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DISTRIBUTION OF VEGETATION ON MESIC FOREST SITES IN RELATION TO SOME CHARACTERISTICS OF THE TREE STAND AND SOIL FERTILITY

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Seloste

TUOREIDEN KANGASMETSIEN KASVILLISUUDEN JAKAUTUMINEN SUHTEESSA ERÄISIIN PUUSTON JA MAAPERÄN TUNNUKSIIN

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Vegetation data collected from a random sample of forest stands representing mesic upland forest sites in selected areas in southern Finland are analyzed and classified using two-way indicator species analysis (TWINSPAN). The tree stand and soil fertility characteristics are analyzed using the LISREL measurement model in order to construct latent variables for describing the site factors. The site factor scores are treated as continuous dependent variables and the vegetation units as independent class variables in order to test statistically the mensurational fitness of the produced vegetation units.

The results are in agreement with the main division of mesic forest sites in the Finnish forest site type classification system: vegetation units which can be related to the *Oxalis-Myrtillus* site type are clearly separated from the remaining units, and the fertility factor indicates a statistically significant difference. The *Myrtillus* site type seems to be edaphically comparatively uniform; the vegetational differences are caused mainly by the tree stand factor. On the other hand, the *Oxalis-Myrtillus* site type seems to be markedly heterogenous: variation in the soil characteristics is clearly reflected in the vegetation composition, particularly in species' richness and in the abundances of exacting herbs, grasses and bryophytes.

1. INTRODUCTION

The Finnish forest site type classification is primarily based on A.K. Cajander's theory on forest site types (Cajander 1909, 1926, 1949, Cajander & Ilvessalo 1921 etc.). Cajander described two main types of mesic forest sites in southern Finland: the *Myrtillus* site type (MT) and the *Oxalis-Myrtillus* site type (OMT) (e.g. Cajander & Ilvessalo 1921). Mesic forest sites are confined mainly to moraine soils. The moisture content of the soil is relatively high. A comparatively thick, well-developed humus layer has more or less the characteristics of raw humus. In undisturbed, mature forest stands, the dominant tree species is Norway spruce (*Picea abies*), but also Scots pine (*Pinus sylvestris*) may occur as a forest-forming tree. The *Myrtillus* site type is characterized by an abundant and more or less continuous moss cover and by a predominance of *Vaccinium myrtillus*, usually accompanied by *Vaccinium vitis-idaea*. The *Oxalis-Myrtillus* site type represents a continuous transition between the preceding type and the grassherb forest class (grass- and herb-rich forests). *Vaccinium myrtillus* is also fairly abundant in this type, but due to the more luxuriant character of the vegetation, i.e. occurrence of relatively exacting herbs and grasses such as *Oxalis acetosella, Melica nutans, Carex digitata* etc., the *Oxalis-Myrtillus* site type can rather easily be identified in the field (cf. e.g. Ilvessalo 1922, Cajander 1926).

The main emphasis in the Finnish forest site type classification is on classifying potential site productivity on the basis of the actual vegetation cover, which is considered to reflect the invariable site factors such as climatical and edaphical conditions (cf. Keltikangas 1959). The descriptions of the site types are primarily based on undisturbed, mature forests. The variation in the vegetation pattern caused by successional stage, disturbances etc. is considered temporary and, thus, of less significance (Cajander 1926). Recent silvicultural activities are, however, so intense that undisturbed, mature forest stands can seldom be found. For this reason, determination of the site type has in many cases been highly subjective (e.g. Vuokila 1965, 1980, see also Kuusela 1982). In the Cajanderian forest site type theory, the site type is also considered to be essentially independent of the tree species composition: although the tree stand evidently has a considerable effect on the vegetation pattern, the site type can be determined unambiguously (Cajander & Ilvessalo 1921). According to Keltikangas (1959), there is a need for supplementary research concerning the application of the forest site type system in forests recently subjected to intensive silviculture. Obviously there is also a need for research concerning the impact of the tree stand on the vegetation composition, which has in many cases been considered to be underestimated (cf. Sarvas 1951, Teivainen 1952, Vuokila 1956). Probably the most objective approach is to examine, simultaneously, the characteristics of the understorey vegetation, the tree stand and the soil, from random sample of forest stands. Random sample provides unbiased statistical treatment of the data.

The present study includes material collected from a set of sample plots situated randomly on mesic forest sites in selected areas in southern Finland. The published material is not sufficient to reveal all the important variation in the vegetation and site factors affecting it, but is expected to show some major features of these topics. Divisive numerical clustering based on indicator values of different plant species is applied in order to derive automatic and objective classification of the actual vegetation. The characteristics of the tree stand and soil fertility form a complex of variables, the effects of which are difficult to examine separately. For this reason, their covariance structure is analyzed with specified measurement models in order to produce complex latent variables for describing their interaction on the vegetation pattern. The aims of the present work are (1) to experiment with the application of a floristically oriented numerical method for the treatment of forest vegetation, (2) to experiment with the application of confirmatory factor models for the treatment of environmental data, and (3) to analyze the major features in the variation of the actual vegetation on mesic forest sites and some essential site factors affecting it. The theoretical implications of the findings are discussed.

The present study was carried out with the co-operation of the Department of Forest Soil Science, the Finnish Forest Research Institute, and was supported by the Academy of Finland. Mr. Pekka Tamminen of the Finnish Forest Research Institute provided the author with the measurements concerning the tree stand and the soil characteristics. Computing work was carried out by the author at the University of Joensuu. The author is also responsible for the vegetation data, which were collected with the assistance of Mr. Jorma Korhonen. Valuable comments on the manuscript were given by Prof. Eino Mälkönen, Prof. Matti Leikola, Dr. Erkki Lipas, Mr. Hannu Mannerkoski and Mr. Jari Oksanen. Mr. John Derome kindly checked the language. The author is grateful to all the above-mentioned, as well as to all the other contributors to the study.

2. MATERIAL AND MEASUREMENTS

The material consists of 106 sample plots, each 16×16 m in size, located in the districts of Lammi, Kuhmoinen and Mänttä (Fig. 1) in the southern boreal vegetation zone (Ahti & al. 1968). The material was collected in 1982. In the field, the sample plots were located randomly using the center points of the coordinate quadrats of selected sheets of the basic ordnance survey map (1:20 000). Only sample plots representing closed forest stands were taken into account in the vegetation analysis.

Six subsamples, 2×2 m in size, were located in the corners (4) and in the centre (2) of each of the sample plots. The vegetation growing on stones, stumps, logs etc. was disregarded. The coverage of the species was investigated using direct estimation of percentage cover. In the material of the present paper, only sample plots representing mesic upland forest sites (MT and OMT) were included. Thus the material used in the present work was reduced to a total of 80 sample plots.

The nomenclature of the plant species follows Hämet-Ahti & al. (1980) (vascular plants) and Koponen & al. (1977) (Bryophyta).

The material concerning the site characteristics was collected from the same sample plots. The ecological data used in the present work consist of the following variables:

(1) Characteristics of the tree stand
- basal area (m^2/ha/tree species)
- dominant age of the stand

(2) Characteristics of the soil
- dry weight of humus (kg/ha)
- ph (H_2O) in humus layer
- total nitrogen content (% dry humus)
- total calcium content (% dry humus)

Information about the measurement methods are given by Tamminen (1982).

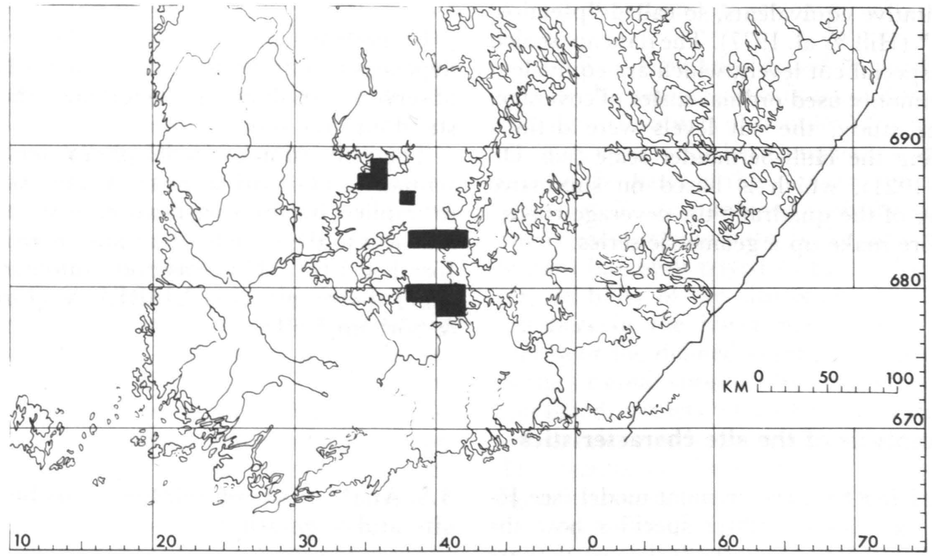

Fig. 1. Location of the study areas.
Kuva 1. Tutkimusalueiden sijainti.

3. METHODS

3.1. Vegetation analysis

The mean coverages of different plant species were calculated for each sample plot. The data were analyzed using two-way indicator species analysis (TWINSPAN, Hill 1979), 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 level of division is reached. A corresponding species classification is produced, and the sample and species hierarchical classifications are used to produce an arranged data matrix. 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. 1977). The data are scaled using special cut levels, which are equivalent to commonly used ordinal scales of coverage. In this study, the cut levels were defined following the Hult-Sernander scale (e.g. Du Rietz 1921), which is based on successive halving of the quadrats; the coverage classes therefore make up a geometric series.

3.2. Analysis of the site characteristics

The LISREL measurement model (see Jöreskog & Sörbom 1981) specifies how the latent variables or hypothetical constructs are measured in terms of observed variables and is used to describe the measurement properties (validities and reliabilities) of the observed variables. Provided that the goodness of fit and the coefficient of determination are acceptable, a set of observed variables can be substituted by a linear combination of the variables (Lawley & Maxwell 1971, Jöreskog & Sörbom 1981).

Latent variables ξ were constructed to describe the effects of the site factors on the understorey vegetation. The measurement model specifying how these hypothetical constructs are measured in terms of the observed variables can be defined as follows:

(1) $\mathbf{x} = \Lambda_x \xi + \delta,$

where x_i:s are the measured ecological characteristics, Λ_x is the regression matrix of $\mathbf{x}$ on ξ, and δ is the vector of the measurement errors of $\mathbf{x}$.

Finally, factor scores regression coefficients representing the estimated regression of ξ on all the observed variables were computed (for formula, see Lawley & Maxwell 1971, p. 109). The coefficient matrix, say, $\mathbf{A}$, was used to compute the estimated factor scores ξ_α for each observation (sample plot) with observed scores $\mathbf{x}_\alpha$ by the means of the formula

(2) $\xi_\alpha = \mathbf{A}\mathbf{x}_\alpha$

Computed factor scores were then used as dependent continuous variables instead of the observed variables characterizing the tree stand and the soil.

The estimation of model parameters is essentially that of fitting the covariance structure implied by the specification of parameter matrices to the sample covariance matrix (see Jöreskog 1973). This was done automatically using the programme LISREL V (Jöreskog & Sörbom 1981).

3.3. Analysis of the relationships between site and vegetation

In statistical analysis, the vegetation units produced by TWINSPAN were treated as independent class variables and site characteristics as continuous dependent variables. One-way analysis of variance with *a posteriori* contrast tests of the group means were used when examining the relationships between the vegetation pattern and site factors. In the multiple range tests, the LSD (least-significant difference) procedure was used. This is essentially a Student's t test between group means, and is exact for unequal group sizes. The computations were carried out using the programme package SPSS (Nie & al. 1975).

4. VEGETATION ANALYSIS

The results of two-way indicator species analysis are summarized in the arranged data matrix (Table 1). The names of the species are abbreviated; the correct names are given in Table 2. The ordinal numbers of the sample plots are given in the upper margin; e.g. the first column represents sample plot number 61. The binary codes in the lower margin represent the sample divisions produced by TWINSPAN; the binary codes in the right margin represent corresponding divisions of species. The table is divided into fields by lines which follow the hierarchical classification of the samples and species.

The maximum level of divisions was defined as 4; the minimum group size for each division was defined as 10. The maximum number of species was limited in the programme specification; in the final tabulation, the 60 most abundant species are presented. However, all the species present in the original data matrix were used in the computations and could appear as indicators. The coverages of different species in the tabulation follow Hult-Sernander scale.

The first division divides the data into two major subsets: sample plots representing herb-rich sites (1) and sample plots representing more heath-like sites (0). The most significant indicators in the first division are *Viola riviniana, Carex digitata* and *Brachythecium* spp., which are very frequent in subset (1) but occur in only a few cases in subset (0). In addition, the high abundance of *Oxalis acetosella* indicates the subset of herb-rich samples, whereas the high abundance of *Dicranum polysetum* indicates the subset of more heath-like samples. The first division is in agreement with the main division of mesic upland forest site types presented by Cajander (1926). Subset (0) represents the *Myrtillus* site type, while subset (1) can be assigned to the *Oxalis-Myrtillus* site type. The species list arranged in the rows of the matrix, as well as the sample list in the columns, can be interpreted to reflect, at least approximately, the overall site fertility.

As regards the subsequent divisions, it should be noted that dichotomous hierarchical clustering methods are comparatively sensitive to random effects (see e.g. Gauch 1982). The main divisions are more reliable than are the divisions produced at lower classification levels; random errors are correspondingly more probable when group sizes are small. For this reason, the results must be evaluated on the basis of the typical species composition in each subset and its ecological interpretability.

The final tabulation based on the four levels of the sample classification divides the data into 10 subsets of samples. The vegetation units used in further comparisons are defined on the basis of this division. Small subsets (n < 5) are combined with the vegetationally most similar subsets. In addition, attention has been payed to the ecological interpretability of the clustering. The ordinal numbers in the lower margin of Table 1 represent the defined vegetation units. Some of the original subsets of samples have been combined; subsets which belong to the same unit are denoted by the same ordinal number. The results of the vegetation analysis are summarized in the following descriptions of the vegetation units.

1. (00): The unit represents markedly xerophilous and light-demanding vegetation, characterized by an abundance of *Vaccinium vitis-idaea, Dicranum polysetum* and *Pleurozium schreberi. Calamagrostis arundinacea* is also fairly abundant. Only a few occurrences of exacting herbs and grasses can be found. The number of species is compa-

Table 1. Hierarchical classification of sample plots and species (TWINSPAN).
Taulukko 1. Näytealojen ja lajien hierarkkinen luokittelu (TWINSPAN).

			67788885566883445555666666777777788445622333345122333445 2 1123 11121111223	
			13824674825038681269034679012456791509781256795377802313452937848044602991356561	
93	Cal	vulg	---11-21----1------------1--------1---	111
90	Dic	poly	54232251242232223212232122122222113311-1212212321111121-1231-1111111111-211-1---11	111
66	Goo	repe	1-11111--1-1-1111---111-1-11--11---------------1--11-----1-1---1-1-1---1-1-------	111
61	Pti	cili	--1--1----------1--------1--1-------1-------------------------------1--1----------1----	111
91	Jun	comm	1--1--11-1-11-----------1---------1------------------------------------1---------1	110
86	Mel	prat	12-2--1112-11--1--111121-1-21---1--1222-1--1--1-12-1111-1211---------------------1	110
81	Car	glob	----------------1-----1-1--1--1---1-------1-------1---------------------------11-------	110
76	Dic	maju	1222-12321313544131214445243-33332221222222323312222232132213113143121121122 2122	1011
70	Pic	abie	1-1-11-1111111-1-1111111-1-111111111-111-11-11111111111111-1-1111111-111111-1--1-	1011
69	Des	flex	1-11-131111112122222122211112122222 1-1231122--3212-2222521331 11--11--2--1-111131	1011
48	Lyc	anno	---------------1-1-----------1--1-111-111-1-------------1---------------------------	1011
84	Vac	viti	-34325522212211-2212232114221221332213222211122311122222221111111111212121211212	1010
83	Ple	schr	4556564455545455253554543546354563462655352334443323433545114223534241445 2242232	1010
82	Vac	myrt	3355644525455543545363564545535555455455334434433354445546123331323333143 2421453	1010
80	Hyl	sple	2133333432352132125411223342534425233131312212221131332224112112113332414 2231125	1010
72	Lin	bore	22222-211111121111113121121111112211---1-1111211211-211312---21-222-111-1-22--2-	1010
62	Pop	trem	---1-1-11-----1--------1-------1---------------------1----1--------1-1-------1--1	1010
59	Pti	cris	---1-------111-----11-----1-----1--1--1---1-1-----1---------11----1----------1-	1010
85	Pol	comm	------1--------1-11-11-2-11--1--1121----11-124314---1---1--1----------1---1----	100
79	Ort	secu	-11--2-------111-1-11-2-111-1---------1-111111111---1-----11-1-1111-1111--1-11-	100
77	Sor	aucu	--1---1151-11111--111-11111--11--1-1-1111111111-111-111-11111-11111111-1111111-	100
64	Hie	muro	-----------1--1-----------1---------1---------------1-------1-----------1-------1--1	100
60	Dic	scop	1111111-1111-111111111-1111-11111-1-22-11-1111-1211111111111111111-1111111111111	100
54	Tri	euro	1--11--111111111111112----1--1---11--111111111111111111111111111111211111111111111	100
42	Luz	pilo	-------1111111-1111111-1-1-11--1111--1-11111111111111-111-1111111111111111111111-1	100
89	Sph	sp	------2---------------1--1----1---21-------41-1-3--------1------------------------	011
71	Aul	palu	------1----------------------------------111-1--------------1--------1-----------------	011
68	Bet	pube	--1---1-----------1--1----------1----1----111-11--1---------1---1----------------1---	011
67	Con	maja	111--------1--1---------------1-------11---------------1-1---1-----1-1--1-1-111--1212	010
55	Mel	sylv	2------2221--1--11111-1112-1111-1---1121111111111311221111111111111111111321131	010
49	Mai	bifo	--1---121321-4-33223322212132 1-121112331433224332333233323313244434332423 2422341	010
47	Cal	arun	3322-11221211--11------111-1--1-1-1-112----1---1-221332111-41121312 1-2112 3551243	010
45	Pyr	mino	---------1----1---------------------------1--1------1---11---------------11-1---------	010
46	Pot	erec	--1--1------1---1---------------1-----1----1-----1	0011
44	Rub	saxa	11-1----1-11--1-2-1--------------------1--312111-2112-11--211211-11111111--122-212	0011
41	Pte	aqui	---1------------1-----1-------------------211-----11-2--1------11--11-----------1-	0011
38	Sol	virg	-------11-11---1-------------------------1111--111-1-11-111-11---1-1-1-1-1--11111111	0011
32	Gym	dryo	---------1---1----1-1---------1------1-11111-1--1--1--1-2-1---1-----2-1421--1-1--	0011
26	Car	digi	---1-----------------1------------------1-1-111-----1111-1-1-11-1111111111111111111-	0011
20	Oxa	acet	------1----1-1--111---1-----1-11-----11112311222121212111114233324314423121-1212-2	0011
19	Pla	sp	----------------1---1---1-------------1----1-1111--1111111-111-1111-1---1------11--	0011
17	Bra	sp	---------1-----3-11--1-1------------------1-111111111-2111111111321412111132131 2121111	0011
15	Rhy	trqu	---1---1------11---1---------------------11--11---1--11-111-1-1--1-1123111 1121-111	0011
13	Dry	cart	---------------------------------1-------1-111111111 1-1--1-11-1111-1-1-11111--------	0011
34	Ger	sylv	---1-----------11------1--1---1111-111---11	0010
25	Vio	rivi	---2--11---1111-1---1-11--1-1111111111111111	0010
24	Vio	cani	--1---------1-1----1---------1--1	0010
21	Lat	vern	-1---1--------1---11-111-1	0010
14	Mel	nuta	---------------1---------------------------11-----1--------11-11-111-111111-1111--11	0010
9	Hep	nobi	--1-------1--121-1-22-1112111--1	0010
53	Equ	sylv	--1--11-1------1----------1----1--11----------	0001
27	Rub	idae	-------------------1-----------------------11------1-------11------1-1-1------------	0001
16	Fra	vesc	---------1------------------------------------11-11-----1111-111--1111--11111-1-11---1	0001
11	Rho	rose	------------1--1------------------------------11-----1-11--1-1-1211-----111-----2---1-	0001
5	Ver	cham	---1--1--------1-------1-11------1---1------1	0001
2	Ane	nemo	--31----1----------11---	0001
33	Poa	nemo	--1--1-1---1----1----1--11--1----------------------	0000
30	Des	caes	--111--1-1---------11---1-----1------------	0000
18	Ver	offi	--1-----111---------11-11-------------------	0000
8	Cir	pili	---1---1----111-11-1-------------------1----	0000
			1 2 3 3 4 5 6 7 7 6	
			00000000000000000000000000000000000000111111111111111111111111111111111111111111	
			00000001111111111111111111111111111111110000000000000000000000011111111111111111111111	
			00000000000000000000000000000000011100000000000000000011100000000000011111111	
			00000011111111111111111111111111 00000000111111111 000000111111	

Table 2. Key to species.
Taulukko 2. Lajiluettelo.

93 *Calluna vulgaris*	64 *Hieracium* spp.	17 *Brachythecium* spp. (mainly *B. curtum* and *B. reflexum*)
90 *Dicranum polysetum*	60 *Dicranum scoparium*	15 *Rhytidiadelphus triquetrus*
66 *Goodyera repens*	54 *Trientalis europaea*	13 *Dryopteris carthusiana*
61 *Ptilidium ciliare*	42 *Luzula pilosa*	34 *Geranium sylvaticum*
91 *Juniperus communis*	89 *Sphagnum* spp.	25 *Viola riviniana*
86 *Melampyrum pratense*	71 *Aulacomnium palustre*	24 *Viola canina*
81 *Carex globularis*	68 *Betula pubescens*	21 *Lathyrus vernus*
76 *Dicranum majus*	67 *Convallaria majalis*	14 *Melica nutans*
70 *Picea abies*	55 *Melampyrum sylvaticum*	9 *Hepatica nobilis*
69 *Deschampsia flexuosa*	49 *Maianthemum bifolium*	53 *Equisetum sylvaticum*
48 *Lycopodium annotinum*	47 *Calamagrostis arundinacea*	27 *Rubus idaeus*
84 *Vaccinium vitis-idaea*	45 *Pyrola minor*	16 *Fragaria vesca*
83 *Pleurozium schreberi*	46 *Potentilla erecta*	11 *Rhodobryum roseum*
82 *Vaccinium myrtillus*	44 *Rubus saxatilis*	5 *Veronica chamaedrys*
80 *Hylocomium splendens*	41 *Pteridium aquilinum*	2 *Anemone nemorosa*
72 *Linnaea borealis*	38 *Solidago virgaurea*	33 *Poa nemoralis*
62 *Populus tremula*	32 *Gymnocarpium dryopteris*	30 *Deschampsia caespitosa*
59 *Ptilium crista-castrensis*	26 *Carex digitata*	18 *Veronica officinalis*
85 *Polytrichum commune*	20 *Oxalis acetosella*	8 *Cirriphyllum piliferum*
79 *Orthilia secunda*	19 *Plagiothecium* spp. (mainly *P. laetum*)	
77 *Sorbus aucuparia*		

ratively low. Dominance by dwarf-shrubs and common forest mosses prevails. In the Finnish forest site type system, this group may be regarded as a transition type between the *Myrtillus* site type and the *Vaccinium* site type.

2. (0100): The unit is clearly of more mesic character than the preceding one. In the Finnish forest site type system, the group clearly represents the *Myrtillus* site type. However, the unit resembles the preceding one in that there are relatively high abundances of certain light-demanding and xerophilous species (e.g. *Calamagrostis arundinacea* and *Juniperus communis*). A significantly lower abundance of *Deschampsia flexuosa* and the absence of *Polytrichum commune* are noticeable differences in comparison with the subsequent units. The general character of the vegetation resembles relatively dry and open forest.
3. (0101 and 011): An abundance of *Vaccinium myrtillus*, *Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum majus* characterizes this unit. Frequent occurrences of e.g. *Polytrichum commune* and *Orthilia secunda* and, on the other hand, a low number of occurrences of light-demanding and xerophilous species, imply a rather moist and mesic loving vegetation. The number of occurrences of herbs, grasses and mosses typical of rich sites is low, except in subset (011), which is included into this unit due to the small group size. In general, the unit represents the typical *Myrtillus* site type, as described by Cajander. The vegetationally somewhat deviating subset (011) reflects the gradual transition between the *Myrtillus* type and the *Oxalis-Myrtillus* type.
4. (1000): The comparatively mesophilous vegetation characterizing this unit indicates that it represents a rather moist site. *Poa nemoralis*, *Dryopteris carthusiana*, *Gymnocarpium dryopteris*, *Orthilia secunda* and seedlings of *Betula pubescens* occur rather frequently. The abundance of *Polytrichum commune* and *Sphagnum* spp. indicates that paludification has taken place at least to some degree. Herbs and grasses occur significantly more frequently than in the preceding units; also *Oxalis acetosella* is more abundant. For this reason, the unit would be assigned to the *Oxalis-Myrtillus* site type in the Finnish forest site type system.
5. (1001): This unit is characterized by an abundance of *Vaccinium myrtillus* and *Pleurozium schreberi*, which is associated with relatively well represented herb and grass vegetation. However,

the coverages of herbs and grasses are comparatively low. In comparison with the subsequent units, more exacting plants (species subsets 0010, 0001 and 0000) are less abundant. The unit can be interpreted to represent the *Oxalis-Myrtillus* site type, dominated by dwarf-shrubs and common forest mosses.

6. (101 and 111): This unit consists of two subsets set apart at the second level of division in the TWINSPAN analysis. Although they have somewhat different vegetation composition, subset (101) seems to be ecologically closer to subset (111) than to subsets (100) and (110). The abundances of dwarf-shrubs and common forest mosses are clearly lower than in the preceding units, whereas the herb and grass vegetation is rich in species and fairly abundant. The abundance of e.g. *Calamagrostis arundinacea, Convallaria majalis, Deschampsia flexuosa* and *Rubus saxatilis* indicates a considerable supply of light. Subset (101) seems to be of somewhat more mesic character than subset (111), but cannot be treated separately due to the small group size.
7. (1100 and 1101): This unit consists of two subsets set apart at the lowest level of division. Due to insignificant vegetational differences between them, subset (110) is treated combined. In this unit, the herb and grass vegetation is luxuriant; *Oxalis acetosella,* in particular, is considerably abundant. *Gymnocarpium dryopteris, Dryopteris carthusiana, Equisetum sylvaticum, Brachythecium* spp. and *Rhytidiadelphus triquetrus* are typical species of this unit. The general character of the vegetation indicates that the corresponding sites are moister and more shaded than those of the preceding unit.

5. ANALYSIS OF THE SITE FACTORS

The most important environmental factors affecting the forest floor vegetation are the supply of light, microclimate (i.e. humidity and temperature), the moisture content of the soil and the edaphical conditions of the site. Not only the supply of light, but also the microclimate are closely connected to the characteristics of the tree stand. In Fennoscandian coniferous forests especially, the dominance of Norway spruce (*Picea abies*) plays a decisive role in determining these factors (e.g. Cajander & Ilvessalo 1921, Brenner 1921, Sarvas 1951, Teivainen 1952, Sirén 1955 etc.). The basal area is a reasonably good variable in estimating the density of the tree stand (e.g. Vuokila 1980). Consequently, both the total basal area of the tree stand and the basal area of Norway spruce individuals in the stand are incorporated in the model describing the properties of the tree stand. In addition, the dominant age is considered to indicate the maturity of the tree stand and is incorporated as a measure of the successional stage.

The correlations between the tree stand measures can be seen in Table 3. Since the forest stands where deciduous trees are predominate are omitted from the material, the low dominance of Norway spruce implies a high dominance of Scots pine. Dominant age appears to correlate negatively with the two measures of basal area; young spruce stands in particular, seem to be denser than old ones. This may arise as a result of selective cuttings carried out in older stands approaching the regeneration stage. It should, however, be noted that only mature and middle-aged stands are included in the study material. Thus the range of the axis is short and the distribution somewhat skewed. Hence the product moment correlations between age and the measures of basal areas can be biased.

In order to substitute the mutually connected effects of the observed variables by a single effect via the latent variable ξ_1 which is later called the tree stand factor, a measurement model was specified following the general formula (1). The results are presented in Table 4. The model includes only two parameter matrices: lambda x is a vector of factor loadings, i.e. the regression matrix of the tree stand measures on ξ_1, and theta delta is a vector of error variances. The squared multiple correlations (R square) for x-variables represent their reliabilities. The coefficient of determination for the x-variables jointly is a generalized measure of the reliability for the

Table 3. Correlations between the ecological characteristics.
Taulukko 3. Ekologisten tunnusten välinen korrelaatiomatriisi.

Variable – *Muuttuja*	1	2	3	4	5	6	7
1. Total basal area – *Puuston pohjapinta-ala*	1.000						
2. Basal area of spruce – *Kuusen pohjapinta-ala*	0.451	1.000					
3. Dominant age – *Valtapuuston ikä*	–0.227	–0.315	1.000				
4. Amount of humus – *Humuksen määrä*	0.110	–0.021	0.211	1.000			
5. pH of the humus – *Humuksen pH*	–0.040	0.237	–0.363	–0.424	1.000		
6. Nitrogen content – *Humuksen typpipitoisuus*	–0.028	0.452	–0.499	–0.311	0.455	1.000	
7. Calcium content – *Humuksen kalkkipitoisuus*	0.032	0.375	–0.272	–0.329	0.694	0.494	1.000

Table 4. Parameter estimates of measurement model for the tree stand. FCR = factor scores regressions.
Taulukko 4. Puuston rakenteen mittausmallin parametrien estimaatit. FCR = fakrotipistekertoimet.

Variable – *Muuttuja*	Lambda x	t-values	Theta δ	t-values	R square	FCR
Total basal area – *Puuston pohjap.ala*	0.570	4.020	0.675	4.318	0.325	0.253
Basal area of spruce – *Kuusen pohja. ala*	0.791	4.580	0.374	1.517	0.626	0.633
Dominant age – *Valtapuuston ikä*	–0.398	–3.280	0.841	6.389	0.159	–0.142
Total coefficient of determination *Mallin kokonaisselitysaste*	0.701					

whole measurement model (see Jöreskog & Sörbom 1981). The t-values are calculated by dividing each parameter estimate by its standard error, and is used to test whether the true parameter is zero. Parameters whose t-values are larger than two in magnitude are normally judged to be different from zero (Jöreskog & Sörbom 1981).

The coefficient of determination is remarkably high, 0.701, indicating that the measurement model is reasonable. It can be seen from the t-values that most of the parameters are considerably significant. Factor loadings of the tree stand measures represent the magnitude of their effects on ξ_1. Here it is seen that the density of Norway spruce has a strong positive effect on the latent variable. The reliability of the parameter is also very high (0.626). The positive effect of the total density is also considerably high, but the error variance is fairly large (0.675). The dominant age affects ξ_1 negatively; this effect may, however, be biased. In addition, the error variance is considerably large. The factor scores regressions show the weight of each variable on computed scores of the tree stand factor. The tree stand factor may thus be interpreted in such a way that high factor scores represent mainly a high dominance of Norway spruce and also somewhat higher density of the tree stand. The dominant age is also possibly lower than in the stands characterized by low factor scores, the main attributes of which are high dominance of pine and lower density. Consequently, high factor scores represent a low illumination level as well as relatively high and constant moisture conditions on the forest floor. Low factor scores represent a rather high illumination level and more xeric conditions.

As regards the edaphical conditions, the properties of the humus layer are a good measure of the nutrient supply in the rhizospheric horizon of the plants (e.g. Aaltonen 1940, Hinneri 1972). Therefore, attention has been paid to the amount of humus material and its chemical properties, instead of to the underlying mineral soil. It has previously been demonstrated that the pH value of the soil and the total contents of nitrogen and calcium reflect the fertility and the productive capacity of the site rather reliably (e.g. Valmari 1921). Accordingly, variables measuring the corresponding characteristics in the humus layer are incorporated in a measurement model. The amount of humus material is omitted from the model, but is used independently in further comparisons.

Correlations between the measured soil characteristics indicate strong mutual connections (Table 3). The acidity of the soil is associated with the calcium content, which affects the availability of nutrients for plants. The strong positive correlation between the nitrogen and the calcium content is probably due to the fact that the rate of nitrogen mineralization is dependent on the calcium content (e.g. Mälkönen 1982).

The parameters of the measurement model are presented in Table 5. The formulation of the model is equivalent to the model for the tree stand factor. The squared multiple correlations, as well as the t-values, indicate high reliabilities of the x-variables. The coefficient of determination is very high, 0.842, indicating that the measurement model is good. The latent variable ξ_2 can be considered to reflect the overall fertility of the site quite well. As regards the factor scores regressions, the calcium content has the highest weight, whereas the weight of the nitrogen content is rather low. High factor scores may be interpreted to indicate high site fertility, whereas low factor scores are associated with less fertile sites. Computed factor scores are treated as a dependent variable, which is later called the fertility factor.

Consequently, two latent variables (i.e. the tree stand factor and the soil fertility factor) and one observed variable (the amount of humus material) are used in further comparisons. It should be noted that the two latent variables were calculated separately, i.e. the correlation between ξ_1 and ξ_2 were fixed to be zero (cf. Jöreskog & Sörbom 1981).

Table 5. Parameter estimates of measurement model for soil fertility. FCR = factor scores regressions.
Taulukko 5. Viljavuuden mittausmallin parametrien estimaatit. FCR = faktoripistekertoimet.

Variable – *Muuttuja*	Lambda x	t-values	Theta δ	t-values	R square	FCR
pH of humus – *humuksen pH*	0.799	8.110	0.362	3.526	0.638	0.349
Nitrogen content – *Typpipitoisuus*	0.568	5.785	0.677	6.492	0.323	0.133
Calcium content – *Kalkkipitoisuus*	0.869	8.818	0.245	2.198	0.755	0.561
Total coefficient of determination *Mallin kokonaisselitysaste*	0.842					

6. RELATIONSHIPS BETWEEN SITE FACTORS AND VEGETATION UNITS

Computed scores for the tree stand factor and the fertility factor, as well as the observed amounts of humus, were allocated according to the division of the sample plots into vegetation units (1–7). The differences between vegetation units were tested statistically in order to examine the ecological character of different vegetation types and to give some information about the dependency of the vegetation pattern on the measured environmental characteristics. The results of the analyses of variance and the multiple range tests are given in Tables 6–8. An asterisk (*) denotes pairs of groups which differ significantly at the 0.05 level. An (o) denotes pairs of groups which differ significantly at the 0.10 level.

The results concerning the tree stand factor are presented in Table 6. The lowest scores are observed in units 1 and 2; they differ significantly from all the other units. The fact that the vegetation of these units is characterized by light-demanding, relatively xerophilous plants fits well to the ecological interpretation of the tree stand factor. Vegetation unit 3 seems to represent a spruce-dominated, dense stand of the *Myrtillus* type, whereas unit 2 resembles a more pine-dominated and open stand of the same site type. Vegetation units 3–7 seem to closely resemble each other: they represent largely spruce-dominated, relatively dense and closed forest stands. The difference between units 6 and 7, although not statistically significant, gives support to the interpretation of the vegetation analysis: the general character of the vegetation in unit 7 indicates moister and more shady conditions than that of unit 6.

The results concerning the fertility factor are presented in Table 7. The differences are very clear and largely in agreement with the forest site type theory: vegetation units related to the *Oxalis-Myrtillus* site type represent statistically significantly more fertile sites than those related to the *Myrtillus* site type.

As regards units 1–3, only a slight difference between units 2 and 3 can be found. The lower fertility in unit 3 may be a result of the accumulation of raw humus, which often takes place in spruce-dominated, dense stands (cf. Aaltonen 1940, Sirén 1955). As far as vegetation units 4–7 are concerned, the fertility index increases in accordance with the ordination produced by TWINSPAN (cf.

Table 6. Distribution of tree stand factor scores in different vegetation units.
Taulukko 6. Puustofaktoripisteiden jakautuminen näytealaryhmittäin.

Multiple range test (LSD) – *Keskiarvojen monivertailu (LSD-testi)*

Group Ryhmä	*Mean Keskiarvo*	1.	2.	4.	3.	6.	5.	7.
1.	–3.653							
2.	3.070							
4.	8.483	*						
3.	9.243	*	°					
6	10.621	*	°					
5.	13.073	*	*					
7.	15.060	*	*					

(*): p = 0.95
(°): p = 0.90

Analysis of variance – *Varianssianalyysi*

F-ratio – *F-suhde* 4.748***

Table 7. Distribution of fertility factor scores in different vegetation units.
Taulukko 7. Viljavuusfaktoripisteiden jakautuminen näytealaryhmittäin.

Multiple range test (LSD) – *Keskiarvojen monivertailu (LSD-testi)*

Group Ryhmä	*Mean Keskiarvo*	3.	1.	2.	4.	5.	6.	7.
3.	1.759							
1.	1.820							
2.	1.849	°						
4.	1.898	*						
5.	2.011	*	*	*				
6.	2.034	*	*	*	*			
7.	2.145	*	*	*	*	°		

(*): p = 0.95
(°): p = 0.90

Analysis of variance – *Varianssianalyysi*

F-ratio – *F-suhde* 12.483***

Table 1). In other words, the order of the samples, as well as the arranged species list, reflects the overall fertility of the site remarkably well; the abundance of exacting herbs, grasses and bryophytes increases in accordance with the site fertility. The fertility of the sites assigned to unit 4 can be related to that of unit 2; the low fertility of the former may be connected to the effects of paludification. Vegetation units 5–7 seem to make up somewhat different fertility classes, although their limits are gradual.

As regards the amount of humus material, analysis of variance indicates no statistically significant differences. The multiple range test, however, indicates that the amount of humus is somewhat higher on sites assigned to unit 3 than in, for example, those assigned to unit 5. The difference may be interpreted by examining the differences in vegetation composition: the somewhat more luxuriant vegetation in unit 5 indicates a faster rate of litter decomposition as well as a faster carbon and nutrient cycle, whereas in unit 3 the accumulation of raw humus has apparently taken place.

Table 8. Amounts of humus (kg/ hectare) in different vegetation units.
Taulukko 8. Humuksen määrän (kg/ ha) jakautuminen näytealaryhmittäin.

Multiple range test (LSD) – *Keskiarvojen monivertailu (LSD-testi)*

Group Ryhmä	*Mean Keskiarvo*	7.	5.	2.	6.	4.	1.	3.
7.	21 306							
5.	27 204							
2.	28 185							
6.	29 213							
4.	32 839							
1.	34 603	°						
3.	36 714	*	*		°			

(*): p = 0.95
(°): p = 0.90

Analysis of variance – *Varianssianalyysi*

F-ratio – *F-suhde* 1.687$^{(\sim°)}$

7. DISCUSSION

7.1. Methods

Divisive classification methods have seldom been used in forest vegetation research. Jeglum & al. (1982) and Jones & al. (1982) applied TWINSPAN for the classification of Canadian forest ecosystems. In Finland, Pakarinen (1982) has used association analysis (Williams & Lambert 1960, Podani 1979) for the numerical classification of southern Finnish forest types. Due to its polythetic nature and the effective use of quantitative information, TWINSPAN can be regarded as the most appropriate method for divisive classification, particularly when the vegetation consists of many constant plant species (Gauch 1982). In its emphasis on indicator species, TWINSPAN resembles the approach used in practical determination of the Finnish forest site types. The method emphasizes specific, relative abundances of different species rather than absolute coverage values. The use of the Hult-Sernander scale as the pseudospecies cut levels also emphasizes the differences at low abundance levels: lower coverages are scaled more accurately than high ones. Hence it follows that the differences between the coverages of abundant, but less informative common forest plants, affect the classification less than the abundance relationships between indicator plants often characterized by a relatively scanty occurrence. However, the sensitivity of TWINSPAN also makes its sensitive to random (ecologically insignificant) variation in species' abundances. Therefore, the divisions of small groups at low classification levels especially, must be interpreted with care; in many cases it would be useful to analyze the vegetation data by more than one numerical methods simultaneously (cf. Jones & al. 1982).

TWINSPAN reconciles the practical need to form vegetation classes for forest mensurational purposes with the reality of vegetation continua by using ordination to classify both the samples and the species. In this application of TWINSPAN, the classification of both samples and species seems to reflect the overall fertility of the site considerably well. The continuous character of the variation in the vegetation pattern, as well as in fertility characteristics, can be seen in the results: abundances of different species change gradually along the vegetation continuum, thus reflecting the gradual change in site quality. Generally speaking, a correspondingly arranged matrix of species and units, based on a larger and more representative material, would probably be a more suitable tool for site evaluation than qualitative descriptions of vegetation in defined, distinct site classes.

From the viewpoint of classification, it is interesting to compare these results with the application of TWINSPAN for Canadian boreal forest vegetation presented by Jones & al. (1982). Although Jones & al. used only presence/absence data instead of coverage classes, their main division of the samples is equivalent to the first division presented in this study: it subdivides the population into those plots with a reasonably well represented herb and grass vegetation from those plots with a poor to non-existent herb and grass vegetation. The method Jones & al. used for treating the soil data was based on the classification and ordination of site properties, independently of vegetation classification, and is thus not comparable with the results presented here. However, if the main emphasis is on evaluating the mensurational fitness of forest vegetation classes, the two-stage method presented here is probably more valid and unambiguous than indirect comparisons between separate classifications.

Confirmatory factor analysis constituted by measurement models has many applications in econometrics and in the social and behavioral sciences (see e.g. Jöreskog 1969, Goldberger 1972, Jöreskog & Sörbom 1981). In the present study, confirmatory factor analysis is applied for the treatment of ecological data.

The fertility of the soil can be regarded as an unobservable, hypothetical latent variable, which affects the biological productivity of the site (cf. Aaltonen 1940). All measurable site characteristics, i.e. nutrient contents, acidity, moisture etc., affect the overall fertility jointly, and often their effects are cumulative or complementary. In the present study, the measurement model for the overall fertility was extremely simple, consisting only of three observed variables and a latent one. The model was specified under the assumption that the pH of the soil and the nitrogen and calcium contents are valid and adequate measures of fertility. The characteristics of the tree stand also form a complex of variables, the effects of which are not easy to examine separately. Although the model presented for the tree stand factor seems to describe well some of the essential characters of the tree stand, it needs further development and testing in a less uniform material. The validity of the models could be improved by incorporating additional variables characterizing the properties of the soil and the tree stratum.

In practical evaluation of the site quality, the main emphasis is on determining the biological productivity of the site. The major difficulty is encountered in the treatment of a great number of site factors, which affect the site productivity jointly. Confirmatory factor analysis provides a statistical tool for the analysis of the covariance structure between the site factors. The method also provides tools for examining the fit of the model and deciding where the lack of fit is. Thus it enables stepwise improvement of the model (cf. Jöreskog & Sörbom 1981).

7.2. Results

The results presented here emphasize the role of exacting herbs and grasses as indicator species, whereas quantitative differences in the abundances of constant forest plants, such as *Vaccinium myrtillus* and common forest mosses, are less informative. As discussed by e.g. Werger & Maarel (1978), there is a shift in the ecological indicator value of a given species. Near the margins of their distribution area, species are more specific environmental indicators than in the more central parts of their distribution area. Near the centre of a species' distribution area, ecological amplitude of the plant fits well to the combination of the governing environmental factors, and thus it is strongly competitive to other species. Towards the margins, the environmental factors (e.g. climatical conditions, calcium content of the soil etc.) change one by one and the tolerance limits of the species for these factors are approached until one factor becomes critical and determines the occurrence or absence of the species (cf. Werger & Van Gils 1976, Holzner 1978, Willems 1978). Species therefore characterize the plant community, and hence also the site, more distinctly near to the margin of their distribution area (cf. Vinogradov 1965). Exacting herbs and grasses reach their maximum abundance in nemoral forests, whereas boreal coniferous forests can be regarded as a marginal distribution area for them. On the other hand, boreal coniferous forests can be regarded as a central distribution area e.g. for the common forest dwarf-shrubs and mosses mentioned above. The striking difference in the species' richness and the exacting character of the vegetation between units 1–3 and 4–7 imply that the tolerance limits of many exacting species are reached simultaneously. Accordingly, the difference reflects changes in some critical site factors.

As emphasized by e.g. Keltikangas (1959, p. 24), the description of the Cajanderian forest site types is based mainly on the species composition, particularly on constant and abundant plant species, and on the relative quantity of certain plant groups: lichens, mosses, herbs, grasses, dwarf-shrubs and shrubs (cf. Cajander 1926, 1949). The floristic differences are, however, stressed in forestry textbooks, where the identification of the forest site types is based on "quide" or "indicator" species (e.g. Lehto 1964). The position of vegetation unit 5 in the fertility axis illustrates the decisive role of exacting herbs and grasses as indicator species: even though the vegetation has many typical characteristics of the *Myrtillus* site type, i.e. the continuous cover of *Pleurozium schreberi* accompanied by *Dicranum* mosses, the abundance of *Vaccinium myrtillus* and *Vaccinium vitis-idaea*, a comparatively low abundance of herbs and grasses etc., the multiple range test separates this unit clearly from the units 1–3. The well represented herb species diversity and the occurrence of *Oxalis acetosella, Viola riviniana* and *Carex digitata* justify the assignment of this unit to the *Oxalis-Myrtillus* site type.

It should, however, be noted that many highly indicative species are far from being completely constant (frequency = 100 % of suitable sites). On the other hand, some comparatively constant indicator species may occur sparsely over a wide range of variation in the site characteristics. For instance, as demonstrated already by Cajander (e.g. Cajander & Ilvessalo 1921, see also Ilvessalo 1922, Tertti 1944, Lehto 1964 etc.), and as can also be seen in Table 1, a low occurrence of *Oxalis acetosella* is an inadequate criterion for distinguishing the *Oxalis-Myrtillus* site type from the *Myrtillus* site type; only when *Oxalis* is accompanied by other exacting plants such as *Viola riviniana, Melica nutans* etc., or is strikingly abundant, can a site dominated by *Vaccinium myrtillus* be assigned to the *Oxalis-Myrtillus* type.

The vegetational heterogeneity within the sample subset assigned to the *Myrtillus* site type (units 1–3) seems to be induced by the variation in the tree stand properties rather than by edaphical heterogeneity. On the contrary, the vegetation differentiation within the sample subset assigned to the *Oxalis-Myrtillus* site type (units 4–7) clearly reflects the variation in the fertility factor. The results give the impression that the *Oxalis-Myrtillus* site type is internally more heterogenous than the *Myrtillus* site type, representing a continuous transition between the mesic heath forests and the grass- and herb-rich forests (cf. Cajander 1926). However, as emphasized by Keltikangas (1959), a Cajanderian forest site type represents a larger amplitude of variation in the site factors than the different plant association types included in it. From this point of view, the obtained results are in agreement with the Cajanderian distinction of two main types of mesic forest sites: the *Myrtillus* site type and the *Oxalis-Myrtillus* site types can be distinguished rather unambiguously in the field, and the fertility factor indicates that there is a statistically significant difference between them. In relation to this difference, the within-type variation observed in the sample subset assigned to the *Oxalis-Myrtillus* site type is insignificantly small.

REFERENCES

AALTONEN, V. T. 1940. Metsämaa. 615 pp. Porvoo.

AHTI, T., HÄMET-AHTI, L. & JALAS, J. 1968. Vegetation zones and their sections in northwestern Europe. Ann. Bot. Fennici 5: 169–211.

BRENNER, W. 1921. Studier över vegetationen i en del av västra Nyland och dess förhållande till markbeskaffenheten. Referat: Studien über die Vegetation im westlichen Nyland (Süd-Finnland) und ihr Verhältnis zu den Eigenschaften des Bodens. Fennia 43(2): 1–105.

CAJANDER, A. K. 1909. Über Waldtypen. Acta For. Fennica 2(3): 1–175.

— 1926. The theory of forest types. Acta For. Fennica 29(3): 1–108.

— 1949. Metsätyypit ja niiden merkitys. Forest types and their significance. Acta For. Fennica 56: 1–69, 1–71.

— & ILVESSALO, Y. 1921. Über Waldtypen II. Acta For. Fennica 20: 1–77.

DU RIETZ, G. E. 1921. Zur methodologischen Grundlage der modernen Pflanzensoziologie. 272 p. Wien.

GAUCH, H. 1982. Multivariate analysis in community ecology. 298 pp. New York.

GOLDBERGER, A. S. 1972. Structural equation methods in the social sciences. Econometrica 40: 979–1001.

HILL, M. O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol. 61: 237–294.

— 1979. TWINSPAN. A FORTRAN Program for Arranging Multivariate Data in an ordered Twoway Table by Classification of the Individuals and Attributes. Ecology and Systematics, Cornell University. Ithaca, New York. 49 pp.

— , BUNCE, R. G. H. & SHAW, M. W. 1975. Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. J. Ecol. 63: 597–613.

HINNERI, S. 1972. An ecological monograph on eutrophic deciduous woods in the SW archipelago of Finland. Annales Univ. Turkuensis Ser. A. 50: 1–131.

HOLZNER, W. 1978. Weed species and weed communities. Vegetatio 38: 13–20.

HÄMET-AHTI, L., JALAS, J. & ULVINEN, T. 1980. Suomen alkuperäiset ja vakiintuneet putkilokasvit. Helsingin yliopiston kasvitieteen laitoksen monisteita 61: 1–111.

ILVESSALO, Y. 1922. Vegetationsstatistische Untersuchungen über die Waldtypen. Acta For. Fennica 20: 1–73.

JEGLUM, J. K., ARNUP, R., JONES, R. K., PIERPOINT, G. & WICKWARE, G. M. 1982. Forest ecosystem classification in Ontario's clay belt: a case study. Proc. Artificial Regeneration of Conifers in the Upper Great Lakes Region, October 26–28, 1982 Green Bay, Wisconsin, p. 111–128.

JONES, R. K., PIERPOINT, G., WICKWARE, G. M. & JEGLUM, J. K. 1982. A classification and ordination of forest ecosystems in the Northern Clay Section of Ontario: A framework for forest management. Proc. International Symposium on the Dynamics of Boreal Forest Ecosystems: Future Research and Management Requirements, August 23–26, 1982 Lakehead University.

JÖRESKOG, K. G. 1969. A general approach to confirmatory factor analysis. Psychometrica 34: 183–202.

— 1973. Analysis of covariance structures. In: Krishnaiah, P. R. (Ed.): Multivariate analysis III. Academic Press, New York, p. 263–285.

— & SÖRBOM, D. 1981. LISREL V. Analysis of Linear Structural Relationships by Maximum Likelihood and Least Squares Methods. International Educational Services, Chicago.

KELTIKANGAS, V. 1959. Suomalaisista seinäsammaltyypeistä ja niiden asemasta Cajanderin luokitusjärjestelmässä. Summary: Finnish feather-moss types and their position in Cajander's forest site classification. Acta For. Fennica 69: 1–266.

KOPONEN, T., ISOVIITA, P. & LAMMES, T. 1977. The bryophytes of Finland: An annotated checklist. Flora Fennica 6: 1–77.

KUUSELA, K. 1982. Maan bonitointi metsätaloudellisena käsitteenä. Metsä ja Puu 3: 4–7.

LAWLEY, D. N. & MAXWELL, A. E. 1971. Factor analysis as a statistical method. 230 pp. London.

LEHTO, J. 1964. Käytännön metsätyypit. 98 pp. Rauma.

MÄLKÖNEN, E. 1982. Metsämaatieteen perusteita. Helsingin yliopiston metsänhoitotieteen laitoksen tiedonantoja 19: 1–107.

NIE, N. H., HULL, C. H., JENKINS, J. G., STEINBRENNER, K. & BENT, D. H. 1975. SPSS. Statistical Package for Social Sciences. 675 pp. New York.

PAKARINEN, P. 1982. Etelä-Suomen suo- ja metsätyyppien numeerisesta luokittelusta. Summary: Numerical classification of south Finnish mire and forest types. Suo 33(4–5): 97–103.

PODANI, J. 1979. Association-analysis based on the use of mutual information. Acta Bot. Acad. Scient. Hungaricae 25: 125–130.

SARVAS, R. 1951. Tutkimuksia puolukkatyypin kuusikoista. Summary: Investigations onto the spruce stands of Vaccinium type. Comm. Inst. For. Fenniae 39(1): 1–82.

SIRÉN, G. 1955. The development of spruce forest on raw humus sites in Northern Finland and its ecology. Acta For. Fennica 62(4): 1–408.

TAMMINEN, P. 1982. Metsämaan viljavuuden alueellinen jakautuminen. Kenttätyöohjeet 1982. Metsäntutkimuslaitos, maantutkimusosasto. Konekirjoite, 6 pp.

TEIVAINEN, L. 1952. Pohjois-Suomen tuoreiden kangasmetsien kasvillisuudesta. Referat: Über die Vegetation der frischen Heidewälder in Nordfinnland. Ann. Bot. Soc. "Vanamo" 25(2): 1–168.

TERTTI, M. 1944. Mikä metsätyyppi? Ohjeita metsätyypin määrääjälle Suomen eteläpuoliskon kovilla mailla. 31 pp. Helsinki.

VALMARI, J. 1921. Beiträge zur chemischen Bodenanalyse. Acta For. Fennica 20: 1–67.

VINOGRADOV, B. V. 1965. Ecological compensation and replaceability, and the extrapolation of plant indicators. In: Chikishev, A. G. (Ed.): Plant indi-

cators of soils, rocks and subsurface waters, pp. 180–187. New York.
VUOKILA, Y. 1956. Etelä-Suomen hoidettujen kuusikoiden kehityksestä. Summary: On the development of managed spruce stands in southern Finland. Comm. Inst. For. Fenniae 48(11): 1–138.
— 1980. Metsänkasvatuksen perusteet ja menetelmät. 256 pp. Porvoo.
WERGER, M. J. A. & GILS, H. VAN 1976. Phytosociological classification problems in chorological border line areas. J. Biogeogr. 3: 49–54.
— & MAAREL, E. VAN DER 1978. Plant species and plant communities: some conclusions. In: Maarel, E. van der & Werger, M. J. A. (Eds.): Plant species and plant communities, pp. 169–175. The Hague.
WILLEMS, J. H. 1978. Observations on North-West European limestone grassland communities: Phytosociological and ecological notes on chalk grasslands of southern England. Vegetatio 37: 141–150.
WILLIAMS, W. T. & LAMBERT, J. M. 1960. Multivariate methods in plant ecology. II. The use of electronic digital computer for association-analysis. J. Ecol. 48: 689–710.

SELOSTE

TUOREIDEN KANGASMETSIEN KASVILLISUUDEN JAKAUTUMINEN SUHTEESSA ERÄISIIN PUUSTON JA MAAPERÄN TUNNUKSIIN

Työssä tarkastellaan Etelä-Suomen tuoreiden ja lehtomaisten kankaiden metsätyyppikuvassa ilmenevää vaihtelua ja siihen vaikuttavia tekijöitä sekä eräiden monimuuttujamenetelmien soveltuvuutta kasvupaikkaluokitusta koskevaan tutkimukseen. Kerätyn peittävyysaineiston pohjalta suoritettiin pintakasvillisuuden lajiston sekä näytealojen ryhmittely kaksisuuntaista indikaattorilajianalyysia (TWINSPAN, Hill 1979) käyttäen. Ryhmien vastaavuutta metsätyyppien avulla ilmaistuihin kasvupaikkaluokkiin tarkasteltiin. Valituille puusto- ja maaperätunnuksille laadittiin mittausmallit (LISREL, Jöreskog & Sörbom 1981), joiden avulla muuttujien kovarianssirakennetta tarkasteltiin. Mallien avulla laskettiin puuston rakennetta ja maaperän viljavuutta mittaavien muuttujien yhteisvaihtelua kuvaavat näytealakohtaiset faktoripisteet, joiden vaihtelua pintakasvillisuuden perusteella määritellyissä kasvupaikkaluokissa tutkittiin varianssianalyyttisesti.

Käenkaali-mustikkatyyppiä (OMT) edustavat metsiköt erottuivat numeerisessa analyysissa selvästi mustikkatyypin (MT) metsiköistä ruohojen ja heinien sekä eräiden vaateliaampien sammalten esiintymisen perusteella (Taulukko 1). Vastaava ero ilmenee myös lasketun viljavuusindeksin keskiarvojen monivertailussa (Taulukko 7).

Mustikkatyyppi näyttää tulosten perusteella edustavan varsin yhtenäistä viljavuusluokkaa: kasvilajiston runsaussuhteissa ilmenevät erot selittyvät suureksi osaksi puuston rakenne-eroilla (Taulukko 6). Sen sijaan käenkaali-mustikkatyyppi muodostaa heterogeenisemman kasvupaikkatyyppiryhmän. Erot viljavuudessa heijastuvat ruohojen ja heinien suhteellisessa osuudessa kasvipeitteestä sekä eräiden vaateliaiden lehtokasvien esiintymistaajuudessa. Pääjakoon (MT–OMT) verrattuna erot ovat kuitenkin selvästi vähemmän merkitseviä.

Tulokset osoittavat, että indikaattorilajianalyysi soveltuu hyvin kasvupaikkaluokitusta koskevan tutkimuksen apuvälineeksi. Saatu ryhmittely ilmentää verraten herkästi epäjatkuvuuksia kasvupaikkatekijöissä sekä soveltuu myös kasvisosiologisten tunnuslajien etsintään. Laaditut maaperän viljavuutta ja puuston rakennetta kuvaavat faktorimallit yksinkertaistivat huomattavasti kasvillisuuteen vaikuttavien tekijöiden samanaikaista tarkastelua. Etenkin viljavuutta kuvaava malli näyttää toimivan hyvin esitetyssä aineistossa. Konfirmatoorista faktorianalyysia voidaan soveltaa mitattujen kasvupaikan tunnusten kovarianssirakenteen tarkasteluun ja sen avulla voidaan kehittää kasvupaikan viljavuutta kuvaavia indeksejä. Menetelmä mahdollistaa mallien sekä siten myös niistä johdettujen indeksien hyvyyden tilastollisen testaamisen.