Understorey Vegetation in Fresh and Herb-Rich Upland Forests in Southwest Lapland

Markku Lehtelä, Juha-Pekka Hotanen and Pentti Sepponen

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Fresh and herb-rich upland forest sites in the northwestern part of the central boreal vegetation zone in Finland were studied with respect to vegetation structure and vegetation–environment relationships (soil, stand characteristics). Two fresh heath vegetation data sets, one from the northern boreal zone and the other from the central boreal zone, were compared with the data of this study using multivariate methods.

The variation in heath forest vegetation within the climatically uniform area was mainly determined by the fertility of the soil (in this case primarily Ca and Mg) and the stage of stand development. The N, P and K content of the humus layer varied little between the vegetation classes. Fertile site types occurred, in general, on coarser-textured soils than infertile site types, may be due to the fact that the sample plots were located in various bedrock and glacial till areas, i.e. to sampling effects.

The place of the vegetational units of the study area in the Finnish forest site type system is discussed. The vegetation of the area has features in common with the northern boreal zone as well as the southern part of the central boreal vegetation zone. The results lend some support to the occurrence of a northern *Myrtillus* type (p.MT) or at least that intermediate forms of fresh and herb-rich mineral soil sites commonly occur in the studied area. It is argued that the older name *Dryopteris-Myrtillus* type (DMT) is more suitable than *Geranium-Oxalis-Myrtillus* type (GOMT) for herb-rich heath sites in the study area.

Keywords forest site type, forest soil, forest vegetation, multivariate methods, site classification.

Authors' addresses *Lehtelä*, Jyväkuja 3 A 2, FIN-80140 Joensuu, Finland; *Hotanen*, The Finnish Forest Research Institute, Joensuu Research Station, P.O. Box 68, FIN-80101 Joensuu, Finland; *Sepponen*, The Finnish Forest Research Institute, Rovaniemi Research Station, P.O. Box 16, FIN-96301 Rovaniemi, Finland **Fax** +358 73 151 4567
E-mail juha-pekka.hotanen@metla.fi

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1 Introduction

The classification of forest sites in Finland has primarily been based on the so-called Finnish forest site type theory (Cajander 1909, 1949). In Cajanderian site type classification, the understorey vegetation is assumed to reflect the primary site conditions (including productivity) adequately (see Nieppola and Carleton 1991, Nieppola 1993). Furthermore, no clear distinction is made between site and vegetation (Oksanen 1990). According to Oksanen (1990), this has led to poorly defined and circular concepts and vague methods of vegetation analysis. Variation due to climate has been included in the system by use of parallel forest site types, in the different sub-zones of the boreal zone (e.g. Kalela 1961, Ahti et al. 1968). For practical forestry the parallel forest site types are combined to form six site types: grove, herb-rich (grove-like) heath, fresh heath, dryish heath, dry heath and barren heath (e.g. Lehto and Leikola 1987).

The forest site types are arranged in a series from rich-and-moist to poor-and-dry, independent of the successional stage (e.g. Cajander 1949). It is assumed that vegetational site classification can also be applied in managed forests, because the understorey vegetation will retain features characteristic of the site type. However, the variation in successional vegetation over a range of edaphic and climatic conditions has not been thoroughly studied and described in detail (cf. Oksanen 1986, Tonteri et al. 1990a,b, Vanha-Majamaa and Lähde 1991, Nieppola 1992), nor are the effects of intensive forestry (thinnings, fertilization, mechanical site preparation etc.) on the development of forest vegetation well known.

The Finnish forest site type system has also been criticized for several other reasons: (1) the effects of the dominant tree species on the understorey vegetation have usually been underestimated, (2) the system is deductive disregarding important variation between the major types, and (3) that identification of type in the field is subjective (Kuusipalo 1985, Nieppola 1986, Hotanen and Nousiainen 1990 and references therein). In addition to this, local problems with forest site type classification are well documented. One example from north Finland is the treatment of fresh upland forests (Teivainen 1952, Kalela 1952, 1961, Sirén 1955, Keltikangas 1959, Kujala 1979, Sepponen et al. 1982, Lehto and Leikola 1987).

The development of multivariate methods has enabled the relationship between vegetation and environmental factors to be analysed in greater depth. Research in Finland has mainly concentrated on the southern boreal vegetation zone (e.g. Kuusipalo 1985, Lahti and Väisänen 1987, Rajakorpi 1987, Heikkinen 1991, Nieppola and Carleton 1991). Sepponen et al. (1982) and Sepponen (1985) mainly treat vegetation from the northern boreal zone and Mikola and Sepponen (1988) and Hotanen and Nousiainen (1990) have investigated forests in the southeastern part of the central boreal vegetation zone.

The aims of this study are (1) to investigate the structure of fresh and herb-rich heath forest vegetation in the northwestern part of the central boreal vegetation zone in Finland, and (2) to elucidate vegetation–environment relationships. This study forms a basis for expanded and more detailed studies on the ecological background regarding the studies of the potential wood production possibilities in the so-called Lapland triangle area (Penttilä and Varmola 1987).

2 Material and methods

2.1 Study Area

The study area is located in the northern part of the central boreal vegetation zone (the Pohjanmaa-Kainuu forest vegetation zone) (Ahti et al. 1968, Kalliola 1973) (Fig. 1). The mean altitude of forest land in the study area is about 66 m above sea level (Mattila 1986). Annual mean precipitation is 500–550 mm, the length of the thermal growing season 140–145 days, and the effective temperature sum (threshold +5 °C) 900–1000 d.d. (Atlas of Finland 1987).

The bedrock in the area is characteristic of the Länsi-Pohja schist zone, which also contains basic rocks (Atlas of Finland 1986). The southern and southeastern parts of the study area belong to the Pudasjärvi granite-gneiss area. The sample plots used in this study are located on glacial till, which is the predominant soil type in the area (Atlas of Finland 1990).

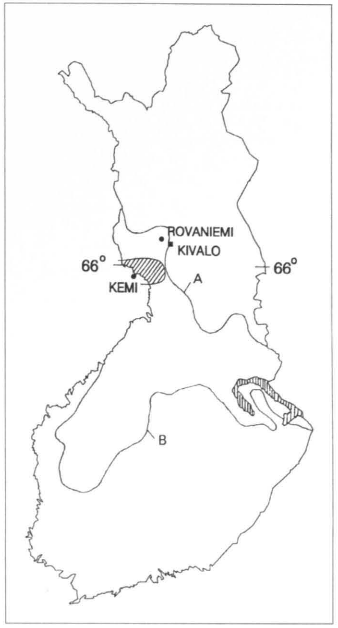

Fig. 1. Location of the study area (diagonal lines = southwest Lapland data) and the border between the northern and central boreal (A) and between the central and southern boreal (B) vegetation zones (Kalliola 1973). ■ = the reference material from Kivalo; vertical lines = the reference material from the state forest management districts of Nurmes and Lieksa.

The predominant site type on upland soils in the area is fresh heath forest. The proportion of grove and herb-rich heath site types out of the productive forest land area is 6–10 %, which is high compared to other parts of the province of Lapland (Atlas of Finland 1988). Grove sites characteristic of the so-called Lapland triangle are located in the area.

2.2 Sample Plots

The permanent sample plots of this study were located on the systematic units (tracts) and plots of the 8th National Forest Inventory (Valtakunnan metsien... 1986). The sample plots were established 1988–89, primarily according to the guidelines of Gustavsen et al. (1988). Among the plots only those containing unpaludified or slightly paludified, fresh and herb-rich heath site types (according to NFI) were included (n = 81).

Plots had to belong to the following development classes to be accepted for the study: (1) seedling or pole stage (RV), (2) middle-aged stand (NK), (3) mature stand (VK), (4) regeneration-mature stand (UK) (Gustavsen et al. 1988). The number of trees on the plot determined the radius and the actual size of the plot (79–1257 m^2). There had to be at least 35 trees on each plot.

The forest site types were classified in the field in accordance with the currently prevailing Pohjanmaa-Kainuu forest site types: fresh heath type = *Deschampsia-Myrtillus* type (DeMT), *Vaccinium-Myrtillus* type (VMT); herb-rich heath type = *Geranium-Oxalis* type (GOMT) (Kalela 1961, Lehto and Leikola 1987). Typical (border) variants of these types were recognized on the basis of site fertility characteristics (Keltikangas 1959). In cases where the coverage of wetland bryophytes (e.g. *Polytrichum commune, Sphagnum capillifolium, S. girgensohnii*) exceeded 10 %, the qualifier "slightly paludified" (s) was added to the forest site type (Table 1). The vegetation and soil samples were collected during 20.6 –24.8.1989.

2.3 Vegetation Analysis

The coverage of the field and bottom layer species was estimated in four quadrats ($2\ m^2$) located systematically on the plots (Fig. 2) using the scale 0.2, 0.5, 0.7, 1, 2, 3, 4, 5, 7, 10, 15, 20,..., 90, 93, 95, 97, 98, 99 and 100 %. Shrubs less than 0.5 m high and tree seedlings were included in the field layer. If an obstacle (e.g. stump, stone, fallen trunk, large tree) occurred in a quadrat, and the coverage of this obstruction was >10 %, the quadrat was moved 1 m towards the centre of the sample plot. If this was not possible, the quadrat was moved 1 m in a clockwise direction with respect to the centre point.

The nomenclature of the vascular plants was in accordance with Hämet-Ahti et al. (1986), *Sphagnum* mosses according to Isoviita (1990),

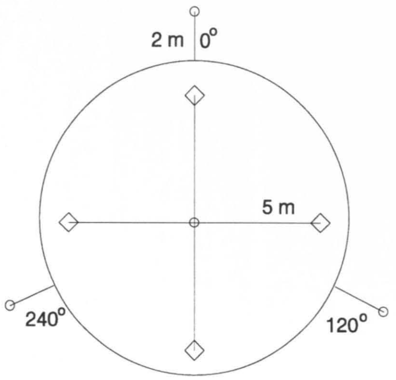

Fig. 2. Location of the three soil sampling points and the vegetation sample plots (4 × 2 m^2).

other mosses according to Koponen (1980), liverworts according to Piippo (1987), and lichens according to Ahti (1981).

2.4 Explanatory Variables

For each tree the diameter at breast height ($d_{1.3}$) and the position were recorded. The stand basal area (m^2/ha) of the plot was calculated on the basis of the diameter of the tallied trees. The mean tree height was calculated from the heights of the sample trees (10–12 trees/plot). Stand age on the plot could not be accurately determined because the majority of the increment cores were rotten. The dominant tree species was taken as the species accounting for at least 70 % of the total stem volume on the plot. In cases where none of the tree species reached this value, the stand on the plot was recorded as a mixed stand. Mixed stands were divided on the basis of the species with the highest volume proportion into spruce-dominated, deciduous-dominated and pine-dominated mixed stands. The canopy coverage on the plot was estimated visually using the scale 0, 5, 10, 15,..., 95 and 100 % (Table 1).

Humus and mineral soil samples (3 sampling points/plot) were taken from outside the sample plot (Fig. 2). In cases where soil samples could not be taken from the prescribed points, e.g. due to stoniness, the sampling point was moved 2 m in a clockwise direction with respect to the centre point. (If soil samples could not be taken from the new point, samples were taken from inside the circular plot, at a point next to each vegetation quadrat). A soil profile of about 30 cm was dug for determination of soil type. The humus samples as well as the mineral soil samples were mixed before analyses. Stoniness was determined using the method of Viro (1952) (Table 1). Soil parameters were also available for the Kivalo area.

The soil samples were analysed at the laboratory of the Rovaniemi Research Station, the Finnish Forest Research Institute. Particle size distribution of the mineral soil samples was determined using a combined sieving and sedimentation method (Niska and Airaksinen 1989). The soil texture class of each plot was determined according to the dominant particle size fraction (Tamminen 1988) (Table 1).

The amounts of acid-extractable nutrients in the soil were determined by extraction with hot 2 N HCl using a weight:volume-ratio of 2:50. Most of the macronutrients (Table 3) were analysed by atomic absorption spectrophotometry. Total nitrogen was determined by the Kjeldahl method. Acid-extractable phosphorus was determined colorimetrically from the same extract (Niska and Airaksinen 1989). The pH and electrical conductivity of the humus samples was determined in distilled water. The organic matter content of the humus samples was determined as the loss in weight on ignition (550 °C). The Kivalo soil samples had been analysed using the same methods.

2.5 Reference Materials

The first reference material was collected in 1981 in the Kivalo area, which is located in the southern part of the northern boreal vegetation zone (Fig. 1). The material consisted of 17 systematically located sample plots from relatively homogeneous, fresh site (*Hylocomium-Myrtillus* type, HMT). The reference plots were located at a mean altitude of about 300 m a.s.l., and were included in the study to represent old spruce stands typical of hill slopes in Peräpohjola (see also Hyvärinen and Sepponen 1988). Annual precipitation in the Kivalo area is 550–600 mm, the length of the thermal growing period 135–140 days, and the effective temperature sum 900–1000 d.d. (Atlas of Finland 1987).

The second reference material was collected in 1981–83 in the Nurmes and Lieksa forestry management districts of the National Board of Forestry (Fig. 1). Systematically located sample plots were part of the 7th National Forest Inventory. Sample plots of the fresh heath type (*Vaccinium-Myrtillus* forest site type, VMT), with a closed tree canopy (TWINSPAN group 1B of Hotanen and Nousiainen 1990, n = 28), were included in the investigation. The mean altitude in the area is about 185 m a.s.l. (Hotanen and Nousiainen 1990), the annual precipitation 550–600 mm, the thermal growing period 145–150 days, and the effective temperature sum about 1000–1100 d.d. (Atlas of Finland 1987). The vegetation of the Nurmes and Lieksa reference material was determined on eight 1 m^2 quadrats and at Kivalo on ten 1 m^2 quadrats.

2.6 Data Analyses

Plotwise mean coverages of the individual plant species were calculated. TWINSPAN classification (Hill 1979) was initially carried out on the material. Plots which differed greatly (n = 12) from the rest of the material were removed on the basis of this classification and preliminary DCA ordination (Hill and Gauch 1980, CANOCO version 2.1: Braak 1987). Such plots (e.g. at the river sides) included spruce swamp sites with a shallow peat layer and groves, and plots whose flora did not represent typical forest vegetation. The most important compositional trends of the variation of the vegetation were detected by global nonmetric multidimensional scaling (GNMDS) using DECODA software (Minchin 1991). GNMDS was applied to a matrix of Bray-Curtis coefficient (see Faith et al. 1987). This matrix of dissimilarities between sample plots was calculated from abundance values of species.

In GNMDS, solutions of 1–4 dimensions were calculated and ten starting configurations in each number of dimensions were used. All possible pairs of ordination configurations were compared using the method of Procrustean analysis (Schönemann and Carrol 1970). A Monte Carlo approach (in DECODA) was used to test the significance of the maximum correlation for environmental variables through the configuration.

After examining the plot of stress vs number of dimensions, plotting the weighted averages of species in the ordination space, fitting vectors of maximum correlation for environmental variables and printing condensed ordered tables with both samples and species along ordination axes it was found that two dimensions were needed in GNMDS. In Procrustean analysis the minimum stress configurations of the two dimensional solutions were all identical.

Both default options and octave scaling were used as the abundance threshold values of pseudo-species in TWINSPAN. The result obtained with octave scaling was ecologically more interpretable, and the classification performed in this way corresponded better to the classification made in the field presumably due to the fact that the material contained rather many constant species with low coverage (Maarel 1979). Three plots were taken as the smallest permitted group size in TWINSPAN. This enabled more precise analysis of the internal structure of the groups and distinction between the border variants. Default parameters were applied in all other cases.

All the species were included in the TWINSPAN classification and GNMDS ordination (Table 2). The properties of the humus layer were tested with one-way analysis of variance using TWINSPAN groups as classes in the ONEWAY (SPSS-X User's Guide 1988). Since the humus variables were characterized by high variation within the groups (Table 3) (cf. also Tamminen 1991) a logarithm transformation was performed for the variables (except pH) before testing.

The reference materials were compared with TWINSPAN and with the DCA ordination in which the reference sample plots could be passively placed in the ordination space (Braak 1987). The axes were detrended by segments and the significance of rare species was reduced by applying downweighting option. The axes were not rescaled. All the species were also included in the comparison analyses, but vegetation descriptions were standardized between the three different data sets.

Table 1. Parameters of the southwest Lapland sample plots. Forest site type: + and – = border variants, (s) = slightly paludified. Dominant tree species (in mixed stands in parentheses): 1 = Scots pine, 2 = Norway spruce, 3 = deciduous species, 4 = mixed stand. Soil type according to the predominant particle fraction: HHt = finer finesand (glacial till), KHt = fine sand (glacial till), HHk = sand (glacial till), KHk = coarse sand (glacial till). Stoniness (Viro 1952): I = low stoniness, II = stoney, III = extremely stoney. Development class: RV = seedling or pole stand, NK = middleaged stand, VK = mature stand, UK = regeneration-ripe stand.

TWINSPAN group	Sample plot no.	Forest site type	Dominant tree species	Soil texture class	Stoniness class	Basal area (m^2/ha)	Canopy coverage	Development class
1	202	GOMT+	2	HHk	II	40	75	UK
1	203	GOMT+	2	HHk	I	36	75	VK
1	252	GOMT+	2	HHk	I	19	55	VK
2	201	GOMT	4 (2)	HHk	I	35	70	UK
2	242	GOMT	2	KHk	I	23	65	VK
2	243	GOMT	2	KHt	I	23	70	VK
2	251	GOMT	2	HHk	I	20	55	VK
2	253	GOMT	2	HHk	II	21	50	VK
2	282	GOMT	4 (3)	KHk	II	39	70	VK
2	283	GOMT	2	HHt	II	14	65	VK
2	93	GOMT	2	KHt	III	13	55	VK
2	281	GOMT–	3	KHk	II	47	75	VK
2	312	GOMT–	2	KHk	II	21	70	VK
2	543	DeMT(s)	2	KHt	II	26	65	VK
3	221	GOMT	3	KHt	III	25	75	VK
3	141	GOMT	2	HHk	I	7	55	RV
3	142	GOMT	4 (3)	KHt	II	10	70	RV
4	241	GOMT	2	KHk	I	19	65	VK
4	393	GOMT	4 (3)	KHt	II	19	75	VK
4	222	GOMT–	4 (3)	HHk	II	26	75	VK
4	311	GOMT–	4 (3)	HHk	II	21	70	VK
4	313	GOMT–	4 (3)	HHk	II	30	80	UK
4	392	GOMT–	2	KHt	II	16	65	NK
4	92	GOMT–	2	KHt	II	13	60	VK
4	441	DeMT	2	KHt	I	19	60	VK
4	442	DeMT	2	KHt	II	20	70	VK
4	443	DeMT	2	KHt	II	17	55	VK
4	81	DeMT	2	KHt	II	13	65	VK
4	82	DeMT	2	KHt	II	8	55	NK
4	223	VMT+	4 (3)	HHk	III	26	75	VK
4	402	VMT+	2	HHk	II	17	65	VK
4	403	VMT+	2	HHk	II	20	70	VK
4	83	VMT+	2	KHt	I	11	60	VK
4	91	VMT+	2	KHt	II	13	65	VK
4	401	VMT	4 (3)	HHk	II	18	75	VK
4	172	VMT	4 (2)	HHt	II	15	65	NK
4	552	VMT	4 (2)	HHk	II	16	60	VK
5	143	GOMT–	4 (3)	KHt	II	5	35	RV
5	181	GOMT–	4 (2)	KHt	II	22	70	VK
5	182	GOMT–	4 (2)	KHt	II	15	75	NK
5	372	VMT+	2	KHt	II	15	65	VK
5	373	VMT+	2	HHt	II	12	55	VK
5	391	VMT+	4 (3)	KHt	II	13	55	NK
5	173	VMT+	4 (3)	KHt	II	12	55	NK
5	183	VMT+	2	KHt	II	10	55	NK
5	161	VMT+(s)	2	KHt	I	26	75	NK
5	171	VMT	4 (2)	HHt	III	11	60	NK
5	371	VMT	2	KHt	II	21	75	VK
6	191	VMT	3	HHk	II	28	65	VK
6	192	VMT(s)	4 (2)	KHt	I	10	65	NK
6	193	VMT	3	KHt	II	43	70	NK
6	301	VMT(s)	2	KHt	I	12	55	NK
6	302	VMT(s)	2	KHt	I	18	70	NK
6	303	VMT(s)	2	KHt	I	9	65	NK
6	162	VMT	2	KHt	II	12	60	NK
6	163	VMT	2	KHt	I	15	70	NK
7	293	VMT(s)	2	KHt	I	11	60	NK
7	361	VMT(s)	2	KHt	I	15	70	VK
7	362	VMT	4 (2)	KHt	I	12	65	VK
7	363	VMT(s)	4 (2)	KHt	I	16	60	VK
7	381	VMT	4 (3)	KHt	I	18	65	VK
7	382	VMT(s)	4 (2)	KHt	I	11	55	VK
7	383	VMT(s)	4 (3)	KHt	I	20	70	NK
7	532	VMT(s)	2	KHt	I	12	60	NK
7	553	VMT	4 (1)	HHk	II	16	70	VK
8	492	VMT–(s)	2	KHt	I	4	35	RV
8	493	VMT–(s)	4 (1)	KHt	I	5	40	RV
8	531	VMT–(s)	4 (2)	KHt	I	14	55	NK
8	533	VMT–(s)	2	HHt	I	6	45	RV

Table 1 contd.

Table 2. Vegetation on the sample plots by TWINSPAN group. Species abundance is according to octave scaling (see Fig. 5).

	1	2	3	4	5	6	7	8
PYROLA ROTUNDIFOLIA	1-1	1-11-------	---	--------------------	-----------	--------	--------1	----
CAREX VAGINATA	1-4	1131-------	13-	--------------------	------1----	--------	---------	----
EQUISETUM PALUSTRE	4--	--1-------4	---	--------------------	-----------	--------	------1--	----
CAREX CESPITOSA	---	--3--------	---	--------------------	-----------	--------	---------	----
CORNUS SUECICA	--3	-5643-1--41	--1	--11--------15--1---	------1----	--------	---------	----
POLYGONUM VIVIPARUM	---	-1-----1---	---	--1-----------------	-----------	--------	---------	----
RHYTIDIADELPHUS TRIQUETRUS	741	4661764-1--	---	--4---------1-------	-----------	--------	---------	----
SPHAGNUM FIMBRIATUM	---	--11-------	---	--------------------	-----------	--------	---------	----
CIRSIUM HELENIOIDES	3--	1---1------	1--	-------------------1	-----------	--------	---------	----
EQUISETUM PRATENSE	455	-1-1-------	---	-------------------1	-----------	--------	---------	----
GOODYERA REPENS	1-1	----------1	---	--------------------	-----------	--------	---------	----
LISTERA CORDATA	--1	1----------	---	--------------------	-----------	--------	---------	----
THELYPTERIS PHEGOPTERIS	-4-	-----------	---	--------------------	-----------	--------	---------	----
VICIA CRACCA	1--	11---------	1--	--------------------	-----------	--------	---------	----
HIERACIUM SYLVATICA	111	11----1----	1--	-------------1-----1	-----------	--------	---------	----
MONESES UNIFLORA	-11	----------1	---	--------------------	-----------	--------	---------	----
PLAGIOMNIUM CUSPIDATUM	-14	----------1	---	--------------------	-----------	--------	---------	----
DAPHNE MEZEREUM	3--	-----------	---	--------------------	-----------	--------	---------	----
GERANIUM SYLVATICUM	454	13113-15113	33-	1-3-----1111-1--11-3	1-------1-3	--------	--------1	----
GYMNOCARPIUM DRYOPTERIS	-65	56556565556	3-3	--11-1----53-1-115-5	13-64-311-4	--------	---------	----
RUBUS SAXATILIS	543	133111--1-1	4--	1-1--1--1--1-------1	33----11113	--------	---------	----
SOLIDAGO VIRGAUREA	133	11313-45431	11-	1111-1--1111-11-1111	131111-1113	----11--	--------1	----
CALAMAGROSTIS CANESCENS	---	----1------	--1	--------------------	-----------	--------	---------	----
DESCHAMPSIA CESPITOSA	---	1--1-------	1-1	--------------------	1----------	--------	---------	----
MAIANTHEMUM BIFOLIUM	131	44331153514	134	15131133113331311131	441111-1111	----11--	---------	----
PARIS QUADRIFOLIA	1-1	-----------	1--	--1-----------------	-----------	--------	---------	----
JUNIPERUS COMMUNIS	1--	31----11---	--1	---11--11-----------	---1------1	--------	--------1	----
DIPHASIASTRUM COMPLANATUM	---	-----------	---	----111------11-1---	-----------	--------	---------	----
MILIUM EFFUSUM	---	-----------	--1	1-------------------	-----------	--------	---------	----
ORTHODICRANUM MONTANUM	---	-----------	--1	------------1-------	-----------	--------	---------	----
MELICA NUTANS	1--	11---------	411	--------------------	-----------	--------	---------	----
POA NEMORALIS	---	----1------	1-1	-------------1------	-----------	--------	---------	----
CONVALLARIA MAJALIS	5--	-----------	131	43-----1------------	-----------	--------	---------	----
CALAMAGROSTIS PURPUREA	1--	-----------	1--	--------------------	------1----	--------	---------	----
BRACHYTHECIUM SPP.	-11	-------1--4	-3-	11-1---1---1-1----1-	111-1111-11	--------	---------	----
CLADONIA CHLOROPHAEA	---	1----------	---	--1-----------------	---------1-	--------	---------	----
CALAMAGROSTIS LAPPONICA	-1-	-----1--1-1	-11	----------------1---	1----1-----	-----1--	---------	----
LINNAEA BOREALIS	415	44433111534	113	45144131111111311113	11111111311	11311--1	11--1---1	----
SORBUS AUCUPARIA	111	--11113-11-	-1-	1--1--111-41-11-111-	1-111111-1-	---11--1	--------1	----
MELAMPYRUM SYLVATICUM	1-1	111-11-1411	111	1111-111-11111111111	131111-1111	1-1--1--	--------1	----
PELTIGERA APHTHOSA	---	-----------	---	---11-1-1---------1-	-1---1-----	--1-----	---------	----
EPILOBIUM ANGUSTIFOLIUM	-1-	1---11----1	1--	--------1--111----1-	1111-1-1113	--111-1-	---------	----
EQUISETUM SYLVATICUM	-57	--41------5	---	--------------------	------1----	1-1----1	--1-31---	-1--
CALAMAGROSTIS ARUNDINACEA	---	11----11---	---	111----------------1	-----------	--------	-1------1	----
LYCOPODIUM ANNOTINUM	143	-41-1113314	14-	4--11---1111111111-1	--111-1----	1311---3	1------13	----
DICRANUM MAJUS	---	-133-451314	1-1	--141-11-1-11-1-11--	1-------111	-411-1--	-1--1--1-	-1--
LUZULA PILOSA	111	11111111111	111	1111--11111111111111	11111111111	-11111--	1---1---1	1-1-
ORTHILIA SECUNDA	1-1	11-11--11-1	---	--1---1----111--1111	1--1-------	1-1-1--1	----11---	----
TRIENTALIS EUROPAEA	111	111-1111411	111	11-111111111111111-1	11111111111	-1111111	----1----	---1
VACCINIUM MYRTILLUS	774	75675787677	565	87787677788885787776	63866647784	77777687	878778676	-513
DESCHAMPSIA FLEXUOSA	1--	1111111351-	143	11111111111111111111	111111-1111	11111111	111111-11	1111
MELAMPYRUM PRATENSE	1--	11-11-1131-	---	--1111--1111-11111-1	1-1-11-1111	-1-1111-	11--11111	--1-
HYLOCOMIUM SPLENDENS	867	87768778888	558	67688888877888878867	56667857783	45436511	778657788	4311
PICEA ABIES	--1	1111-1-11-1	11-	1111111-11111-1111-1	111-11111-1	1113111-	-1-11----	1111
VACCINIUM VITIS-IDAEA	645	77574543544	665	66757665435655545476	76566657666	56765656	466664637	4555
DICRANUM SCOPARIUM	-14	1111453-11-	313	31331114341311434331	54413551111	145534-1	41131-11-	3143
POPULUS TREMULA	---	-1---1--1-1	---	--1----1----1-3---1-	-1-111--11-	------5-	---------	--1-
CLADONIA SPP.	---	-----------	---	--------------------	--1--1---1-	--------	---1-----	----
PELTIGERA CANINA	---	-----------	---	-1--------------1---	-11--1-1---	--------	--1-----1	----
PLAGIOTHECIUM SPP.	---	----1------	---	-----11---11-1----1-	-111-------	-------1	---------	1-1-
DICRANUM FUSCESCENS	---	----1------	---	---------1----111-1-	13--11-----	----1---	1-----1--	----
CLADONIA FURCATA	---	-----------	---	1-1--1---1----------	111--------	-1-1----	1--------	----
PINUS SYLVESTRIS	---	-----------	---	--------------1----1	-----------	--------	---------	1---
PTILIUM CRISTA-CASTRENSIS	---	-----------	1-1	3---511133--1-------	-1---1----1	-11-----	--111-1--	----
BETULA PUBESCENS	--1	-111-1--1--	1--	--1-1-1-1----------1	--1----1---	1--11---	-----11-1	11-1
BARBILOPHOZIA LYCOPODIOIDES	---	---1--1111-	1-1	---1---1111-1-------	------1---3	-11--1--	-----1131	----
DICRANUM POLYSETUM	135	11564----11	3-4	-131163313111-131311	41411345753	33433343	31-54511-	6141
PLEUROZIUM SCHREBERI	646	77477645776	868	58778887887667888778	88765768877	77888873	988887758	8888
CLADINA RANGIFERINA	---	-----------	1--	-11--11-1-11----1-1-	111111--111	-1-111--	1111-1--1	1111
ONCOPHORUS WAHLENBERGII	---	-----1-----	---	--------1-------1---	-----1----1	--------	---------	-111
POLYTRICHUM JUNIPERUM	---	-----------	1--	----11--3-----------	11---1--111	----1-1-	-1-1-----	1--1
CLADONIA CORNUTA	---	1----1----1	-11	-----1--1--11-1-1-11	11111111111	--1111--	-111--1-1	1111
CLADINA ARBUSCULA	---	-----------	---	-----1--1-----------	-1--11--11-	----1-1-	-1-1----1	111-
CLADONIA FIMBRIATA	---	-----1-----	--1	-----1--1-----1-1-1-	----111-1-1	--111111	---1-----	1111
ICMADOPHILA ERICETORUM	---	-----------	---	--------------------	---11------	----11--	---------	----
LEDUM PALUSTRE	---	-----------	---	---3-----1----------	-----------	--------	141---1--	--1-
DICRANUM BERGERI	---	-----------	---	--------5-----------	-----1-----	--------	---1-----	1-33
EMPETRUM NIGRUM	---	-----------	1--	--511111-1----111111	31--11-1114	--------	453444335	1135
VACCINIUM ULIGINOSUM	1--	1-41-------	4--	--13-----1----------	---------4-	----1---	13-3-3341	5-64
CLADONIA PYXIDATA	---	-----------	---	--------1---1---1---	1-------1--	---1----	---1---11	1111
CLADONIA SULPHURINA	---	-----------	---	----------------1---	-----1-1-1-	---1----	-1-1-1--1	-11-
CLADONIA BOTRYTES	---	-----------	---	--------------------	-----1----1	---1----	---1-----	1--1
RUBUS CHAMAEMORUS	---	-----------	---	--------------------	-----------	--------	-------11	----
SPHAGNUM ANGUSTIFOLIUM	---	-----------	4--	--------------------	-----------	--------	----146-5	---4
AULACOMNIUM PALUSTRE	---	-----------	---	---------1----------	-----------	--------	-------1-	5-11
POLYTRICHUM STRICTUM	---	-----------	---	--------------------	-----1-----	----1-3-	---111---	1331
HYPNUM CUPRESSIFORME	---	-----------	---	--------------------	-----------	--------	---------	3-3-
POLYTRICHUM COMMUNE	---	---415-1131	---	---4-----11--3111---	-1111--1--1	787736-1	-54577667	7767
PYROLA CHLORANTHA	---	-----------	---	--------------------	-----------	--1-----	-1-------	----
CLADONIA DEFORMIS	---	-----------	---	--------------------	-----------	------11	--1------	----
SPHAGNUM GIRGENSOHNII	--4	-----7-----	---	--------------------	-----------	7-------	---4-6---	----
CAREX GLOBULARIS	-41	--1-------5	---	--11---------------1	------1----	141---13	-111-1111	11-1
POHLIA NUTANS	--1	-----------	---	--------------------	-----------	------11	---------	----
CLADONIA CENOTEA	---	-----------	---	--------------------	-----------	--1--1--	---------	----

Table 3. The chemical and physical properties of the humus layer. HMT = the reference material from Kivalo. Significance of one-way analysis of variance is shown.

TWINSPAN group	n	Thickness of humus layer, cm x̄	S.D.	Organic matter, % x̄	S.D.	pH x̄	S.D.	Electrical conductivity x̄	S.D.
1	(3)	8.7	2.1	69	4	5.5	0.3	1271	274
2	(11)	8.8	1.8	78	8	4.8	0.4	1576	584
3	(3)	7.0	1.9	56	19	5.2	0.3	1585	238
4	(20)	6.9	1.5	69	11	4.5	0.3	1579	405
5	(11)	7.8	6.7	67	9	4.5	0.3	1389	675
6	(8)	9.5	2.1	77	11	4.2	0.3	960	319
7	(9)	8.6	2.3	86	6	4.1	0.4	1005	377
8	(4)	6.9	1.7	82	5	3.9	0.1	1106	491
HMT	(17)	6.9	1.0	78	16	4.2	0.2	-	-
F		2.2*		3.2**		14.3***		3.1**	

	N x̄	S.D.	Ca x̄	S.D.	P x̄	S.D.	K x̄	S.D.	Mg x̄	S.D.	Fe x̄	S.D.	Al x̄	S.D.	Mn x̄	S.D.	Na x̄	S.D.
	%		mg · 100^{-1}															
1	1.11	0.25	1668	476	34	6	68	12	195	43	98	102	32	19	373	421	164	30
2	1.39	0.12	966	515	42	13	94	37	154	74	44	25	25	13	119	92	127	28
3	1.08	0.26	946	218	46	15	97	24	222	59	81	45	28	8	230	111	168	33
4	1.15	0.17	580	263	45	8	109	28	97	41	33	14	16	5	121	89	146	40
5	1.19	0.34	493	207	41	7	100	29	75	29	37	30	22	25	148	146	135	32
6	1.26	0.28	246	72	46	11	86	21	69	28	67	43	37	17	20	9	127	33
7	1.18	0.12	369	223	35	5	74	25	82	65	41	22	21	11	35	43	87	9
8	1.21	0.11	319	149	31	3	62	5	53	4	20	4	13	4	21	13	97	10
HMT	1.06	0.18	271	57	38	8	105	25	57	12	29	13	35	22	-	-	-	-
F	2.4*		18.5***		2.5*		3.3**		12.0***		3.9***		4.0***		7.9***		5.6***	

3 Results

3.1 GNMDS Ordination

On the first axis the sample plots were located running from left to right approximately in the order GOMT+, GOMT, GOMT–, DeMT, VMT+, VMT and VMT–, i.e. in accordance with the fertility series of the forest site types (Fig. 3). Some overlapping occurred.

The 1st axis in the ordination, i.e. the main compositional gradient (coenocline), primarily seems to represent the variation in site fertility. Demanding species such as *Equisetum pratense, Rhytidiadelphus triquetrus* and *Plagiomnium cuspidatum* obtained low scores along GNMDS1. On moving to the right, the species were replaced by others, with less demanding site requirements – the species at the end of the axis were ones characteristic of northern (poor) fresh and dryish heath sites and their paludified variants, e.g. *Empetrum nigrum, Cladina arbuscula, C. rangiferina, Polytrichum commune, P. strictum* and *Aulacomnium palustre* etc. (Fig. 4).

However, the variables which displayed strongest monotonic trends across the ordination, notably Ca, Mg (and pH), stand basal area and canopy coverage were located at angles to the axes (Fig. 3). For instance, the degree of shading in terms of e.g. canopy coverage is connected with the first axis (fertile sites are denser than poor sites) but also with the second compositional gradient. Thus, the axes represent ecological complex factors (cf. Økland 1990)

The dominant tree storey on the plots which received high scores on the 2nd axis had been thinned a few decades earlier, and the present dominant storey was either a rather sparse pole stand or a middle-aged stand. *Dicranum majus* and a spruce swamp species *Sphagnum girgensohnii*, for instance, which are species which thrive in the shade, received low scores on the

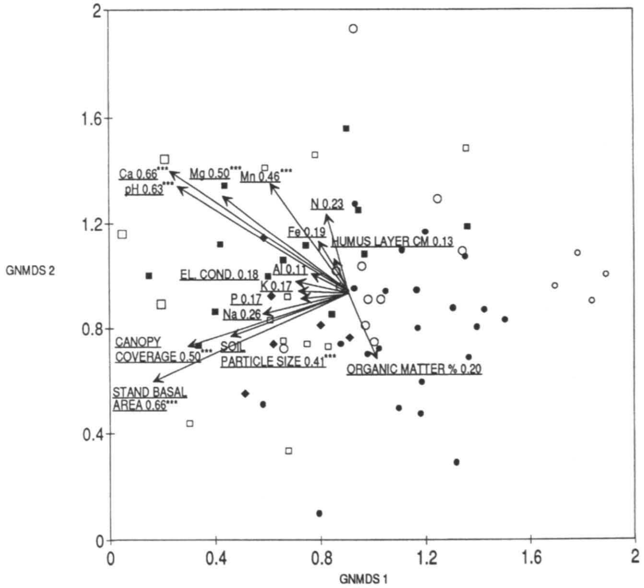

Fig. 3. GNMDS ordination of the samples. □ = GOMT+, ■ = GOMT, □ = GOMT–, ◆ = DeMT, ○ = VMT+, ● = VMT, ○ = VMT–. The vectors represent the correlations of environmental variables between the two-dimensional ordination space.

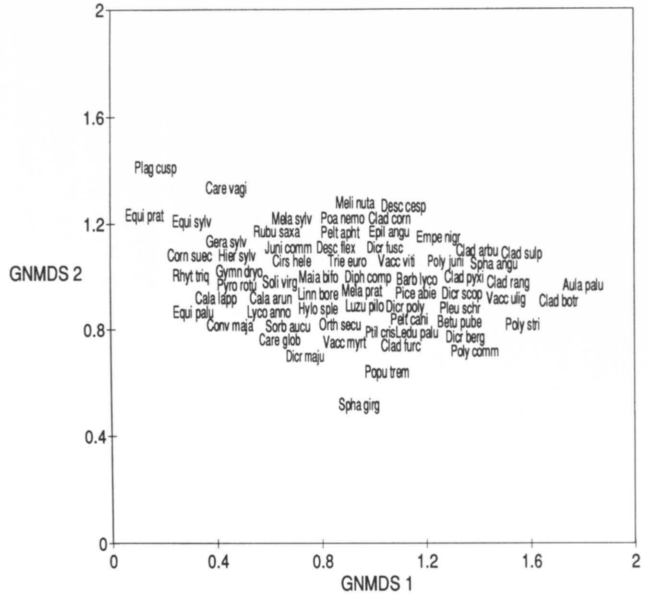

Fig. 4. Weighted averages of most frequent species (cf. Table 2) in GNMDS ordination (parallel to Fig. 3).

2nd axis, while correspondingly the light-favouring species, e.g. *Deschampsia cespitosa, Melica nutans* and *Epilobium angustifolium* had high scores (Fig. 4). A few of the low-shade, herb-rich heath plots were located up to the left in the ordination. The acid-extractable calcium content was high on these sample plots.

The dominant particle size in the mineral soil increased to the left in the ordination (Fig. 3). Thus, in this material the fertile site types occurred, on the average, more frequently on coarser-textured soils than the infertile site types. For instance, most of the herb-rich upland sites were located on either coarse sand or sand glacial till (KHk, HHk), whilst all the DeMT plots and most of the VMT plots were located on fine sand glacial tills (KHt) (Table 1).

The correlations of the thickness of humus layer and the organic matter content of humus layer within the ordination space were low (Fig. 3, see also Table 3). The soils at the infertile end of the material were compacted, with subsequent slight paludification (cf. Table 1).

Also the nitrogen content and the acid-extractable phosphorus and potassium contents displayed weak trends through the ordination configuration. The maximum correlation for the manganese content was quite high (Fig. 3); the values were highest at the fertile end and lowest in the infertile groups of the material (Table 3).

3.2 TWINSPAN Classification

The main division on the left side of the TWINSPAN classification separated all the herb-rich heath sites, the fertile VMT border variants, the DeMT plots and five VMT plots (Fig. 5, Table 1). Most of the plots classified as VMT and the infertile VMT variants were separated on the right hand side. Most of the plots on the right hand side of the main division were characterized by slight paludification.

The most fertile (GOMT+) and most infertile (VMT–) border variants were separated into their own groups (1 and 8), but a number of different types occurred in groups 4 and 5 (Table 1). The groups contained sample plots with a rather even spread of different species of tree. The deciduous-dominated mixed stands were concentrated in these groups, which may be due to the heterogeneous number of site types and border variants. Compared with the group 4 the group 5 (*Epilobium angustifolium*) contained younger development classes (Table 1).

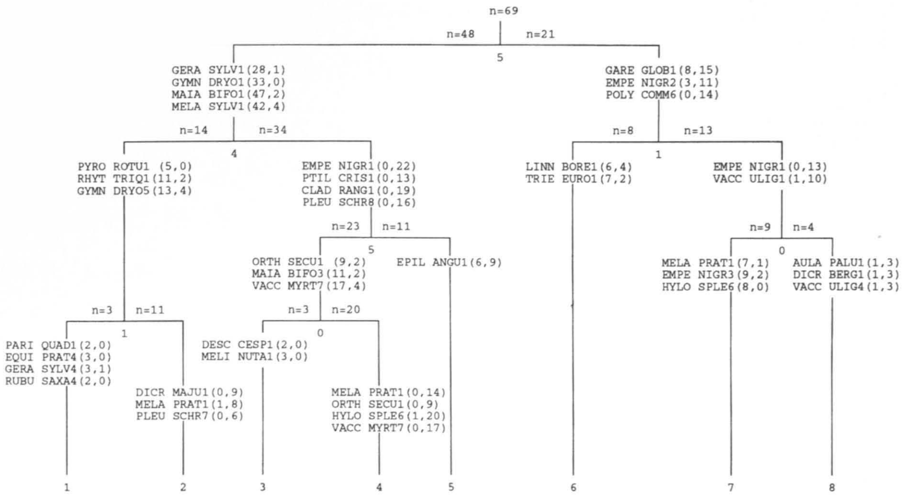

Fig. 5. TWINSPAN classification of the fresh and herb-rich upland forests of southwest Lapland. The most important indicator species are denoted using abbreviations, e.g. MAIA BIFO = *Maianthemum bifolium* (cf. Table 2). Octave scaling (number after the abbreviation) was used for the indicator species abundances as follows way: 1 = +, 2 = 0.5–1 %, 3 = 1–2 %, 4 = 2–4 %, 5 = 4–8 %, 6 = 8–16 %, 7 = 16–32 %, 8 = 32–64 %, 9 > 64 %. The number of borderline cases is indicated at each division.

The species in TWINSPAN group 3 (GOMT) were more demanding and light tolerant than those in group 4, e.g. *Melica nutans* and *Deschampsia cespitosa* (Fig. 5, Table 2). Of the three plots in the group, two in fact represented pole stage stands (RV) (Table 1). All the plots in groups 6 and 7 had been classified in the field as VMT. The flora in group 6 was slightly more demanding and there were clearly more middle-aged stands than in group 7.

3.3 Relationship between the Vegetation of the SW Lapland Heath Sites and the Reference Material

In the comparison analyses the difference between the SW Lapland fresh heath sites and the Kivalo HMT sites was somewhat clearer than that for the VMT plots of the Lieksa and Nurmes forestry management area (Figs 6 and 7). In the DCA ordination the HMT plots were mainly separated from the other fresh heath sites on the 2nd axis. Liverworts (*Hepaticae* spp.) were exceptionally abundant on the Kivalo HMT plots; *Dicranum majus*, for instance, was also rather abundant. The Lieksa and Nurmes VMT plots were well mixed with the VMT plots of this study in the ordination (apart from the paludified and pole-stage stands at the top and bottom on the right).

In the TWINSPAN classification the Lieksa and Nurmes plots were all in the same group, apart from one slightly paludified plot. Howev-

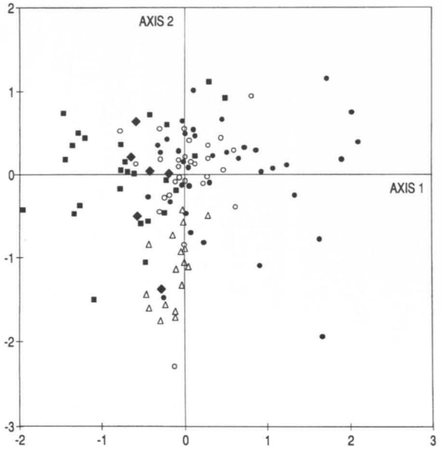

Fig 6. DCA ordination of the sample plots in southwest Lapland and the reference materials (cf. Fig. 1). southwest Lapland: ■ = GOMT, ◆ = DeMT, ● = VMT; △ = HMT from Kivalo, ○ = VMT from Nurmes and Lieksa. The reference sample plots are passively placed in the ordination. Eigenvalues of the axes: 1. = 0.285, 2. = 0.094.

er, the same group also included many of the VMT plots of this study (Fig. 7). (The class was not clearly divided areally at the lower division levels, 4th to 6th). The three Kivalo HMT plots were separated from the group in question, and the indicator species again included *Hepaticae* spp. The sample plots on fresh heath sites, where wetland species occurred, were separated on the right in the dendrogram on the second division level of TWINSPAN. The third division level clearly distinguished the five plots with slight pine bog characteristics from those with spruce swamp species.

4 Discussion

The results show that variation in the vegetation on different heath sites within a climatically relatively uniform area is primarily determined by the fertility of the soil and the stage of development of the tree stand (cf. Lahti and Väisänen 1987, Tonteri et al. 1990a,b). The lengths (and the eigenvalues in Fig. 6) of the most important axes in the ordination analyses were, in fact, not very high compared to those reported in many other studies (e.g. Sepponen 1985, Kuusipalo 1985, Hotanen and Nousiainen 1990, Heikkinen 1991, Nieppola and Carleton 1991, Økland and Eilertsen 1993). The main reason for this is that the range of variation along the major environmental complex-gradients (soil fertility, successional stage) was restricted. The occurrence of wetland vegetation on heath sites is a common phenomenon in the humid conditions prevailing in northern Finland, especially in young stands with compacted soils where the ground easily becomes waterlogged after the removal of the tree stand (also Sarvas 1937).

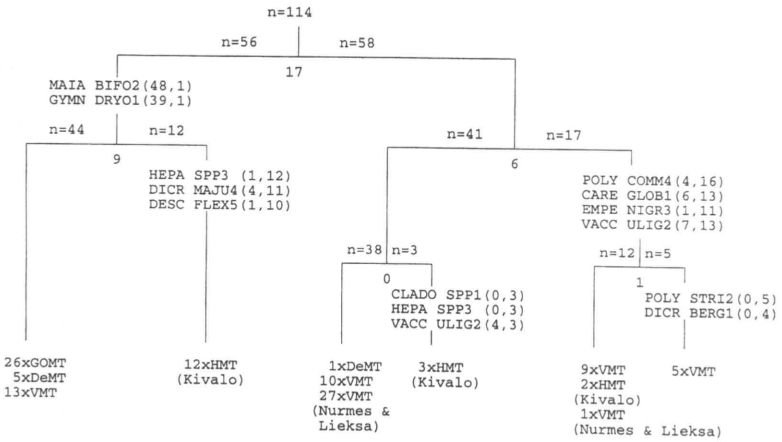

Fig 7. TWINSPAN classification of the southwest Lapland data and the reference materials. For explanations, see Fig. 5.

Identification of the forest site type in deciduous and mixed stands is problematic, for instance, due to the effects on the light climate. In addition, deciduous litter contains more nutrients than conifer litter, and also decomposes at a faster rate (Heinonen 1991 and references therein). Thus nutrient cycling in deciduous-dominated stands is faster than that in coniferous-dominated stands (Kellomäki 1991). For this reason the ground vegetation in deciduous and mixed stands is usually different from the corresponding type in coniferous stands (Lahti and Väisänen 1987); it usually appears more luxuriant (Mielikäinen 1980, Tonteri 1988). Most of the deciduous stands and deciduous-dominated stands in this material were classified as VMT+ or better.

There are differences in the texture class distribution of the forest site types, but no site type occurs exclusively on a particular soil type (Urvas and Erviö 1974, Sepponen 1985) (cf. the *Pyrola* site type). When moving from fertile and moist sites to more infertile and drier ones, the proportion of coarse soil fractions usually increases and that of fine ones correspondingly decreases (Aaltonen 1941). However, this is somewhat dependent on the material and subject to local variation, and in this study an opposite result was obtained: almost all those plots occurring on the coarsest texture classes represented the more fertile forest site types (also Teivainen 1952). This is presumably due to the fact that the plots were located in various bedrock and glacial till areas, i.e. to sampling effects. The coarse fractions have such high nutrient contents that fertile site types are possible. The chemical composition had, in this case, a greater regulating effect than the texture. The result may also be affected by the fact that the soil texture classification was based on the predominant particle size class, and no overall picture of the particle size distribution was obtained.

The vegetation on fresh heath sites was very variable in the study area. Some of the plots clearly represented the VMT type or paludified variants of it. The absence of *Calluna vulgaris* in this material (Table 2) makes it an exception to the VMT site type description (Kalela 1961, Kalliola 1973, Sepponen et al. 1982, Lehto and Leikola 1987, Hotanen and Nousiainen 1990). This species is relatively demanding with respect to light and it is normally present in pine-dominated stands on fresh heath sites and in young successional stages (e.g. Kuusipalo 1985, Tonteri et al. 1990a, Hotanen and Nousiainen 1990). Apart from a few pole-stage stands, the VMT plots in this study had a rather closed canopy and were mainly spruce-dominated. On the other hand, *Calluna vulgaris* is known to decrease in frequency on moving northwards in the Pohjanmaa-Kainuu and Peräpohjola zones (Kalliola 1973).

Some of the fresh heath sites, primarily the plots in TWINSPAN groups 4 and 5, had vegetation that is more demanding than that of VMT. This was also apparent in the case of a number of nutrient parameters (e.g. electrical conductivity, pH, Ca). The vegetation on these plots rather closely resembled that of DeMT, which occurs rather frequently in the southern parts of the central boreal vegetation zone. However, the indicator species, *Deschampsia flexuosa*, has a considerably higher abundance in the DeMT descriptions (e.g. Kalliola 1973) than on the plots of this study (Table 2). The structure of the vegetation on the plots in question also appears to correspond rather well, perhaps even better than with DeMT, with the vegetation of the northern *Myrtillus* type (p.MT) earlier in use (Ilvessalo 1937, Kalela 1952, Kujala 1979, Sepponen et al. 1982).

The site type p.MT does not occur in the site type description currently in use (Lehto and Leikola 1987), and it has most probably been incorporated into VMT and DeMT of the central boreal vegetation zone, or even partly into GOMT (Kalela 1952, 1961), as well as partly into the HMT of the northern boreal vegetation zone (or *Ledum-Uliginosum*, LUT, and *Geranium-Myr-*

tillus, GMT) (Keltikangas 1959, cf. Sepponen et al. 1982). In this material the nine difficult border cases in relation to Kivalo HMT plots on the left of the second division level in the comparison classification (Fig. 7) were the plots of groups 4 and 5. However, on the Kivalo plots e.g. *Hepaticae* spp. and *Deschampsia flexuosa* were abundant (see also Keltikangas 1959, Eurola et al. 1991). In the Future perhaps more detailed attention to hepatics (e.g. determination to species) should be paid (in the Finnish forest vegetation studies). Most of the Kivalo plots appeared to have vegetation which was slightly more demanding than the Peräpohjola HMT mineral soil sites mentioned in the literature (Kalliola 1973, Kujala 1979, Sepponen et al. 1982).

On the basis of the above-mentioned description, relatively demanding species, individually even species of herb-rich mineral soil sites (e.g. *Geranium sylvaticum*, *Gymnocarpium dryopteris*, *Cornus suecica*) occur on the sites of the p.MT type. These species occurred perhaps slightly more abundantly on the plots of this study than in the above descriptions. This may be partly the reason (and because the p.MT type was not in use) why the plots in groups 4 and 5 of TWINSPAN were often classified in the field as VMT+ and GOMT–. Since, in addition to the fertility status, the tree stand (volume, development stage, tree species composition) has a considerable effect on the ground vegetation, classification problems are real ones.

The overall appearance of the site on fresh mineral soils became less fertile, and also more luxurious, with a reduction in crown shading following thinning (Lähde 1984, Lehto and Leikola 1987, Hotanen and Nousiainen 1990, Vanha-Majamaa and Lähde 1991). For instance, *Vaccinium myrtillus*, *Linnaea borealis* and *Hylocomium splendens* decrease sharply in abundance and more *Polytrichum* spp. and *Vaccinium vitis-idaea* appear in the stand. *Calluna vulgaris* and in northern Finland especially lichens and *Empetrum nigrum* become more abundant on clear-cut areas. At the same time many grasses (e.g. *Deschampsia flexuosa*, *Agrostis capillaris*, *Calamagrostis* spp. etc.) and herbs (e.g. *Trientalis europaea*, *Maianthemum bifolium*, *Epilobium angustifolium* etc.) increase in abundance. In this study the developmental stage of the tree stand (pole stage) may partly explain the infertile mark of the vegetation of the plots (VMT–) of TWINSPAN group 8.

The results of this study would appear to support the occurrence of the p.MT type, or at least that intermediate forms of fresh and herb-rich mineral soil sites commonly occur in the studied area (also Kuusipalo 1985). The site index of the tree stand of p.MT presumably differs from that of VMT, but the differences compared to DeMT and GOMT appear to be unclear (Kalela 1952). The site index of p.MT in the Peräpohjola area (northern boreal) is greater than that of HMT (Ilvessalo 1937). Information will be obtained about the stand site index of these plots later after remeasurements of the stands.

Oxalis acetosella did not occur on the herb-rich heath plots of this study, apart from on a few exceptional plots removed from the material (see Material and methods). The species occurs in the studied area at the northern limits of its distribution (Kujala 1964), and it is not common or abundant on herb-rich heath sites in the area. Owing to the absence of the classifying species, for instance DMT (*Dryopteris-Myrtillus* type) would be a more suitable name for the herb-rich upland forest site type (normally GOMT) (Kujala 1979, Sepponen et al. 1982). Compared to this material, *Gymnocarpium dryopteris* and *Geranium sylvaticum* occur relatively more abundantly in the Peräpohjola herb-rich heath type GMT (*Geranium-Myrtillus*) (Kalliola 1973).

Despite favourable climatic (slightly marine) conditions to the latitude and nutrient rich soil the vegetation in the study area contains features of the northern boreal vegetation zone. However, a part of the fresh heaths resembles the fresh heath forests of the southern part of the central boreal zone. The vegetation of the area is miscellaneous and variable. If one wants to define the forest site type strictly, the currently prevailing forest site types of the central and northern boreal zones are inadequate.

The borders of the vegetation zones especially in northern Finland (topography, exposition) are ambiguous, e.g. the Peräpohjola forest site types are to be found in the Pohjanmaa-Kainuu zone, and vice versa. When we also take into account the strong anthropogenic impact on the vegetation it is understandable that forestry, and often also forestry research, has become reconciled to using the forest site types in the classification (Lähde 1984). In such cases it is essential, taking into account the case in hand, to distinguish fresh heath sites from herb-rich heath sites. On herb-rich heath sites the above-mentioned field layer species of herb-rich heath sites should occur in moderate amounts. There is also reason to pay attention to the bottom layer because *Rhytidiadelphus triquetrus*, for instance, often occurs relatively abundantly in closed stands on herb-rich heath sites.

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