinct, stable and mature plant communities. Plants tend to form ecological species groups with relatively similar resource requirements and, in general, the number of species potentially capable of occupying a forest site increases along with the increase in resource richness. Accepting the continuum concept of vegetation, distinguishing between relatively indifferent "core" forest plants and highly indicative "marginal" forest plants, and a consideration of the species' distributional limits and environmental requirements for soil resources and light in particular, would provide a firm basis for the use of plants as site indicators. On such a basis of individualistic concept of plant associations, it could be possible to eliminate terminological and other inconsistences such as the arbitrary distinction between successional and mature plant communities, and the existence of a zonal type series for uplands but not for peatlands (Mikola 1982).

The approach used in the present study differs from the Cajanderian one most fundamentally in that the continuum character of vegetation has been emphasized, and the operational site classification has been made following the apparent discontinuities encountered in a vegetation gradient imposed from a truly random sample of stands. The presented classification shows a considerable convergence with the Finnish forest site type system, although the identification criteria and the presumed status of the types in the presented hierarchical system differ somewhat from those implied in the Cajanderian forest site type series. In summary, the present study proves that there is a valid correlation between vegetation and site quality, but it must be kept in broad terms; it must be recognized that the understorey vegetation is affected also by the species composition, age and density of the tree stand, and by past management practices. It seems likely that an operational classification system for forest site evaluation can be developed by different methods with a fundamentally different theoretical basis without changing the major outlines of the system, but improving its practical applicability. In conclusion, the presented "objective" classification and the Cajanderian one both presumably approach the "natural" classification of forest sites in southern Finland. However, an indirect classification study based on vegetation characteristics sheds only a little light on the underlying diversification of sites, which is presumably a result of the geological history of the soils and the consequent development of different types of forest ecosystem.

7. CONCLUDING REMARKS

In the Finnish forest site type system, site quality evaluation is principally based on rather qualitative descriptions of normal stands on presumably different site types. The concept of site type is imprecisely defined; the system is strongly deductive in nature, constituting an arbitrary simplification of the complex reality of forest ecosystem. In addition, there is a lack of unambiguous criteria and practical procedures for allocating an individual stand to a site type. Correct use of the system requires considerable ecological knowledge on the part of the forester; a large number of vegetational and environmental characteristics have to be taken into account simultaneously. Identification of the site type is evidently particularly subjective in successionally young forest stands, which form the most part of the present commercial forests.

The present study material consists of a random sample of actual forest stands in southern Finland. The major environmental gradient underlying the vegetation composition gradient is evidently connected to the nutrient regime of the humus layer. The humus layer is itself a product of the vegetation, including the tree stand, and it is therefore self-evident that its nutrient contents are well adapted to the composition of the plant community. The primary causal agents of the diversification of upland forest sites are presumably associated with the characteristics of the mineral soil. The soils of different geological genesis differ from each other as regards their minerological, textural and structural properties. In addition, topogenic factors evidently play an important role in governing moisture regime, microclimatical conditions and light regime of the site. These properties presumably control the long-term processes which modify the ecosystem so that the differences in vegetation and humus layer develop concurrently during the development of different types of site. The present study sheds only a little light on the question of these causal processes. The material involves till soils mainly, and both the chemical and physical properties of the soil seem to intergrade relatively continuously. However, a slight change in the availability of a single or a few soil resources may result as a considerable change in the vegetation composition so that apparent discontinuities can be found.

Presumably the most important environmental discontinuities underlying the vegetational differences seem to be connected to the differences in the soil moisture regime and in the calcium release of the parent material. The major division of the vegetation data set appears to reflect a fundamental difference in soil moisture content between the mesic and xeric sites. This difference, however, can have many causes, including textural properties of the soil, topogenic factors and the thickness of the superficial soil, or an interaction of several of these factors. The vegetation growing on calcium-rich soils seems also to differ clearly from other types of vegetation. This division appears to be reflected in many ecological properties of the site, including the composition of the humus layer. It should be noted, however, that the calcium content changes gradually from a type of parent material to another, and that truly lime-rich soils are infrequent in southern Finland (see Aaltonen 1951, Kalliola 1973).

The produced vegetation classification largely corresponds to the Finnish forest site type system as applied in southern Finland, and reflects the overall fertility of the soil very clearly. However, resource partitioning between plant species is evidently a question of sharing the proportion of a relative amount of available light and a limiting soil resource (Tilman 1982). Hence it follows that the tree stand, as a major factor limiting light availability on the forest floor, and the soil nutrient regime have a concurrent, additive effect on the understorey vegetation. The fact that forest succession can be understood as an analogous gradient along the supply ratio of a limiting soil resource and light availability is also an important point (Tilman 1985). This could provide a framework for considering spatial and temporal patterns of community replacement simultaneously, e.g. in a two-dimensional space formed by a spatial gradient (say, from poor to fertile sites) and temporal gradient (successional series of stands).

In forestry, site types are primarily used for the estimation of productive capacity. In this, a continuous index would, of course, be highly desirable. However, attempts to develop such an index on the basis of vegetation characteristics are probably bound to fail for several reasons (see Vallée & Lowry 1972). A hierarchical system such as presented in this study should provide an effective tool foor adjusting the forest site type system, and for improving its practical applicability. It is possible, based on the type of hierarchical approach presented in this study, to develop a practical, successive key for site definition in which only a few attributes have to be considered at a time. This kind of approach reduces the dependency of site evaluation on the individual's interpretation of the descriptions and, therefore, also reduces the probability of misclassification. In addition to the understorey vegetation, a proper and accurate site classification should also consider the tree stand and soil properties (cf. Hägglund 1981, Jones & al. 1983). The ecosystem approach should form a proper framework for the compilation of present knowledge in this respect. Particularly organized in a flexible hierarchical system, it should permit integration of classification to cover the needs and purposes of practical forestry and natural sciences, and facilitate international cooperation.

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SELOSTE

Ekologinen tutkimus Etelä-Suomen kangasmetsien kasvupaikkaluokituksesta

Tutkimuksen tausta ja tavoitteet

Maassamme käytössä oleva kangasmetsien kasvupaikkaluokitusjärjestelmä perustuu A. K. Cajanderin (1926) kehittämään metsätyyppiteoriaan, jonka mukaan primääriset kasvupaikkatekijät – ilmaston ja maaperän ominaisuudet – määräävät paikalle syntyvän pintakasvillisuuden rakenteen niin tarkasti, että pintakasvillisuutta voidaan käyttää metsämaan viljavuuden välillisenä ilmaisimena. Metsätyyppijärjestelmä on suunniteltu nimenomaisesti käytännön metsätalouden tarpeisiin. Tyyppien lukumäärä on sen vuoksi pyritty pitämään mahdollisimman pienenä. Samalla on jouduttu tinkimään tyyppien kuvausten ekologisesta täsmällisyydestä: metsätyyppien sisäinen vaihtelu on varsin suurta sekä kasvillisuuden että maaperän ominaisuuksien suhteen (Keltikangas 1959). Metsätyyppien katsotaan muodostavan kasvupaikan puuntuottokykyä vastaavan perussarjan, jossa maan vesi- ja ravinnetalous ovat määrääviä tekijöitä. Perussarjat on kuvattu erikseen kullekin ilmastolliselle kasvillisuusvyöhykkeelle (Kalela 1961). Tässä tutkimuksessa on keskitytty Etelä-Suomen metsäkasvillisuusvyöhykkeeseen.

Metsätyyppien kuvaukset perustuvat suurimmalta osin tutkimuksiin, jotka on tehty kutakin tyyppiä luonteenomaisesti edustavissa, jokseenkin luonnontilaisissa ja täysin sulkeutuneissa metsiköissä (Cajander 1949). Nykyisin valtaosa metsistämme edustaa nuorempia sukkessiovaiheita, ja metsien käsittely on Cajanderin ajoista olennaisesti muuttunut. Tämä on synnyttänyt keskustelua metsätyyppien sovellutuksen objektiivisuudesta nykyisin vallitsevissa olosuhteissa (Kuusela 1982, Vuokila 1980, 1982). On myös varsin ilmeistä, että nimenomaan metsätalouden tarpeisiin kehitetty luokitusjärjestelmä ei palvele yhtä hyvin ekologisesti tarkempaa luokitusta vaativaa biologista tutkimusta. On edelleen muistettava, että metsätyyppijärjestelmää ei vielä ole kehitetty valmiiksi; keskeneräisyyttä ovat korostaneet sekä Cajander itse että järjestelmää myöhemmin edelleen kehittäneet metsätieteilijät (ks. Keltikangas 1959). Nykyisen ekologisen tietämyksen valossa voidaan myös eräät Cajanderin metsätyyppiteorian keskeiset, kasviyhdyskuntien muodostumisen lainalaisuuksia koskevat hypoteesit ottaa uuden tarkastelun kohteeksi.

Käsillä oleva tutkimus perustuu satunnaiseen otokseen eri osissa Etelä-Suomea sijaitsevia metsikkönäytealoja. Aineisto edustaa siten periaatteessa alueen metsissä tällä hetkellä vallitsevia olosuhteita. Satunnaisotos mahdollistaa myös tilastollisten monimuuttujamenetelmien harhattoman käytön aineiston analysoinnissa. Tutkimuksen tarkoituksena on analysoida metsäkasvillisuudessa esiintyvää vaihtelua sekä tämän vaihtelun yhteyksiä maaperän ja puuston tunnuksissa esiintyvään vaihteluun. Lähtökohtana on hypoteesi, jonka mukaan metsäkasvillisuuden vaihtelu on luonteeltaan jatkuvaa (kontinuumi) eikä siitä voida erottaa "luonnollisia" viljavuusluokkia. Tuloksia tarkastellaan Cajanderin metsätyyppiteorian sekä eräiden uudempien, kasviyhdyskuntien muodostumista koskevien teorioiden valossa. Toisena tavoitteena on tutkia ekologisesti mielekkään, operationaalisen metsäekosysteemiluokituksen kehittämismahdollisuuksia sekä mahdollisuuksia kehittää metsätyypeille määrityskaava, jonka käyttö olisi mahdollisimman riippumaton määritystä suorittavan henkilön tulkinnoista ja asiantuntemuksesta.

Aineisto ja menetelmät

Tutkimuksessa mitattiin 410 näytealaa, jotka sijoittuvat eri osiin Etelä-Suomea kuvan 1 osoittamalla tavalla. Aineisto on satunnaisotos populaatiosta, jonka muodostavat em. alueilla sijaitsevat kivennäismaiden puustoltaan sulkeutuneet metsiköt. Näytealoilta mitattiin puusto relaskopoimalla, puuston pituusboniteetti (H_{100}) (Gustavsen 1980), kasvillisuudesta tehtiin lajikohtainen peittävyysanalyysi kuudelta 2×2 m:n ruudulta sekä otettiin maanäytteet humuskerroksesta (16) ja kivennäismaasta (4). Lisäksi mitattiin kasvupaikan fysiografisia tunnuksia kuten topografinen asema, rinteen suunta ja kaltevuus sekä kasvukauden tehoisa lämpösumma interpoloiden (Tamminen 1982). Maanäytteistä määritettiin kivennäismaan raekokotunnukset seulomalla ja liettoanalyysiä käyttäen. Kivisyys mitattiin rassilla Viron (1952) menetelmää käyttäen. Sekä humus- että kivennäismaanäytteistä määritettiin kokonaistyyppi ns. Kjeldahl-menetelmällä, pH (vesi), P-, Ca-, K- ja Mg-kokonaispitoisuudet sekä helppoliukoisen fosforin ja vaihtuvien kationien (Ca, K ja Mg) pitoisuudet (Halonen & al. 1983).

Kasvillisuusanalyysin perusmenetelmänä käytettiin rinnasteista indikaattorilajianalyysia (TWINSPAN) (Hill 1979a), joka järjestää sekä kasvilajit että näytealat taulukkomuotoon aineistossa pääasiallisesti vallitsevan vaihtelusuunnan mukaisesti (liite). Lisäksi ohjelma tulostaa taulukkomuodossa lajien ja näytealojen hierarkkisen luokittelun ns. jakavalla menetelmällä sekä eri lajien indikaattoriarvot kunkin jaon yhteydessä (liite, kuvat 5 ja 6). Kasvillisuuden perusteella muodostettujen luokkien välisiä ekologisia eroavuuksia selvitettiin erotteluanalyysillä, jossa kriteerimuuttujina käytettiin mitattuja kasvupaikan viljavuustunnuksia sekä puuston tunnuksia. Luokkien edustamien kasvupaikkojen keskimääräisen puuntuottokyvyn välisiä eroja tutkittiin varianssianalyysin avulla, jossa kriteerimuuttujana käytettiin pituusboniteetti-indeksiä.

Tulokset

Kasvillisuuden perusteella muodostettujen luokkien todettiin kutakuinkin vastaavan Cajanderin (1926) esittämää luokittelua, kuitenkin siten että luokat eivät ole selvärajaisia vaan liittyvät toisiinsa enemmän tai vähemmän kontinuuminomaisesti. Puuston lajikoostumuksella ja tiheydellä todettiin olevan erittäin merkittävää vaikutusta pintakasvillisuuden rakenteeseen. Maaperän ominaisuuksien osalta luokkien välisiä eroja selittävät parhaiten humuskerroksesta mitatut kokonaistyppi- ja fosforipitoisuudet sekä happamuus. Kivennäismaan ominaisuuksissa ei sen sijaan vastaavia luokkien välisiä eroja ollut selvästi havaittavissa. Voidaan kuitenkin päätellä, että maan vesitaloudella on ratkaiseva vaikutus pintakasvillisuuden muotoutumiseen. Tämä vaikutus on osittain epäsuora ja liittyy puuston säätelemiin valaistusoloihin.

Tutkimusaineistoon sisältyvät metsämaat voidaan jakaa kahteen pääluokkaan (ks. kuvat 5 ja 6): tuoreet kasvupaikat (klusterit 1–4) sekä kuivat kasvupaikat (klusterit 5–6), joista edelliset ovat satunnaisesta näytteenotosta johtuen aineistossa vallitsevia. Kuiviin kasvupaikkoihin sisältyy sekä hiekkamaiden ja karkearakeisten moreenimaiden karuja metsämaita että kalliokasvupaikkoja. Perusjako kahteen pääluokkaan heijastuu erittäin selvästi sekä kasvillisuudessa että metsämaan kemiallisissa ja fysiologisissa tunnuksissa; myös puuntuottokyky (mitattuna pituusboniteetin avulla puulaji huomioiden) on kuivilla kasvupaikoilla merkitsevästi alhaisempi kuin tuoreilla kasvupaikoilla. Kasvillisuuden tunnuksista suurin indikaattoriarvo on eräillä tuoreiden kasvupaikkojen ruohovartisilla kasveilla (tärkeimpänä oravanmarja) sekä kuiville kasvupaikoille luonteenomaisella jäkäläisyydellä. Ekologiselta kannalta katsoen perusero on vesitaloudessa, jonka epäsuotuisuus kuivilla kasvupaikoilla saattaa johtua monista eri syistä (kivennäismaan vedenläpäisevyys, kasvupaikan topografinen asema, maapeitteen ohuus jne.). Tuoreiden kasvupaikkojen (klusterit 1–4) välillä vallitsevat floristiset ja ekologiset eroavuudet ovat enemmän tai vähemmän diffuuseja. Kasvillisuuden perusteella muodostetuista klustereista voidaan kuitenkin erottaa ravinnetaloudeltaan selvästi eriarvoisia kasvupaikkaluokkia.

Selvimmin omaksi ryhmäkseen tuoreita kankaita edustavista metsikkönäytealoista erottuvat viljavimmat kasvupaikat (klusteri 1, ks. kuva 5 ja liite), joiden indikaattorilajeja ovat mm. sormisara, käenkaali (suhteellisen runsaana esiintyessään), nuokkuhelmikkä ja metsäorvokki; yleisesti ottaen varpujen (mm. mustikka) peittävyysosuus on näillä kasvupaikoilla alhaisempi kuin vähemmän viljavilla tuoreilla kasvupaikoilla. Humuskerros on multavampaa ja sen kalsiumpitoisuus selvästi korkeampi kuin muilla tuoreilla kasvupaikoilla. On todennäköistä, että kallioperän minerologisilla ominaisuuksilla (kemiallinen koostumus, rapautuvuus, johon vaikuttaa mm. biotiitin suhteellinen osuus ym.) on ratkaiseva vaikutus kalkin määrään maaperässä ja sitä kautta viljavimpien kasvupaikkojen ja niille tunnusomaisen kasvillisuuden muotoutumiseen.

Muilta osin tuoreiden kasvupaikkojen kasvillisuus on luonteenomaisesti varpu- ja sammalvaltaista. Kasvillisuuden perusteella nämä kasvupaikat on kuitenkin mahdollista jakaa suhteellisen yksiselitteisin kriteerein kolmeen ryhmään (klusterit 2–4). Klusteri 2 asettuu humuskerroksesta mitattujen ravinnearvojensa puolesta viljavimpien kasvupaikkojen (klusteri 1) ja klusterien 3–4 muodostaman ryhmän välimaastoon. Tunnusomaista klusterin 2 kasvillisuudelle on ruohojen suhteellisen runsas esiintyminen: metsäalvejuuri, käenkaali ja oravanmarja (suhteellisen runsaana esiintyessään) ovat tärkeimpiä indikaattorilajeja. Silmiinpistävin ekologinen eroavuus klusteriin 1 verrattuna on klusterin 2 kasvupaikoille tyypillinen paksu kangashumuskerros. Klusterit 3 ja 4 edustavat humuskerroksesta mitattujen ravinteisuustunnusten puolesta samanarvoisia kasvupaikkoja. Kasvillisuuden osalta tärkeimmät eroavuudet ovat valoa vaativien lajien (mm. kanerva ja puolukka) runsaus klusterin 4 näytealoilla ja varjossa viihtyvien lajien (mm. isokynsisammal, metsäkerrossammal ja metsämaitikka) runsaus klusterin 3 näytealoilla. Floristisia eroja selittävät puuston säätelemät erot valaistusoloissa ja mikroilmastossa: klusteri 3 edustaa kuusivaltaisia, klusteri 4 selvästi mäntyvaltaisia näytealoja.

Kuten perinteiset metsätyypit, myös tässä tutkimuksessa numeerisin menetelmin muodostetut kasvillisuusklusterit ovat sisäisesti varsin heterogeenisiä. Omaksi ryhmäkseen voidaan erottaa mm. useassa eri klusterissa esiintyvät soistuneet näytealat (ks. liite). Eroavuuksia on myös maaperän fysiologisissa ominaisuuksissa ja topografisesta asemasta johtuvissa mikroilmastollisissa olosuhteissa. Muodostettuja klustereita vertailtiin perinteisiin metsätyyppeihin pituusboniteettina mitatun puuntuottokyvyn (puulajin vaikutus vakioituna) sekä niiden floristisen rakenteen perusteella. Kasvillisuudeltaan rehevin klusteri 1 sijoittuu keskimääräiseltä viljavuudeltaan varsinaisten lehtojen ja kangasmetsätyypin OMT välimaastoon (on huomattava, että varsinaisten lehtometsien osuus tutkimusaineistossa on pieni ja yli 90 % klusterin 1 kasvupaikoista voidaan mm. maannoksen perusteella määrittää kuuluvaksi kangasmetsien pääryhmään). Klusteri 2 edustaa viljavuudeltaan metsätyyppiä OMT, klusterit 3 ja 4 puolestaan metsätyyppiä MT (floristiselta rakenteeltaan klusteri 3 näyttää vastaavan varsin tarkasti metsätyyppioppaissa kuvattua mustikkatyyppiä). Klusterit 5 ja 6 edustavat selvästi kuivia kankaita, keskimäärin puolukkatyyppiä (VT) karumpia kasvupaikkoja.

Johtopäätökset

Pintakasvillisuuden perusteella muodostetut klusterit eroavat selvästi toisistaan humuskerroksesta mitattujen ravinnearvojen, pituusboniteetin sekä puuston varjostusvaikutuksen (ks. Kuusipalo 1985) suhteen. Humuskerroksen ravinteisuuden sekä pituusboniteettina mitatun viljavuuden välillä vallitsee varsin suoraviivainen riippuvuussuhde (kuva 11). Myös puuston tiheys ja puulajikoostumus on riippuvainen kasvupaikan viljavuudesta (kuva 12). Riippuvuus ei kuitenkaan ole lineaarinen, sillä tietyllä kasvupaikan viljavuuden tasolla valtapuuston muuttuminen kuusivaltaiseksi aiheuttaa varsin ratkaisevan muutoksen pintakasvillisuuden saaman valon määrässä (kuva 10). Tämä puolestaan vaikuttaa pintakasvillisuuteen siten, että keskimääräistä ravinteisuutta (metsätyyppiä MT) edustavissa metsiköissä, joissa sekä mänty että kuusi yleisesti esiintyvät valtapuulajina, pintakasvillisuus saa valaistuksen lisääntyessä kuiville kasvupaikoille tunnusomaisen leiman. Viljavammilla kasvupaikoilla valtapuu on useimmiten kuusi, karummilla taas lähes aina mänty, joten vastaava puulajin vaihtumisen aiheuttama vaikutus ei useinkaan tule esiin. Sen sijaan suurelta osin viljavuudesta riippuvainen puuston tiheys ja latvuston peittoala vaikuttavat kasvillisuuteen sekä viljavilla että karuilla kasvupaikoilla. Esimerkiksi osa klusterien 2 ja 3 välisistä floristisista eroista voidaan selittää siten, että edelliselle tunnusomaisen, tiheämmän ja kattavamman puuston aiheuttama mikroilmaston suurempi humidisuus sekä varjostusvaikutus suosivat klusterille tunnusomaisia ruohoja.

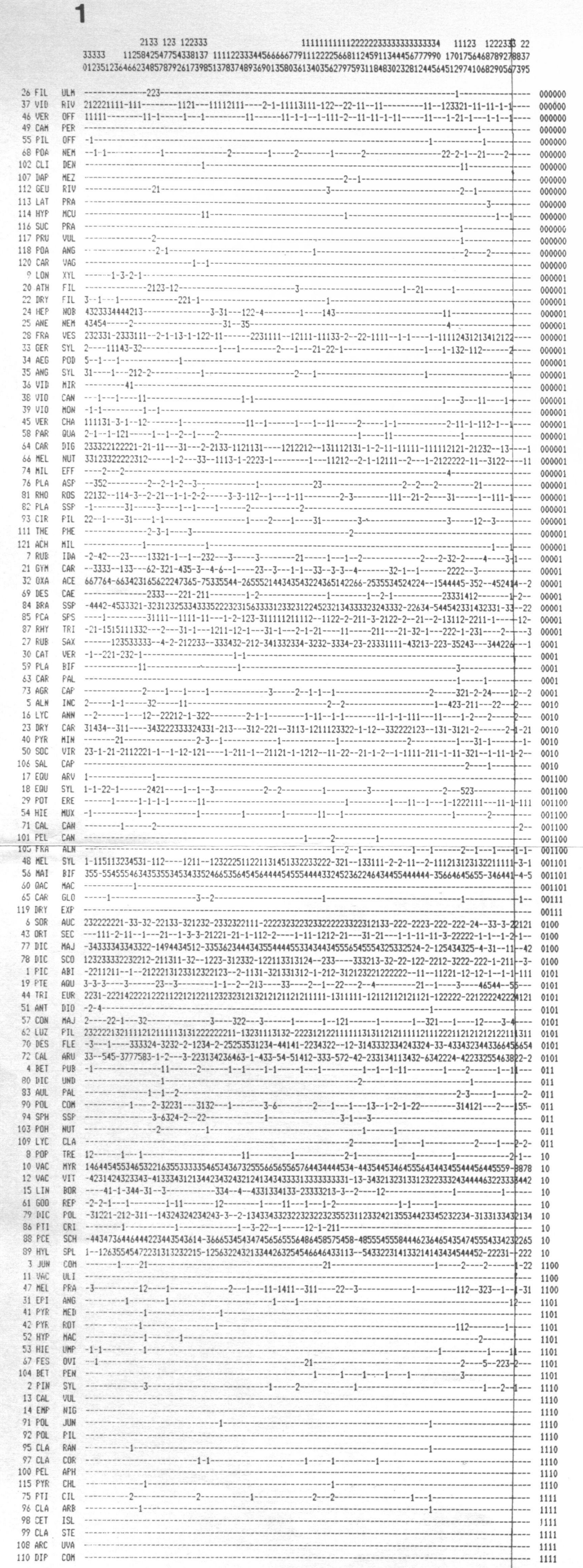
Humuskerroksen ravinnetunnusten ja kasvillisuuden (puusto mukaanlukien) välinen kiinteä vuorosuhde on luonnollinen ilmiö, koska humuskerros on sitä muodostavan kasvillisuuden tuotetta. Kivennäismaasta mitatuissa kemiallisissa ja fysikaalisissa tunnuksissa ei vastaavaa kiinteää vuorosuhdetta voitu havaita. Tämä johtunee osittain siitä, että varsinkin moreenimaiden viljavuutta on vaikea mitata yksiselitteisesti laboratoriossa määritellyin tunnuksin. Voidaan kuitenkin olettaa, että eri tavoin ja erilaisesta alkuperästä syntyneet maaperämuodostumat poikkeavat toisistaan minerologisten, fysikaalisten ja topografisten ominaisuuksiensa suhteen niin suuresti, että nämä ominaisuudet pystyvät säätelemään metsäekosysteemien erilaistumista humuksen ravinnetalouden ja kasvillisuuden suhteen sukkession edetessä (vrt. Sepponen 1985). Myös humuskerroksen viljavuustunnukset voidaan siten lukea ”sekundäärisiin” kasvupaikkatekijöihin, jotka vain epäsuorasti kuvastavat varsinaisia primäärejä kasvupaikkatekijöitä. Primääristen kasvupaikkatekijöiden vaikutuksia on kasvillisuuden ja humuskerroksen tunnusten avulla vaikea erottaa toisistaan, koska ekosysteemin muotoutumiseen vaikuttavat samanaikaisesti hyvin monet tekijät ja ekosysteemin bioottisten ja abioottisten komponenttien monimutkaiset vuorovaikutukset.

Tutkimuksen alussa asetetun hypoteesin metsäkasvillisuuden kontinuum-luonteesta voidaan todeta saaneen tutkimuksen tuloksista vahvistusta: muodostetut klusterit ovat enemmän operationaalisia kuin luonnollisia viljavuusluokkia. Kuitenkin tulokset vahvistavat myös Cajanderin metsätyyppijärjestelmän eräitä perusperiaatteita: perussarjan yksiulotteisuus saa vahvistusta ravinnetunnusten määrävästä vaikutuksesta kasvillisuusgradienttiin, ja klusterien väliset floristiset eroavuudet vastaavat suurin piirtein Cajanderin (1926) esittämää luokittelua. Cajander näyttää kuitenkin aliarvioineen puuston vaikutusta pintakasvillisuuteen; myös luokituksessa itsessään ja etenkin sen kvantitatiivisissa kriteereissä on ilmeistä tarkentamisen varaa nykyisiin talousmetsiin sovellettuna.

Tämänkin tutkimuksen perusteella pintakasvillisuus osoittautuu varsin käyttökelpoiseksi kasvupaikkojen luokitusperustaksi, mikäli puuston kehitysasteen ja puulajisuhteiden vaikutukset otetaan riittävässä määrin huomioon. Kasvillisuuden avulla voidaan kuitenkin päästä ainoastaan varsin karkeaan luokitteluun. Tulosten perusteella näyttää siltä, että nykyistä metsätyyppijärjestelmää olisi syytä tarkentaa etenkin OMT:n ja MT:n sekä myös MT:n ja VT:n välisen rajanvedon osalta. Aineisto ei tutkimuksen tässä vaiheessa ole riittävä konkreettisten tarkennusten perustelemiseen, mutta kuvassa 13 on havainnollistettu erästä mahdollisuutta täsmentää metsätyypin määrityksen kriteerejä ekologisesti mielekkäällä tavalla. Hierarkkisesti rakennettu määrityskaava lähtee ekologisesti perustavimman laatuisesta erosta tuoreiden ja kuivien kasvupaikkojen välillä. Tämän jälkeen edetään kussakin puukuvion haarautumiskohdassa määritellyin floristisin kriteerein varsinaisiin ”metsätyyppeihin”. Lähestymistapa antaa mahdollisuuden suorittaa metsätyypin määrittäminen varsin luotettavasti ja yksiselitteisesti käyttäen tunnuksina ainoastaan muutamien viljavuusluokalleen tyypillisten ja niille suotuisilla kasvupaikoilla konstanttien kasvilajien esiintymistä ja karkeaa runsausarviota. Olennaisesti metsätyyppijärjestelmää paremman ekosysteemiluokituksen kehittäminen edellyttää kuitenkin käsillä olevan tutkimuksen kaltaisten ekstensiivisten luokitustutkimusten kytkentää ekosysteemin eri komponenttien välillä vallitseviin vuorovaikutuksiin ja kausaalisuhteisiin pureutuviin tutkimuksiin.

SPECIES ABBREVIATIONS

FIL	ULM	Filipendula ulmaria
VIO	RIV	Viola riviniana
VER	OFF	Veronica officinalis
CAM	PER	Campanula persicifolia
PIL	OFF	Pilosella officinarum
POA	NEM	Poa nemoralis
CLI	DEN	Climacium dendroides
DAP	MEZ	Daphne mezereum
GEU	RIV	Geum rivale
LAT	PRA	Lathyrus pratensis
HYP	MCU	Hypericum maculatum
SUC	PRA	Succisa pratensis
PRU	VUL	Prunella vulgaris
POA	ANG	Poa angustifolia
CAR	VAG	Carex vaginata
LON	XYL	Lonicera xylosteum
ATH	FIL	Athyrium filix-femina
DRY	FIL	Dryopteris filix-mas
HEP	NOB	Hepatica nobilis
ANE	NEM	Anemone nemorosa
FRA	VES	Fragaria vesca
GER	SYL	Geranium sylvaticum
AEG	POD	Aegopodium podagraria
ANG	SYL	Angelica sylvestris
VIO	MIR	Viola mirabilis
VIO	CAN	Viola canina
VIO	MON	Viola montana
VER	CHA	Veronica chamaedrys
PR	QUA	Paris quadrifolia
CAR	DIG	Carex digitata
MEL	NUT	Melica nutans
MIL	EFF	Milium offusum
PLA	ASP	Plagiochila asplenioides
RHO	ROS	Rhodobryum roseum
PLA	SSP	Plagiomnium spp.
CIR	PIL	Cirriphyllum piliferum
THE	PHE	Thelypteris phegopteris
ACH	MIL	Achillea millefolium
RUB	IDA	Rubus idaeus
GYM	CAR	Gymnocarpium dryopteris
OXA	ACE	Oxalis acetosella
DES	CAE	Deschampsia caespitosa
BRA	SSP	Brachythecium spp.
PCA	SPS	Plagiothecium spp.
RHY	TRI	Rhytidiadelphus triquetrus
RUB	SAX	Rubus saxatilis
LAT	VER	Lathyrus vernus
PLA	BIF	Plantanthera bifolia
CAR	PAL	Carex pallescens
AGR	CAP	Agrostis capillaris
ALN	INC	Alnus incana
LYC	ANN	Lycopodium annotinum
DRY	CAR	Dryopteris carthusiana
PYR	MIN	Pyrola minor
SOL	VIR	Solidago virgaurea
SAL	CAP	Salix caprea
EQU	ARV	Equisetum arvense
EQU	SYL	Equisetum sylvaticum
POT	ERE	Potentilla erecta
HIE	MUX	Hieracium murorum
CAL	CAN	Calamagrostis canescens
PEL	CAN	Peltigera canina
FRA	ALN	Frangula alnus
MEL	SYL	Melampyrum sylvaticum
MAI	BIF	Maianthemum bifolium
DAC	MAC	Dactylorhiza maculata
CAR	GLC	Carex globularis
DRY	EXP	Dryopteris expensa
SOR	AUC	Sorbus aucuparia
ORT	SEC	Orthilia secunda
DIC	MAJ	Dicranum majus
DIC	SCO	Dicranum scoparium
PIC	ABI	Picea abies
PTE	AQU	Pteridium aquilinum
TRI	EUR	Trientalis europaea
ANT	DIO	Antennaria dioica
CON	MAJ	Convallaria majalis
LUZ	PIL	Luzula pilosa
DES	FLE	Deschampsia flexuosa
CAL	ARU	Calamagrostis arundinacea
BET	PUB	Betula pubescens
DIC	UND	Dicranum undulatum
AUL	PAL	Aulacomnium palustre
POL	COM	Polytrichum commune
SPH	SSP	Sphagnum spp.
POH	NUT	Pohlia nutans
LYC	CLA	Lycopodium clavatum
POP	TRE	Populus tremula
VAS	MYR	Vaccinium myrtillus
VAC	VIT	Vaccinium vitis-idaea
LIN	BOR	Linnaea borealis
GOO	REP	Goodyera repens
DIC	POL	Dicranum polysetum
PTI	CRI	Ptilium crista-castrensis
PLE	SCH	Pleurozium schreberi
HYL	SPL	Hylocomium splendens
JUN	COM	Juniperus communis
VAC	ULI	Vaccinium uliginosum
MEL	PRA	Melampyrum pratense
EPI	ANG	Epilobium angustifolium
PYR	MED	Pyrola media
PYR	ROT	Pyrola rotundifolia
HYP	MAC	Hypochoeris maculata
HIE	UMB	Hieracium umbellatum
FES	OVI	Festuca ovina
BET	PEN	Betula pendula
PIN	SYL	Pinus sylvestris
CAL	VUL	Calluna vulgaris
EMP	NIG	Empetrum nigrum
POL	JUN	Polytrichum juniperinum
POL	PIL	Polytrichum piliferum
CLA	RAN	Cladina rangiferina
CLA	COR	Cladonia cornuta
PEL	APH	Peltigera aphthosa
PYR	CHL	Pyrola chlorantha
PTI	CIL	Ptilidium ciliare
CLA	ARB	Cladina arbuscula
CET	ISL	Cetraria islandica
CLA	STE	Cladina stellaris
ARC	UVA	Arctostaphylos uva-ursi
DIP	COM	Diphasiastrum complanatum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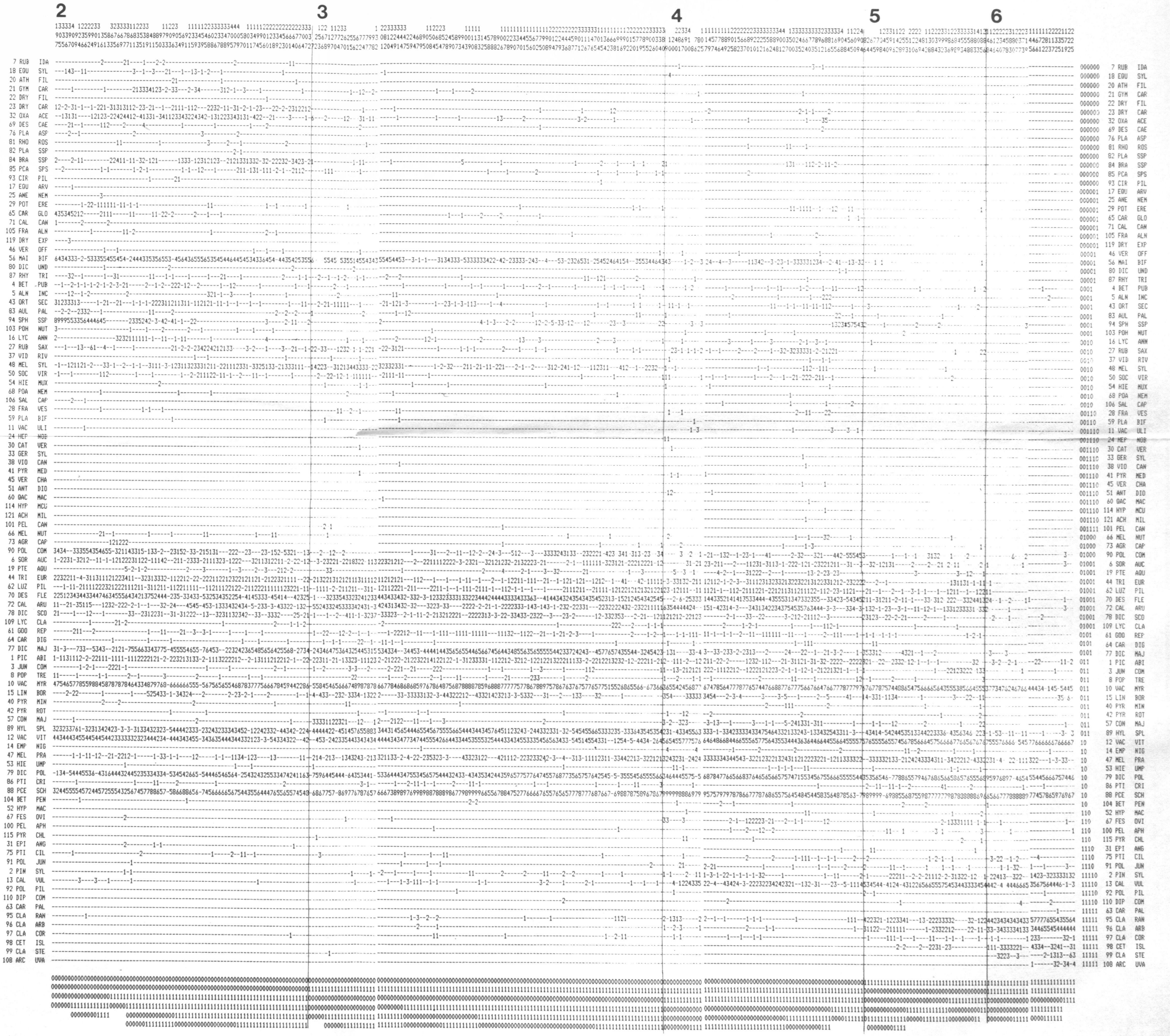
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ODC 542+114.521+187 ISBN 951-651-069-8

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The vegetation and a number of physical and chemical soil properties were studied on a random sample of closed upland forest stands in southern Finland. Two-way indicator species analysis (TWINSPAN) was applied in a hierarchical clustering of samples and plant species. Discriminant analysis and analysis of variance were applied in order to find environmental correlations of the vegetation clustering. The understorey vegetation was found to be jointly dependent on site fertility and on the tree stand, especially the tree species composition. Although the forest vegetation appears to be distributed rather continuously along an axis of increasing site fertility, relatively unambiguous site classification can be based on the appearance of indicator species and species groups.

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ODC 542+114.521+187 ISBN 951-651-069-8

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The vegetation and a number of physical and chemical soil properties were studied on a random sample of closed upland forest stands in southern Finland. Two-way indicator species analysis (TWINSPAN) was applied in a hierarchical clustering of samples and plant species. Discriminant analysis and analysis of variance were applied in order to find environmental correlations of the vegetation clustering. The understorey vegetation was found to be jointly dependent on site fertility and on the tree stand, especially the tree species composition. Although the forest vegetation appears to be distributed rather continuously along an axis of increasing site fertility, relatively unambiguous site classification can be based on the appearance of indicator species and species groups.

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ISBN 951-651-069-8

Arvi A. Karisto Oy:n kirjapaino
Hämeenlinna 1985