BOREAL ENVIRONMENT RESEARCH 13 (suppl. B): 48–66
ISSN 1239-6095 (print) ISSN 1797-2469 (online) © 2008
Helsinki 25 November 2008

Response of boreal forest vegetation to the fertility status of the organic layer along a climatic gradient

Maija Salemaa[1], John Derome[2] and Pekka Nöjd[1]

[1] Finnish Forest Research Institute, Vantaa Research Unit, P.O. Box 18, FI-01301 Vantaa, Finland
[2] Finnish Forest Research Institute, Rovaniemi Research Unit, P.O. Box 16, FI-96301 Rovaniemi, Finland

Received 30 Jan. 2008, accepted 1 July 2008 (Editor in charge of this article: Jaana Bäck)

Salemaa, M., Derome, J. & Nöjd, P. 2008: Response of boreal forest vegetation to the fertility status of the organic layer along a climatic gradient. *Boreal Env. Res.* 13 (suppl. B): 48–66.

Relationships between boreal understorey vegetation and chemical composition of the organic layer, stand productivity and climatic factors were studied on 27 coniferous monitoring plots along a S–N gradient in Finland using ordination techniques (fitting environmental vectors and surfaces to the NMDS pattern). Total N, exchangeable Ca and Mg, BS, pH and organic layer thickness formed the subset of variables with maximum correlation with plant community composition. Of the stand parameters, site index (H_{100}), volume and basal area correlated best with the vegetation pattern. Our results support the hypothesis that site productivity can be predicted on the basis of the occurrence of understorey plants. This was especially true in herbaceous plants, where the number of species well depicted the site index on both pine and spruce plots. We present quantitative evidence that the response curves along an extensive nitrogen gradient varied between species representing dwarf shrubs, herbs, grasses, mosses and lichens.

Introduction

The climatic and edaphic conditions are the primary factors affecting differentiation of the understorey vegetation in boreal forests. The implication of this relationship, which assumes that the composition of the understorey vegetation reflects the fertility and productivity status of the site, forms the basis for the Finnish forest site type classification (Cajander 1909, 1949, Ilvessalo 1922, Kuusipalo 1985), and is a well-established tool in practical forestry in all the Fennoscandian countries (Dahl *et al.* 1967, Hägglund and Lundmark 1977, Økland and Eilertsen 1993, Giesler *et al.* 1998). The same premise also underlies the widely used central-European Ellenberg system (Ellenberg *et al.* 1991, Diekmann and Falkengren-Grerup 1998, Hill *et al.* 2000, Grandin 2004), which gives indicator values to plant species along gradients depicting e.g. soil fertility, water availability and climatic conditions. Both classification systems, despite being widely applied, still lack quantitative and experimental verification. Therefore, more knowledge is required about the dependence of the composition of the understorey vegetation on soil properties and climate.

The understorey vegetation and the organic layer of boreal forests develop concurrently and interact in many ways (Kuusipalo 1985). Vascular plants depend on the organic layer for their supply of nutrients and water (Nilsson and

Wardle 2005). On the other hand, the understorey vegetation has a considerable impact, through plant litterfall, on the composition, microbiological processes and nutrient cycling of the organic layer (Saetre 1999, Kanerva and Smolander 2007, Hilli *et al*. 2008). The overstorey trees also have a considerable influence on the understorey vegetation through shading and regulation of the moisture and nutrient levels (Kuusipalo 1985, Barbier *et al*. 2008).

Analysis of the extensive vegetation data of the Finnish national forest inventories (NFI) using multivariate methods (3rd NFI 1951–1953: Lahti and Väisänen 1987; 8th NFI 1985–1986: Tonteri *et al*. 1991a, 1991b) has shown that the main gradient in the understorey vegetation of upland forests in Finland ranks the habitats from “dry-and-poor” to “moist-and-rich”, and expresses site fertility and forest productivity. Nieppola and Carleton (1991) found this relationship in a relatively large data covering mature Scots pine stands in southern Finland. Nieppola (1993) also investigated how the occurrence and number of species are related to site productivity. However, in these studies the fertility status of the site was determined indirectly using the site index (H_{100}, dominant tree height at the age of 100 years). The chemical and physical properties of the soil have been determined for subjectively classified forest site types in many studies in Finland (e.g. Valmari 1921, Urvas and Erviö 1974, Sepponen 1985, Tamminen 2000). Only a few studies (Kuusipalo 1984, 1985) have analysed the relationships between forest vegetation, soil nutrients and site indices using a continuum approach and applied multivariate ordination and clustering methods.

According to Økland and Eilertsen (1993), the main task of research on forest vegetation is to identify the major vegetational gradients, the ecological complex gradients that cause them, and the spatial scales on which they operate. The species composition and structure of the vegetation varies along ecological gradients in accordance with the differing habitat requirements and tolerances of the individual species. Improved knowledge of the species-specific responses to many abiotic (e.g. moisture, nutrients, light and temperature) and biotic factors is needed in order to better understand the vegetation–environment dynamics of boreal forests.

In this study, we analyse how the understorey vegetation is related to the large-scale variation in site fertility, stand characteristics and climatic factors on a set of coniferous, intensively monitored upland plots in Finland. Our data enable us to test how well the understorey vegetation reflects the nutrient level of the growth substrate using quantitative data on the vegetation, tree stand and soil chemistry that represents all the boreal bio-geographical zones, and the complete latitudinal gradient running through Finland. We hypothesise that site productivity, as expressed by the site index (H_{100}), correlates positively with total nitrogen concentrations in the organic layer and can therefore be predicted on the basis of the occurrence of the understorey plant species. Our specific aims are:

- to identify the most important chemical variables in the organic layer and stand characteristics that correlate best with the vegetation pattern,
- to investigate whether the vegetation-environment relationship is linear or non-linear, and
- to determine the abundance (cover) curves of plant species representing different functional groups along the nitrogen, calcium and acidity gradients of the organic layer.

Material and methods

Study sites

The 14 Norway spruce (*Picea abies*) and 13 Scots pine (*Pinus sylvestris*) Level II plots are a part of the European intensive (Level II) monitoring plot network, established under the EU-Forest Focus and UN/ECE-ICP Forest monitoring programmes, and represent the hemi-boreal, southern, middle and northern boreal vegetation zones in Finland (Fig. 1). As the distance between the southernmost (Solböle No. 28) and northernmost plots (Kevo No. 22) is over 1100 km, the material is strongly affected by a south–north climatic gradient. The plots were selected subjectively to be approximately representative of the prevailing climatic conditions, tree species

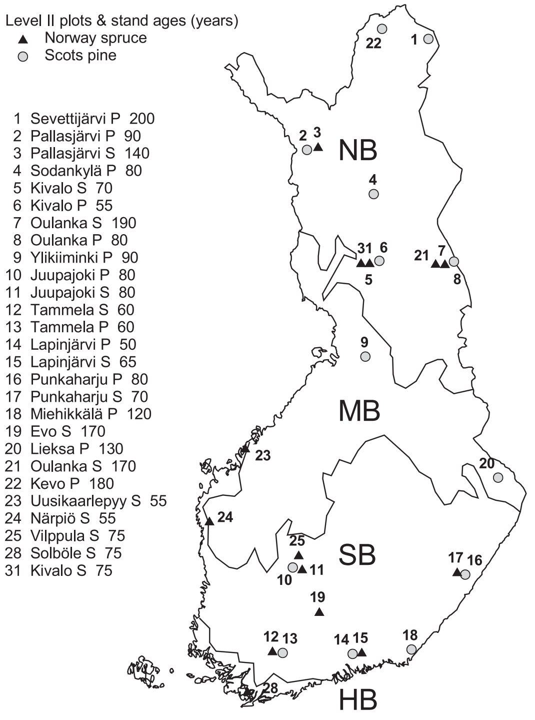

Fig. 1. The location of the plots and the distribution of the vegetation zones in Finland. HB = hemi-boreal, SB = southern boreal, MB = middle boreal, NB = northern boreal. P = Scots pine plot and S = Norway spruce plot. The age of the stands (years) is given after the plot name.

and site types in Finland. In the final selection, however, factors related to the other monitoring activities (e.g. deposition, soil solution and meteorological monitoring) on the plots, such as logistical aspects and financial restraints, played a decisive role. The soil texture on the spruce plots is till and on the pine plots sorted glaciofluvial material, and the soil type on all the plots is podzol.

Twenty three of the 27 stands are located in semi-natural, commercial forests managed according to standard silvicultural regimes. With a few exceptions (primarily Nos. 2, 5 and 6), the stands were mature and represented a late phase of succession. Silvicultural thinnings, which would strongly affect the species composition, were not carried out in any of the stands during the period 1994–2000. Four of the stands (Nos. 19, 20, 21 and 22) are located in strict nature conservation areas and have not been subjected to forest management for several decades (Kokko *et al*. 2002). The mean age of these uneven-aged stands (130–180 years) is considerably older than most of managed stands (Fig. 1), and they also contain an appreciable admixture of other tree species. The basic stand characteristics are given in Derome *et al*. (2007).

Estimation of plant species cover

The understorey vegetation was inventoried on the 27 plots during July–August in 2003. The bottom layer (mosses, liverworts and lichens) and the field layer (vascular plants, height < 50 cm: herbs, grasses, sedges, dwarf shrubs and tree seedlings) were investigated. Altogether 16 sample quadrats, each 2 m^2 (1.41 × 1.41 m), were marked out systematically (4 × 4 design) on the plot (30 × 30 m) reserved for vegetation monitoring (Fig. 2). The cover of the individual plant species on the 2 m^2 quadrats was assessed using the following scale: 0.01% (solitary or very sparsely growing shoots), 0.1%, 0.2%, 0.5%, 1%, 2%, …, 99%, 100%. The mean cover of each species was calculated over an area of 400 m^2 (the Common Sample Area), which is used in all the countries participating in the Forest Focus/ICP Forest monitoring programme. Species (mostly bryophytes and lichens) occurring on the monitoring area (400 m^2), but not on the quadrats, were given the cover value of 0.01%. Two to four botanists inventoried the vegetation, and field tests were carried out to calibrate their individual assessment levels.

Chemical composition of the organic layer and particle size distribution of the underlying mineral soil

The thickness of the organic layer was measured at 120 points on each plot. Samples of the organic layer outside each vegetation quadrat were taken using a soil auger (diam. 58 mm) in 2003. The 16 samples were combined to give one composite sample per plot. The samples were dried and milled to pass through a 1 mm sieve. pH was measured in water. Loss in weight on ignition (LOI) was determined by ashing the samples in a muffle furnace at 550 °C for 3 hours. Exchangeable K, Ca, Mg, Zn, Mn, Na and extractable P and S were determined by inductively coupled plasma atomic emission spectrometry (ICP/AES) after extraction with 1 M ammonium acetate (pH 4.65) + 1% EDTA. Total N and C were determined on a CHN analyser. All concentrations are expressed on an organic matter basis (LOI) in order to reduce the variation caused by the unavoidable inclusion of mineral soil in the organic layer samples. Cation exchange capacity (CEC) and base saturation (BS) were determined using extraction with 0.1 M $BaCl_2$, and titration to an end-point of 7.8, on samples taken from the adjacent plot reserved for destructive sampling (e.g. soil and soil solution sampling). The particle-size distribution was determined gravimetrically on mineral soil samples taken from the subsoil (depth 20–50 cm). The proportion of the finest particles (< 63 μm), i.e. clay + silt, was calculated.

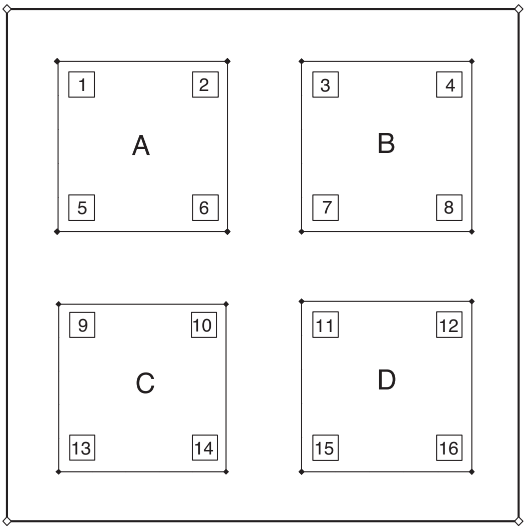

Fig. 2. The plot (30 × 30 m = 900 m^2) used for the inventory of the understorey vegetation. Plant species cover was assessed on the small sample quadrats (16 × 2 m^2). Additional plant species found growing outside the small quadrats were recorded within areas of 4 × 100 m^2 (A–D) forming the monitoring area.

Stand characteristics

Tree species, breast-height diameter (DBH) and tree height were measured on every tree with a DBH of at least 4.5 cm on each plot in 1999–2000. KPL software (Heinonen 1994) was used to transform the individual tree measurements into stand-level characteristics (basal area, dominant height, mean height, cubic volume). Taper curve functions by Laasasenaho (1982) were used for estimating the individual tree volumes. Ten dominant trees on the buffer area around each plot were cored in order to determine the age of the dominant tree layer. The site index (H_{100}) was calculated using the functions of Gustavsen (1980) with dominant height and stand age as input variables.

Weather and climatic factors

Plotwise values for the effective temperature sum (threshold +5 °C) and annual precipitation in 2003 were derived from model interpolations based on measurements made by the Finnish meteorological institute (Ojansuu and Henttonen 1983). The de Martonne index indicating humidity (Tuhkanen 1980) was calculated using the following equation:

$$H = P/(T + 10), \qquad (1)$$

where P = annual precipitation (mm), and T = annual mean temperature (°C).

Statistical analyses

We used global non-metric multidimensional scaling (NMDS) (Minchin 1987) in ordinating the vegetation data of the 27 plots in order to find the main compositional gradients (R programme, MetaMDS in Vegan library, Oksanen 2007). A two-dimensional solution using the Bray-Curtis coefficients as a measure of dissimilarity in floristic composition between the sample plots was chosen for the final method. The third dimension did not provide any essentially new information and is not presented. Species scores were calculated as cover-weighted averages of the sample scores.

We divided the plots on the vegetation continuum into Cajanderian forest site types (for short description, *see* e.g. Lahti and Väisänen 1987) according to the ordination pattern and occurrence of indicator species. We then calculated the site type specific means (± SE) for the cover percentages of the plant species separately for south (hemi-boreal, southern and middle boreal zones) and north (northern boreal zone) Finland (Fig. 1). Corresponding parameters were calculated for the climatic, organic layer, soil texture and stand variables. It was not possible to perform statistical tests between the site types owing to the small number of plots.

Maximum correlations between the environmental variables and the ordination pattern (plot scattergram) were calculated using a linear vector fitting procedure ("Envfit") of Vegan. The significance of the correlations was assessed with Monte Carlo tests (1000 permutations). In addition to the vectors, we fitted non-parametrically smoothed surfaces of the selected environmental variables on the ordination space in order to evaluate whether the vegetation-environment relationship was linear or non-linear. The smooth surfaces were fitted using generalized additive models (GAM, gaussian distribution of error) with thin plate splines (Wood 2000), and their significance was tested by permutation tests ($n = 1000$) (cf. Virtanen *et al*. 2006). If the relationship was linear, the fitted surface was a plane and its R^2 was close to that of the vector; but if the relationship was non-linear, R^2 was higher for the surface than for the vector. The best subset of variables giving the maximum rank correlation with plant community dissimilarities (ordination pattern) was calculated using the "Bioenv" procedure in the Vegan library (Oksanen 2007).

We fitted linear regressions between the H_{100} index and total N concentration in the organic layer separately for the pine and spruce plots. Pearson correlations were calculated between the H_{100} index and the selected variables of the organic layer and climate, and between the number of species in different plant groups and the N concentration of the organic layer and the H_{100} index. We modelled the cover distributions of the selected vascular and bryophyte species, the sum of lichens, as well as the number of species, in relation to the N gradient using GAMs (R programme, Mgcv library, Wood 2006). The cover of the vascular plants was also modelled to the C/N ratio, pH and exchangeable Ca concentration of the organic layer. We used the quasi-poisson distribution of the error and log as a link function in the models. The deviance test (χ^2-test) was applied to decide which of the possible error distributions to choose. The degree of freedom was automatically selected with generalized cross-validation in the GAMs, with an upper limit of 4 df. Corresponding models were constructed for the number and cover of species in relation to the H_{100} index.

Results

Ordination analysis of the vegetation

The plots were located in accordance with the dominating tree species (spruce plots on the right and pine plots on the left) and the fertility level of the organic layer along the main compositional gradient (Fig. 3a). The most fertile herb-rich heath forests were located on the right, mesic heaths in the centre, followed by sub-xeric and xeric heaths on the left. The corresponding Cajanderian forest site types in the different boreal zones are given in Table 1. Within each site type the northern plots were located slightly to the left of the southern ones, indicating a more severe climate or lower fertility. The second gradient shifted from lower to higher latitudes, and separated the younger succession stages (lower part of the ordination space) from the older northern stands. Of the unmanaged plots, Evo No. 19 and Kevo No. 22 were slightly isolated, whereas Lieksa No. 20 and Oulanka No. 21 were located relatively close to the managed plots representing the corresponding forest types.

The arrangement of the species scores corresponded to the general fertility and succession pattern of the plots. The demanding bryophyte species (e.g. *Brachythecium* spp.) on the right were replaced by generalist bryophytes in the centre (e.g. *Pleurozium schreberi* and *Dicranum polysetum*), and by drought-tolerant lichens (e.g. *Cladina rangiferina*) on the left in the species ordination (Fig. 3b). For vascular plants, the focus on demanding herbs (e.g. *Mainthemum bifolium*) and grasses (e.g. *Calamagrostis arundinacaea*) was on the right, in generalist species

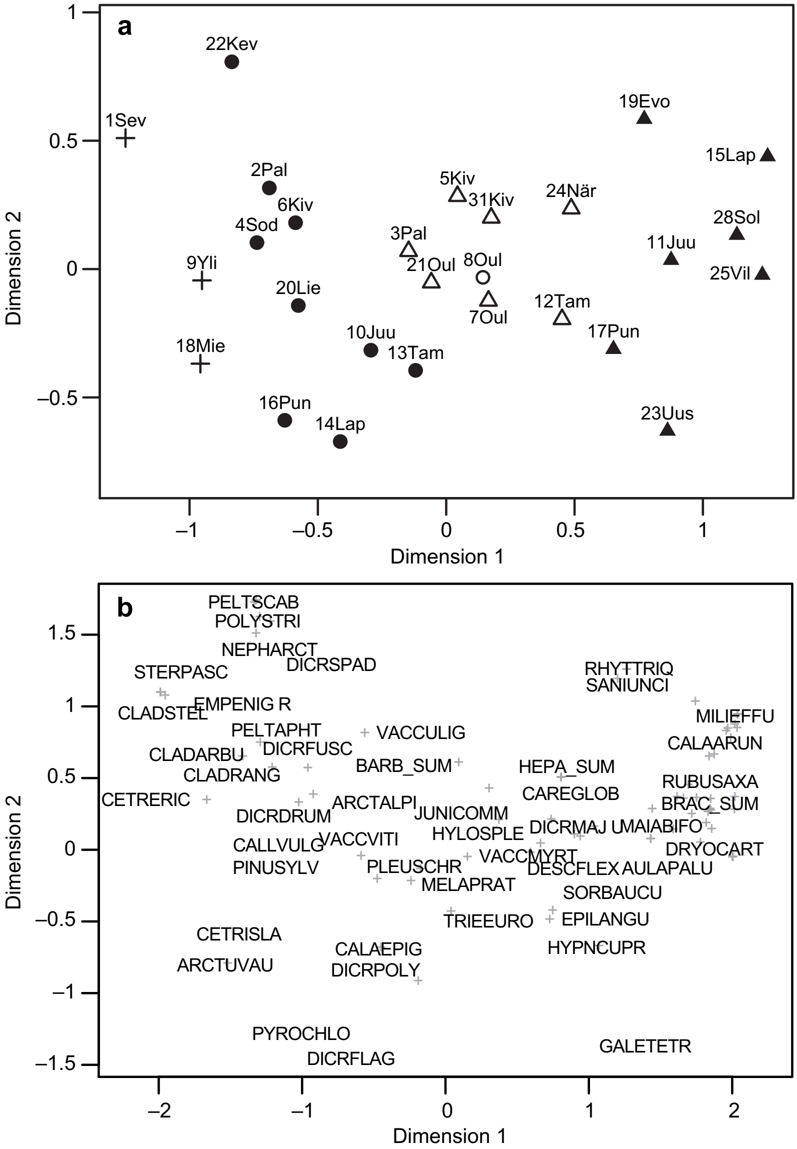

Fig. 3. Global non-metric multidimensional scaling (NMDS) of the vegetation data on the 13 Scots pine (circles and crosses) and 14 Norway spruce plots (triangles) in 2003. — **a**: Ordination of the sample plots. Site types: filled triangle = herb-rich heath forest; open triangle or circle = mesic heath forest; filled circle = sub-xeric heath forest; cross = xeric heath forest. — **b**: Weighted averages of the species. The most abundant species labeled with names, other marked with crosses. Abbreviations of the species names are created from the first four letters of the generic and species names. BRAC_SUM = *Brachythecium* spp., HEPA_SUM = Hepatics species, other than *Barbilophozia*, BARB_SUM = *Barbilophozia* spp.

Table 1. Distribution of the plots according to site types and corresponding Cajanderian (1909) forest site types in the hemi-boreal, southern, middle and northern boreal zones.

Site type	Hemi-boreal	Southern boreal	Middle boreal	Northern boreal
Herb-rich heath forest	OMT No. 28	OMT Nos. 11, 15, 17, 19, 23, 25		
Mesic heath forest		MT Nos. 12, 24		HMT Nos. 3, 5, 7, 8, 21, 31
Sub-xeric heath forest		VT Nos. 10, 13, 14, 16	EVT No. 20	EMT Nos. 2, 4, 6, 22
Xeric heath forest		CT No. 18	ECT No. 9	UVET No. 1

OMT = *Oxalis–Myrtillus* type, MT = *Myrtillus* type, VT = *Vaccinium* type, CT = *Calluna* type, EVT = *Empetrum–Vaccinium* type, ECT = *Empetrum–Calluna* type, HMT = *Hylocomium–Myrtillus* type, EMT = *Empetrum–Myrtillus* type and UVET = *Uliginosum–Vaccinium–Empetrum* type.

(e.g. *Vaccinium myrtillus*) in the centre, and in the least demanding species adapted to nutrient-poor, acidic substrates (e.g. *Calluna vulgaris*) on the left. The abundance of moisture-demanding liverworts (e.g. *Barbilophozia* spp.) increased towards the northern old stands, which can provide suitable humidity and coarse woody debris for their growing substrates.

The mean values for the cover and number of species in the understorey vegetation and for the environmental variables on different site types, are given for the southern and northern plots in Tables 2 and 3, respectively. Southern herb-rich heath plots maintained a high number of vascular plants and bryophytes, while northern subxeric and xeric plots had species-rich bryophyte and lichen communities (Table 2).

Explanatory variables

Vegetation differentiation was explained by several inter-correlated environmental variables. The maximum correlations between all the studied environment variables and the NMDS ordination configuration (Fig. 3a) are given in Table 4. Examples of different variables are presented as fitted vectors and surfaces on the ordination space in a panel figure (Fig. 4). The climatic, organic layer, soil texture and stand variables are henceforth treated separately.

Climate

The combination of climatic variables (out of a maximum of four) giving the best rank correlation with the vegetation pattern was effective temperature sum, annual precipitation and humidity index ($r = 0.241$). Effective temperature sum (max–min = 1462–763 degree days, d.d.) and annual precipitation (max–min = 714–400 mm) decreased from south to north, whereas humidity and altitude had the maximum values on the northern hills. All the climatic variables showed a non-linear relationship with the ordination pattern (R^2 values for surfaces were higher than linear R^2 values) (Fig. 4 and Table 4), which may explain the relatively low rank correlation for the subset of variables. Temperature isoclines for the spruce stands paralleled with dimension 1 (x-axis), but those for the pine stands with dimension 2 (y-axis), resulting in marked curvature on the fitted surface.

Organic layer and soil texture

Total nitrogen (N), exchangeable calcium (Ca) and magnesium (Mg) concentrations, base saturation (BS), pH and thickness of the organic layer formed the subset of variables for the organic layer (out of a maximum of 14, Na excluded) that gave the maximum rank correlation ($r = 0.592$) with the plant community composition. In general, the main vegetation gradient was strongly related to the total N concentration, which increased from the xeric and subxeric pine plots towards the herb-rich heath plots dominated by spruce (Fig. 4 and Table 3). The surface pattern for the C/N ratio (not shown) was almost the same as that for N, but the direction of the values was the opposite (maximum in xeric plots). Of the macronutrients (N, P, K, Ca, S and Mg), only P and K had relatively low R^2 values for both the fitted vectors and surfaces. The surfaces of P and K were clearly unimodal, with maximum values on the “high” altitude Oulanka and Pallasjärvi plots. The P/N ratio (not shown) had a similar surface pattern as P (Fig. 4), with the lowest values on the southern herb-rich and mesic heaths (Table 3). Calcium, Mg, BS and pH increased towards the southern herb-rich heaths, i.e. from the lower left to the upper right in the ordination space. The pH values correlated strongly ($p < 0.001$) with Ca and BS (Table 5). Also extractable sulphur (S) (not shown) increased towards the herb-rich heaths, but from the upper left to the lower right. CEC (not shown) had a very similar surface pattern to that of BS. Of the micronutrients (Mn and Zn), only Mn (not shown) correlated with the ordination pattern, following a linearly increasing trend from the lower left to the upper right. Manganese had strong positive correlation ($p < 0.001$) with pH, Ca, BS and the proportion of fine particles (Table 5). The Na concentrations were highest on the plots subjected to a marine influence (Nos. 1, 22 and 23).

The relationships between the vegetation and the variables most strongly depicting site fertility

Table 2. Means and standard errors of the mean (SE) of the cover of the selected plant species and the number of species in the species groups in the four site type classes. South = hemi-boreal, southern and middle boreal zone, North = northern boreal zone. *n* = number of plots. “Other woody species” includes dwarf shrubs and shrubs and trees (height < 50 cm). “*Cladina* sum” = reindeer lichens, “*Cladonia* sum” = cup lichens, and “other lichens” = *Cetraria* spp., *Stereocaulon* spp. and the leather lichens (*Peltigera* spp. and *Nephroma arcticum*), – = species not found.

Species group	Herb-rich heath forest South (*n* = 7)		Mesic heath forest				Sub-xeric heath forest				Xeric heath forest		
			South (*n* = 2)		North (*n* = 6)		South (*n* = 5)		North (*n* = 4)		South (*n* = 2)		North (*n* = 1)
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean
Dwarf shrubs													
Calluna vulgaris	–		–		0.03	0.03	1.53	1.15	2.81	2.41	4.39	1.76	–
Empetrum nigrum	–		–		0.95	0.86	0.20	0.17	9.79	4.42	0.81	0.81	26.20
Vaccinium myrtillus	10.81	4.10	22.22	16.28	43.59	4.52	16.03	4.04	9.79	1.69	5.64	3.21	0.39
Vaccinium vitis-idaea	1.51	0.72	6.67	4.08	10.02	1.65	19.45	5.35	13.81	2.84	17.22	5.78	19.56
Other woody species	2.39	0.90	2.69	0.14	1.69	0.71	1.09	1.01	1.47	0.52	0.25	0.18	0.52
Number of species	6.7	0.6	9.00	4.00	7.8	1.6	7.2	1.1	9.3	0.5	6.0	0	5
Herbs													
Maianthemum bifolium	6.60	1.80	3.65	1.40	–		0.36	0.32	0	0	–		–
Oxalis acetosella	3.96	1.12	0.02	0.02	–		–		0	0	–		–
Trientalis europaea	0.63	0.21	0.94	0.64	0.02	0.02	1.96	1.18	0	0	–		–
Other herb species	7.34	3.13	0.90	0.07	0.57	0.27	0.06	0.02	0	0	0.01	0	–
Number of species	17.0	2.7	10.5	0.5	4.3	0.5	4.6	1.0	1.0	0.6	0.5	0.5	0
Grasses & sedges													
Calamagrostis arundinacea	1.37	1.01	0.26	0.13	–		0	0	–		–		–
Deschampsia flexuosa	2.35	1.68	1.98	1.30	1.74	0.56	0.75	0.46	0.29	0.23	–		–
Luzula pilosa	0.44	0.18	0.17	0.14	0.14	0.09	0.02	0.01	–		–		–
Other grass species	0.67	0.37	0.13	0.12	–		0.10	0.10	–		–		–
Number of species	6.3	1.2	4.5	0.5	1.8	0.4	1.8	0.7	0.8	0.3	0	0	0
Bryophytes													
Dicranum polysetum	0.73	0.29	6.69	2.19	0.60	0.19	17.16	7.28	1.64	0.68	8.98	7.28	0.01
Dicranum scoparium	2.01	0.53	4.41	1.64	2.56	0.57	0.30	0.17	1.93	0.78	0.32	0.12	–
Hylocomium splendens	8.67	4.09	9.09	0.71	40.36	5.19	8.66	4.69	1.39	1.25	0.08	0.08	–
Pleurozium schreberi	26.65	7.43	32.69	5.81	31.35	7.89	48.09	7.95	50.91	10.70	51.13	2.38	7.88
Other mosses	10.79	3.22	7.58	2.80	8.71	2.17	4.61	2.92	7.74	1.96	0.19	0.04	3.68
Hepatics sum	1.46	0.89	0.02	0.02	2.48	1.27	0	0	1.40	0.78	0.01	0	4.10
Number of species	22.9	2.5	19.5	0.5	18.8	1.5	8.2	1.4	20.8	2.3	8.5	2.5	20.0
Lichens													
Cladina sum	–		0.04	0.04	0.01	0	0.13	0.09	4.43	1.03	9.78	6.65	38.32
Cladonia sum	0.03	0.02	0.01	0	0.01	0	0.07	0.04	2.03	0.84	2.85	2.45	3.98
Other lichens	–		0	0	0.02	0.02	0.04	0.04	1.60	1.10	0.27	0.06	0.40
Number of species	1.4	0.6	2.0	1.0	4.5	1.8	6.4	1.7	19.0	3.4	17.5	1.5	21.0

Table 3. Means and standard error of the mean (SE) of the environmental variables characterising the climate of the plot, organic layer, soil texture and tree stand in the four site types. *See* Table 2 for further explanations. Exch. = exchangeable, Extr. = extractable, om = organic matter.

Environmental variable	Herb-rich heath forest South (n = 7)		Mesic heath forest				Sub-xeric heath forest				Xeric heath forest		
			South (n = 2)		North (n = 6)		South (n = 5)		North (n = 4)		South (n = 2)		North (n = 1)
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean
Altitude (m a.s.l.)	94.1	25.6	86.5	56.5	265.0	11.0	116.8	22.1	206.0	40.2	69.0	21.0	105.0
Eff. temp. sum (d.d.)	1327.9	33.9	1322.5	24.5	911.8	26.2	1318.4	41.9	864.5	66.4	1276.5	113.5	763.0
Annual precipitation (mm)	588.0	29.2	530.8	2.3	521.0	14.8	618.2	30.1	466.6	41.5	564.9	88.7	399.7
Humidity index	41.8	2.2	37.0	0.2	50.2	0.3	44.9	2.9	45.9	2.7	42.3	3.8	40.5
Organic layer													
Thickness (cm)	3.6	0.4	3.4	1.4	3.7	0.4	3.1	0.1	2.5	0.6	2.5	1.1	1.1
pH	3.9	0.1	3.7	0.0	3.7	0.1	3.6	0.1	3.6	0.0	3.4	0.1	3.4
Total N (g kg^{-1} om)	21.4	0.7	20.5	1.1	13.0	0.2	14.9	0.7	11.5	1.0	14.7	2.6	12.8
Extr. P (mg kg^{-1} om)	171.0	36.6	104.0	25.9	491.8	32.7	242.0	28.2	256.9	41.0	222.1	11.7	274.5
Exch. K (mg kg^{-1} om)	978.9	69.8	831.6	88.6	1352.9	35.4	853.2	71.6	915.7	49.3	790.6	43.6	736.3
Exch. Ca (mg kg^{-1} om)	3485.1	615.0	2018.4	12.5	2346.0	172.4	2205.9	158.3	1642.7	54.6	1662.3	641.2	1610.1
Exch. Mg (mg kg^{-1} om)	608.6	68.1	388.6	42.9	447.7	25.4	317.9	21.5	374.6	52.8	207.0	16.6	491.9
Extr. S (mg kg^{-1} om)	275.5	13.7	228.8	16.4	246.7	16.2	220.8	10.7	198.2	15.2	197.8	20.7	176.1
Exch. Mn (mg kg^{-1} om)	569.4	221.4	153.3	15.1	596.0	110.8	197.9	24.4	245.3	72.6	96.3	7.0	109.5
Exch. Zn (mg kg^{-1} om)	30.6	8.7	24.9	5.4	25.4	3.0	29.9	1.5	19.9	2.3	27.4	3.1	20.3
Exch. Na (mg kg^{-1} om)	101.9	21.7	86.5	17.9	46.2	1.7	65.9	9.6	72.6	22.5	66.9	0.5	135.4
C/N ratio	24.1	0.8	25.0	1.2	39.8	0.8	35.0	2.4	44.9	3.1	38.9	5.0	41.8
P/N ratio	8.1	1.8	5.2	1.5	37.8	2.4	16.6	2.7	23.2	4.5	15.7	3.6	21.5
CEC (meq kg^{-1} om)	360.9	21.6	379.9	44.1	293.0	13.7	285.0	17.1	267.8	27.2	283.5	67.1	325.7
BS%	68.9	5.4	67.5	6.0	60.4	2.5	55.7	2.0	49.5	1.3	43.7	7.1	54.7
Mineral soil													
Fine particles (clay + silt) (%)	41.3	10.9	21.3	20.3	36.3	3.6	9.2	4.8	31.7	8.7	17.0	13.9	13.4
Stand													
Number of stems per ha	711.6	108.5	733.5	22.5	1321.2	160.5	699.6	150.7	1152.0	234.4	472.5	94.5	300.0
Volume (m^3 ha^{-1})	362.0	38.8	245.6	24.3	119.5	12.1	233.1	15.0	98.1	19.5	124.4	24.9	71.8
Basal area (m^2 ha^{-1})	32.6	3.3	26.7	1.2	19.2	1.3	23.8	1.9	16.6	2.7	15.0	0.8	12.5
Stem diameter (cm)	24.1	1.3	21.2	1.6	13.2	1.0	20.9	1.5	12.2	1.4	20.1	2.7	21.6
Tree height (m)	21.9	1.0	17.7	2.3	10.3	1.0	19.1	1.2	9.4	1.6	16.7	3.0	10.2
Stand age (years)	84.3	14.6	57.5	2.5	120.8	21.5	80.0	13.8	101.3	27.3	105.0	15.0	200.0
Site's H_{100} index (m)	29.5	1.6	31.2	1.3	15.1	1.5	25.4	0.8	13.6	2.2	18.1	2.2	8.7

(N, C/N ratio and BS) and which were related to soil acidity (pH, Ca) were close to linear, whereas K, P and Mg showed a non-linear response that was probably modified by local factors such as topography (altitude) or the parent soil material. The thickness of the organic layer had a low correlation with the vegetation pattern, although it increased linearly from the xeric pine plots to the moister spruce plots. Similarly, the proportion of fine particles (clay + silt) in the mineral soil was the highest in the herb-rich heath plots dominated by spruce, but there was great variation in the soil texture within the forest site types, and the correlation with the vegetation gradient remained relatively low.

Tree stand

The vegetation gradient was differentiated by the overstorey tree species: the more fertile, moist sites dominated by spruce were located on the right, and the nutrient-poor, drier pine plots on the left in the ordination space. The subset of stand variables (out of a maximum of 7) giving maximum correlation with the variation in the plant community comprised the site index (H_{100}), basal area and volume ($r = 0.460$). Tree species was not included in the model because it correlated too strongly with the other stand characteristics. The number of stems per ha did not explain the ordination pattern. Stand age increased linearly towards the northern plots in the upper part of the ordination space, but its correlation was lower than that for the variables depicting tree size (Fig. 4). Basal area and volume (not shown) had similar correlations with the vegetation pattern, and showed a non-linear increasing trend towards the fertile site types. H_{100} had an almost linear relationship with the main fertility gradient of the vegetation, and it increased from the upper left to the lower right in the same way as the total N concentration.

Species responses to the fertility gradient and the site index

Different functional plant groups showed varying distributions in their cover and species richness along the fertility gradient (Fig. 5). The cover distribution of bryophytes depended on the taxonomic group (Fig. 5a). The most common species, *Pleurozium schreberi*, had a high cover on almost all the plots, showing an increasing trend towards the northern N-poor sites. The curves of *Hylocomium splendens* and *Dicranum polysetum* were unimodal, with maximum cover on the left and in the centre of the N gradient, respectively. On the other hand, the cover of *Dicranum majus* increased slightly towards the N-rich and that of lichens to the N-poor end of the gradient.

Evergreen ericaceous dwarf shrubs dominated on the sites with a relatively low pH, low N

Table 4. Maximum linear correlations (R^2) of the environmental variables with the NMDS ordination pattern (*see* Figs. 3 and 4). The variables are ranked from high to low correlation in each variable group. The significance of the correlations (*p*) was calculated using the Monte Carlo test. Exch. = exchangeable, Extr. = extractable. *n* = 27 plots.

Variable	R^2	$p <$
Effective temperature sum	0.493	0.001
Annual precipitation	0.333	0.008
Altitude	0.122	0.214
Humidity index	0.051	0.535
Organic layer		
Total N	0.665	0.001
C/N ratio	0.660	0.001
pH	0.600	0.001
BS	0.581	0.001
Extr. S	0.533	0.001
Exch. Mg	0.515	0.001
Exch. Ca	0.422	0.001
CEC	0.361	0.001
Exch. Mn	0.272	0.026
Thickness	0.180	0.094
P/N ratio	0.150	0.141
Exch. K	0.089	0.324
Exch. Zn	0.073	0.441
Extr. P	0.057	0.475
Exch. Na	0.033	0.655
Mineral soil		
Fine particles (clay + silt) (%)	0.233	0.042
Stand		
Tree species	0.683	0.001
H_{100}	0.674	0.001
Height	0.540	0.001
Volume	0.492	0.001
Basal area	0.476	0.001
Diameter	0.336	0.009
Age	0.295	0.020
Number of stems	0.025	0.736

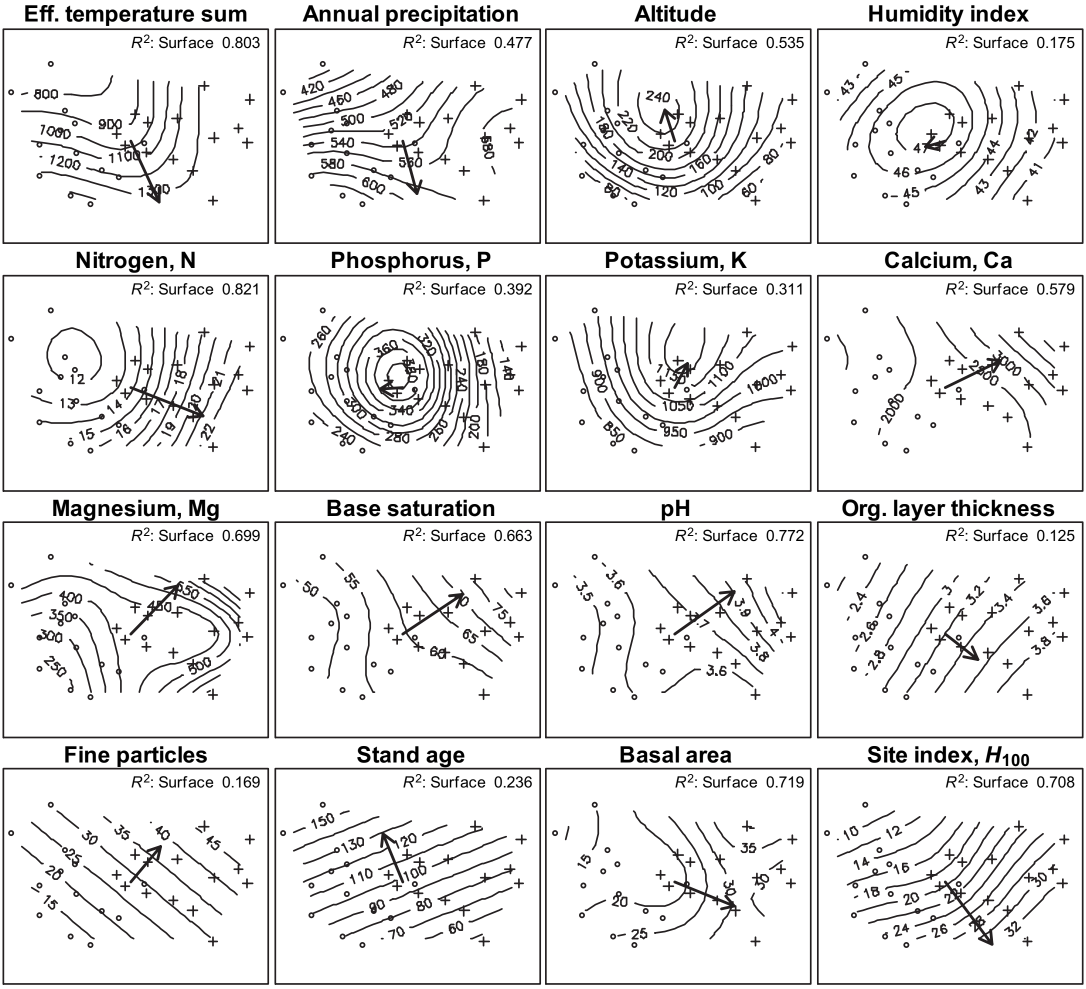

Fig. 4. Non-metric multidimensional scaling (NMDS) ordination (same as in Fig. 3a) with fitted environmental vectors and non-linear GAM surfaces. The vectors show the direction and magnitude of the linear correlations of the environmental variables with the plot scores. The surfaces depict the smooth trends between the environmental variables and plot scores. Crosses indicate the position of the spruce plots, and circles of the pine plots.

and Ca concentrations and high C/N ratio in the organic layer, whereas grasses and herbs were the most abundant at the opposite end of the fertility gradient (Fig. 5b–e). The deciduous dwarf shrub *Vaccinium myrtillus* had the maximum cover between these groups. The most common vascular plant species reached their maximum cover along the N gradient in the following order: *Calluna vulgaris* (lowest N) < *Empetrum nigrum*, *Vaccinium vitis-idaea* < *Vaccinium myrtillus* < *Deschampsia flexuosa* < *Maianthemum bifolium* (Fig. 5b and Table 3).

The H_{100} values ranged from 8.2 to 26.7 m on the pine and from 10.2 to 34 m on the spruce plots. The H_{100} values increased with increasing total N concentrations in the organic layer on the plots of both species (Fig. 6a). The Pearson correlation between the H_{100} values and N concentrations was higher for the spruce plots than for the pine plots (Table 6). On the pine plots the exchangeable Ca concentration had higher correlation than that for N. High H_{100} values invariably occurred on the nitrogen-rich plots. The nitrogen-poor plots, however, represented a rather wide range of site index values. H_{100} values near and even below 10 occurred on the northernmost plots, reflecting the severe, near sub-arctic climatic conditions in northernmost Finland. When

Table 5. Pearson correlations between the chemical variables of the organic layer. Fine part. = Percentage of fine particles. $n = 27$ plots. Correlations significant at $p < 0.05$ are in boldface. *See* Table 3 for explanation of variable names.

	pH	N	P	K	Ca	Mg	S	Mn	Zn	Na	C:N	P:N	CEC	BS
N	**0.582**													
P	−0.248	**−0.596**												
K	0.259	−0.234	**0.792**											
Ca	**0.829**	**0.503**	−0.140	0.286										
Mg	**0.595**	**0.535**	−0.039	0.321	**0.708**									
S	**0.459**	**0.566**	0.092	**0.395**	**0.435**	**0.579**								
Mn	**0.743**	0.151	0.289	**0.617**	**0.794**	**0.573**	**0.443**							
Zn	**0.671**	0.255	−0.048	0.211	**0.732**	**0.385**	0.217	**0.786**						
Na	0.011	**0.521**	**−0.466**	**−0.394**	0.011	**0.488**	**0.351**	−0.184	−0.063					
C:N	**−0.613**	**−0.966**	**0.557**	0.199	**−0.514**	**−0.493**	**−0.574**	−0.160	−0.240	**−0.454**				
P:N	−0.329	**−0.755**	**0.962**	**0.716**	−0.251	−0.157	−0.057	0.219	−0.105	**−0.516**	**0.730**			
CEC	**0.614**	**0.716**	**−0.409**	−0.015	**0.580**	**0.606**	0.332	**0.394**	**0.491**	**0.438**	**−0.680**	**−0.514**		
BS	**0.838**	**0.586**	−0.104	0.336	**0.775**	**0.656**	**0.419**	**0.643**	**0.571**	0.012	**−0.596**	−0.224	**0.668**	
Fine particles	**0.458**	0.208	0.187	**0.498**	**0.608**	**0.624**	**0.492**	**0.699**	**0.382**	0.080	−0.191	0.119	**0.419**	**0.440**

the northern plots (effective temperature sum 700–1100 d.d.) were analysed separately, there was no notable correlation between the N concentration and H_{100}. The N concentrations on the northernmost plots (Sevettijärvi No. 1 and Kevo No. 22) were slightly higher than those in central Lapland, and this had a clear effect on the results. The effective temperature sum, as well as the annual precipitation, correlated positively with the H_{100} values of both species (Table 6).

The correlations between the number of species and the N concentration in the organic layer varied in the different plant groups (Fig. 5f and Table 7). The number of herb species correlated the best with the N concentration on both the pine and spruce plots, as well as in the combined data. The number of grass species also showed a positive trend with the N concentration, especially on the spruce plots. On the other hand, the species richness of dwarf shrubs and lichens on the spruce plots, and of hepatics on the pine plots, correlated negatively with the N concentration in the organic layer. In general, the relationship between the species numbers and H_{100} (Fig. 6b) was relatively similar to that for the N concentration (Fig. 5f). On the pine plots the number of herb species correlated even better with H_{100} ($r = 0.735$) than with the N concentration ($r = 0.531$) (Table 7). The cover curves of the species or species groups along the H_{100} gradient were, in most cases, wide and did not give any clear indication of the productivity level (Fig. 6c and d).

Table 6. Pearson correlations between the site index (H_{100}) values of Scots pine and Norway spruce plots and the variables of organic layer and climate giving the highest correlation with the vegetation pattern. *See* Table 3 for explanation of the variable names.

	Scots pine ($n = 13$)	Norway spruce ($n = 14$)
Total N	0.523°	0.898***
pH	0.352	0.314
Exch. Ca	0.648*	0.211
Exch. Mg	−0.543°	0.213
BS	0.310	0.227
Org. layer thickness	0.386	−0.144
Eff. temperature sum	0.896***	0.909***
Annual precipitation	0.850***	0.478°

Statistical significance: *** = $p < 0.001$, * = $p < 0.05$, ° = $p < 0.10$. n = number of plots.

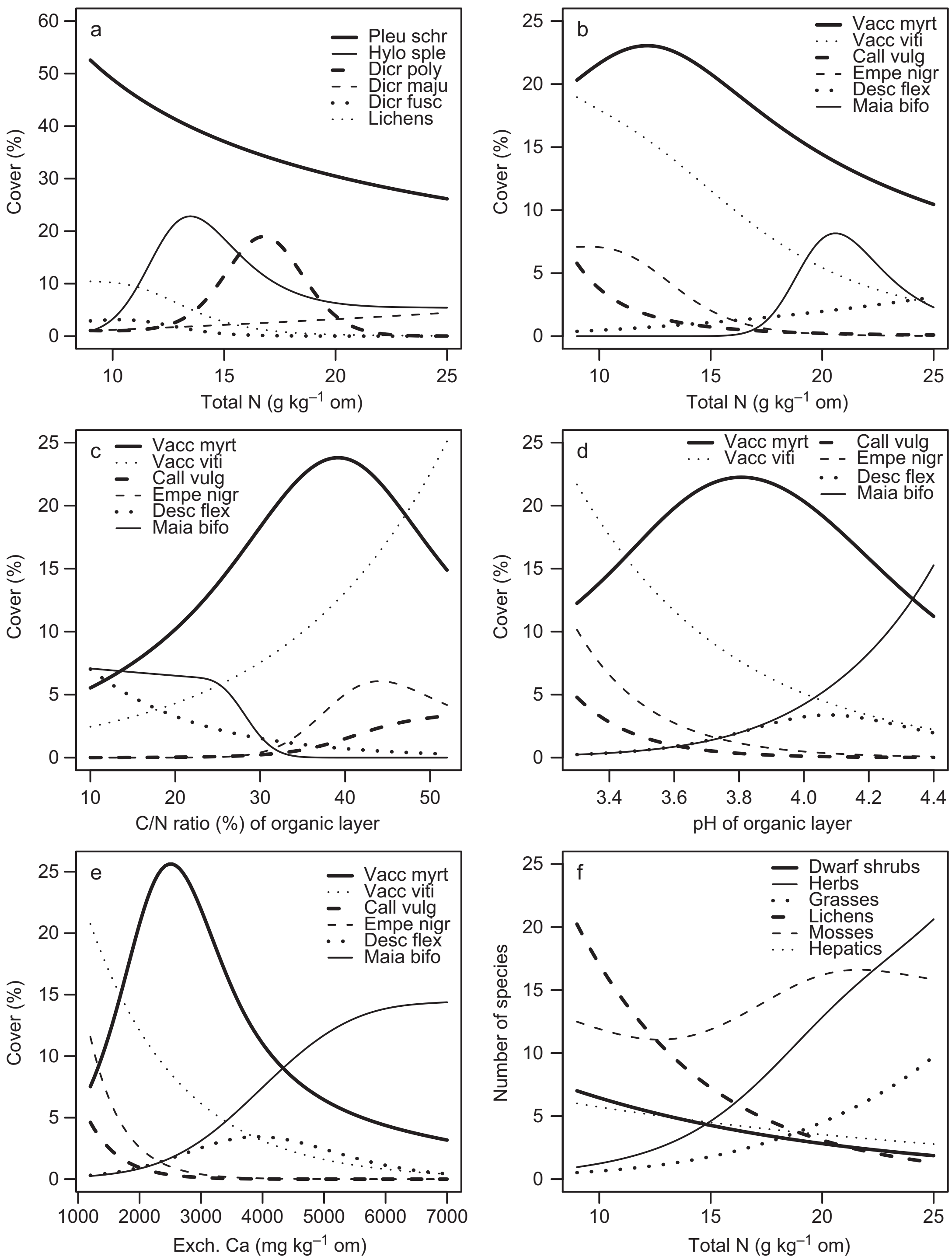

Fig. 5. (**a**) The cover of the selected bryophyte species and the sum of lichens in relation to the N gradient of the organic layer. The cover of the selected vascular plant species in relation to (**b**) N, (**c**) C/N ratio, (**d**) pH, and (**e**) Ca gradient of the organic layer. (**f**) The number of species in different functional plant groups in relation to the N gradient of the organic layer. om = organic matter content. All the curves are the predictions given by GAM models. The values for N were ln-transformed in the models.

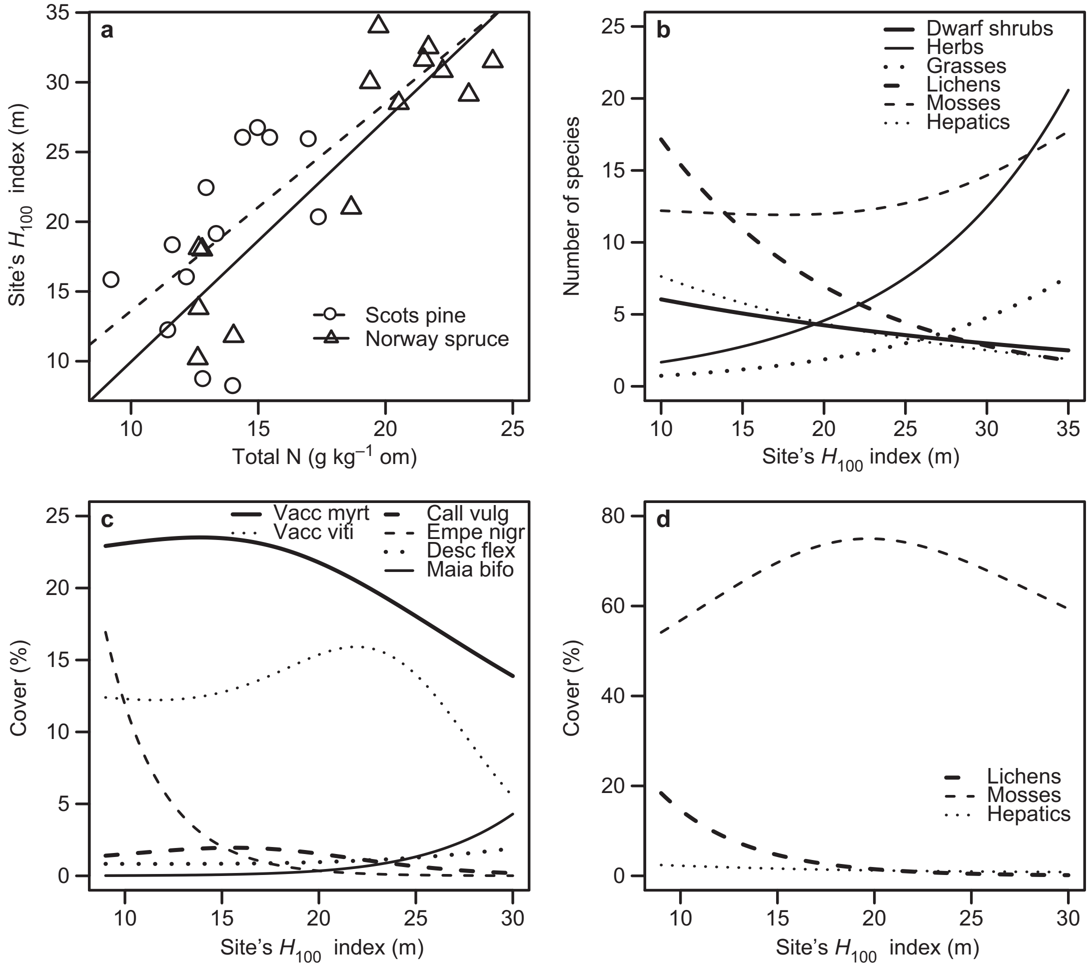

Fig. 6. — **a**: The site's H_{100} index in relation to the N gradient in the organic layer (linear regression lines marked for the Scots pine and Norway spruce plots). — **b**: The number of species. — **c**: The cover of selected vascular plant species. — **d**: Sum of mosses, lichens and liverworts in relation to the H_{100} index. om = organic matter content. The curves in **b**–**d** are the predictions given by GAM models.

Table 7. Pearson correlations between the species numbers in different plant groups and the total N concentration in the organic layer and the site's H_{100} index.

	Scots pine (*n* = 13)		Norway spruce (*n* = 14)		All plots (*n* = 27)	
	Total N	H_{100}	Total N	H_{100}	Total N	H_{100}
Dwarf shrubs	–0.329	–0.401	–0.673**	–0.632*	–0.656***	–0.586**
Herbs	0.531°	0.735**	0.717**	0.617*	0.793***	0.663***
Grasses	0.454	0.492°	0.687**	0.587*	0.764***	0.619***
Hepatics	–0.533°	–0.886***	–0.391	–0.394	–0.216	–0.493**
Mosses	–0.474°	–0.601*	0.357	0.420	0.457*	0.268
Lichens	–0.182	–0.791**	–0.648*	–0.550*	–0.549**	–0.659***

Statistical significance: *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, ° = $p < 0.10$. *n* = number of plots.

Discussion

The strong climatic shift from south to north, combined with the range in properties of the organic layer, formed a complex environmental gradient that affected both the understorey vegetation and the tree stands. In many cases it was impossible to separate the independent effects of the inter-correlated environmental factors on the vegetation. The age of the stands also increased towards the north, which added variation to the results. The difference between the unmanaged and managed plots appeared to be obscured by the effect of stand age. Our results support earlier findings concerning the vegetation–soil relationships in boreal forests (e.g. Cajander 1949, Dahl *et al.* 1967, Økland and Eilertsen 1993, Giesler *et al.* 1998), that the most important chemical variables in the soil causing broad-scale differentiation of the boreal understorey vegetation are N, pH and BS. Our results also indicate that the relationships between these variables and the dominant vegetation gradient were close to linear, although one or two plots (e.g. Uusikaarlepyy No. 23, which was located relatively close to a fur farm) caused irregularities in the overall pattern. However, the importance of N for the vegetation pattern was not so clear when only part of the climatic gradient was investigated. In northern Finland for instance, the vegetation was also related to the P and K concentrations in the organic layer.

Many studies have shown that N deficiency is one of the primary ecological factors that limit the biological production of boreal forests (e.g. Tamm 1991). In our study, only the total N concentration of the organic layer was determined. Generally, only about 1% of the total N is available to plants in mineral form (NH_4 and NO_3) in boreal forests (Smolander *et al.* 2005). Current knowledge, however, emphasizes that plants can also take up some N in organic forms (e.g. amino acids) via mycorrhizal associations (Näsholm *et al.* 1998). Read (1991) suggested that, in regions with a cool, humid climate, low pH and slow rate of decomposition, organic N and ammonium are the main sources of N for plants. Species possessing ectomycorrhizal (ECM) and ericoid mycorrhizal (ERM) associations should predominate in these regions. Experimental evidence has shown that ECM and ERM fungi can mobilise N and P from organic polymers (Read and Perez-Moreno 2003). In contrast, in warmer, drier regions with a higher pH and more rapid N mineralization and nitrification, nitrate is the prevailing N source for plants. In these regions, plants with arbuscular mycorrhizae (AM) form dominant communities and these plant species can assimilate amino acid N (Read and Perez-Moreno 2003).

Our results on the distribution of vascular plant species along the total N gradient are consistent with Read's (1991) hypothesis. The two most abundant dwarf shrubs (*Vaccinium myrtillus* and *V. vitis-idaea*), which possess ERMs, were found on all the plots, but their abundance increased towards the N-poor plots at high latitudes. Mäkipää (1999) did not find differences in the ecological N optima between these two species in the material from southern Finland, but in our data *V. myrtillus* had the maximum cover at higher N level than *V. vitis-idaea*. The evergreen dwarf shrubs, *Calluna vulgaris* and *Empetrum nigrum*, reached their maximum cover on more acidic and nutrient-poor soils than the *Vaccinium* species. The dominance of evergreen dwarf shrubs in nutrient-poor environments can be explained by their low rates of nutrient loss (Aerts 1995) and their polyphenolic-rich leaves and litter (Jalal *et al.* 1982), which accumulate in the organic layer and can be decomposed by their own fungal partner (ERM) (Read and Perez-Moreno 2002). On the other hand, the herbs (e.g. *Maianthemum bifolium*, *Rubus saxatilis* and *Oxalis acetosella*) and grasses (e.g. *Calamagrostis arundinacea*), which possess AMs, were the most abundant on southern plots with higher N concentrations and somewhat higher pH. The most common grass, *Deschampsia flexuosa*, which is known to be able to take up the amino acid glycine (Näsholm *et al.* 1998), was also present on the northern plots.

The moss and lichen layer of boreal forests is known to respond to a complex of factors, including moisture and light conditions, as well as the structural properties of the organic layer (Økland and Eilertsen 1993, Rydgren 1996). Bryophytes obtain almost all of their water and nutrients from precipitation and throughfall, but some of them also obtain nutrients from water that has been in contact with the organic layer (Bates

1992). The N retention ability of different boreal bryophyte species varies, and this can control the between-species interactions. For instance, the dominance of *Pleuroziumin schreberi* may be due to its high biomass production per tissue N concentration (Salemaa *et al.* 2008). Bryophytes (DeLuca *et al.* 2002), and leather lichens (Kallio *et al.* 1972) in the northern N-poor regions have epiphytic cyanobacteria, which are able to biologically fix N. The vegetation–soil dynamics on the northern plots, where the cover of feathermosses often exceeds 50% and the occurrence of leather lichens (*Nephroma* sp. and *Peltigera* sp.) is not rare, may be influenced by the presence of N-fixing organisms.

In addition to N, the BS of the organic layer also correlated positively with the broad-scale vegetation differentiation in our data. BS (i.e. the proportion of base cations occupying the exchange sites on organic soil particles), which is mainly used to depict the acid-buffering capacity of soils, is also an indicator of the availability of Ca, Mg and K to plants. BS had a higher positive correlation with pH than with the N concentration. On some of the plots classified as herb-rich heath forests (e.g. Punkaharju No. 17 and Uusikaarlepyy No. 23), the N concentration in the organic layer was relatively high (20 and 24 g kg^{-1}, respectively), but the BS low (54% and 47%). Specific local conditions, e.g. the Uusikaarlepyy plot is located on an acid sulphate soil, and the Punkaharju plot on a partly paludified site earlier subjected to slash-and-burn agriculture, undoubtedly explain this unusual relationship.

On the plots located in the northern boreal zone, the P and K concentrations in the organic layer were better explanatory variables of the vegetation pattern than the total N concentration. This was probably due to the fact that herb-rich heaths were absent from the plot network in the northern boreal zone, and the range of N concentrations was narrower than in the south. On the other hand, local geological conditions affect the high P and K concentrations on plot Nos. 7, 8 and 21 in the Oulanka area, which is characterized by phosphate-rich alkaline bedrock.

Although the broad-scale differentiation of the vegetation was clearly associated with the chemical composition of the organic layer, in some cases there was greater variation in the structure of the vegetation than in the chemical properties of the organic layer between the site types. In these cases, factors other than the chemical composition of the organic layer, such as the moisture conditions, shading by the tree stand etc., play an important role in determining the composition of the understorey vegetation.

In addition to soil nutrients, climatic factors also had a considerable influence on the vegetation pattern. Solantie (2005) suggested that the effective temperature sum, duration of the vegetation period and the maximum soil frost penetration, are the most important factors determining the zonation of forest vegetation in Finland, and also presented evidence that these factors predict forest productivity. One typical feature in the boreal climatic gradient is that, although precipitation decreases from south to north, the soil moisture content is higher in the north owing to the lower rate of evapo-transpiration caused by the cooler conditions (Solantie 1987). Thus many moisture-demanding plant species that grow on peatlands in the south (e.g. *Vaccinium uliginosum*) have found suitable habitats also on heaths in the north. In general, fine-textured soils retain moisture and are relatively fertile, whereas coarse-textured soils are highly permeable to water, and hence drier, and have much lower nutrient concentrations (Urvas and Erviö 1974, Sepponen *et al.* 1979). In our study, however, the main vegetation gradients did not correlate well with the proportion of fine particles in the soil.

Tree species was a primary attribute for the vegetation structure in our material, because the more fertile plots were dominated by Norway spruce and the less fertile ones by Scots pine. The prevailing tree species has regenerated naturally on the majority of the plots, and thinnings have directed the succession towards single tree-species stands on the managed plots. Tree species affects the vegetation through light transmittance, chemical composition of the throughfall, soil nutrient concentrations and properties of the litter (Økland and Eilertsen 1993, Barbier *et al.* 2008). In general, Norway spruce shades the understorey more than Scots pine. Furthermore, the chemodiversity of trees, e.g. in needle monoterpene levels, may affect the occurrence of specific plant species in the local environment (Iason *et al.* 2005).

The H_{100} values varied within a very wide range, indicating considerable differences in production potential between the stands. The H_{100} values of different tree species growing on the same site are seldom fully comparable. In Finnish conditions, however, Norway spruce and Scots pine have relatively similar site indices under similar conditions (Vuokila and Väliaho 1980). The H_{100} value of the stands correlated positively with the N concentration in the organic layer for both species, but the correlation was higher for Norway spruce. Tamminen (1993) reported a corresponding relationship in a study that included over 1200 stands in southern Finland. However, other factors can also explain the variation in the H_{100} index (Tamminen 1993); in our data the considerable variation in H_{100} on the northern, nutrient-poor sites was obviously related to the cold climate. According to Nieppola (1993), the presence of individual plant species, and especially the number of herbs, is a good indicator of the site index in Scots pine stands in southern Finland. In contrast, the species cover was poorly related to site index. The same conclusion can be drawn from both the Scots pine and Norway spruce plots and the extensive latitudinal gradient in our material.

In this paper, we presented quantitative evidence that the most important factors behind the extensive "fertility gradient" of boreal forest vegetation, were the total N, exchangeable Ca and Mg concentrations, and the BS and pH of the organic layer. We conclude, that our results support the hypothesis that the site index H_{100} correlates with the N concentration of the organic layer, although the correlation was weaker for Scots pine than for Norway spruce and not so clear in the north. Furthermore, the plant species composition, especially the number of herb and grass species, well indicated the site index, despite the small size of the material. The description of the vegetation continuum along an extensive climatic gradient using multivariate methods will also enable us to make hypotheses e.g. on how climate change or eutrophication may alter the understorey vegetation in the future.

Acknowledgements: We are grateful to Prof. Jari Oksanen for providing statistical advice in the data processing stage, and to Päivi Merilä and Raisa Mäkipää for comments on the manuscript. We express our sincere thanks to Leena Hamberg, Liisa Sierla, Tiina Tonteri and Anneli Viherä-Aarnio for participating in the field work, and to Nijole Kalinauskaite and Sampsa Lommi for identifying the bryophyte and lichen samples. Part of the monitoring material utilized in the study was collected with co-funding provided within the framework of the EU/Forest Focus Programme (Regulation (EC) No. 2152/2003).

References

Aerts R. 1995. The advantages of being evergreen. *TREE* 10: 402–407.

Barbier S., Gosselin F. & Balandier P. 2008. Influence of tree species on understorey vegetation diversity and mechanisms involved - a critical review for temperate and boreal forests. *For. Ecol. Manage*. 254: 1–15.

Bates J.W. 1992. Mineral nutrient aquisition and retention by bryophytes. *J. Bryol*. 17: 223–240.

Cajander A.K. 1909. Über Waldtypen. *Acta For. Fenn*. 1: 1–175.

Cajander A.K. 1949. Forest types and their significance. *Acta For. Fenn*. 56(6): 1–71.

Dahl E., Gjems O. & Kielland-Lund J. 1967. On the vegetation types of Norwegian conifer forests in relation to the chemical properties of the humus layer. *Medd. Norske Skogsforsøksvesen* 85: 501–531.

DeLuca T.H., Zackrisson O., Nilsson M.-C. & Sellstedt A. 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. *Nature* 419: 917–920.

Derome J., Lindgren M., Merilä P., Beuker E. & Nöjd P. 2007. Forest condition monitoring under the UN/ECE and EU programmes in Finland. *Working Papers of the Finnish Forest Reserach Institute* 45: 11–20.

Diekmann M. & Falkengren-Grerup U. 1998. A new species index for forest vascular plants: development of functional indices based on mineralization rates of various forms of soil nitrogen. *J. Ecol*. 86: 269–283.

Ellenberg H., Weber H.E., Düll R., Wirth V., Werner W. & Paulissen D. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* 18: 1–248.

Giesler R., Högberg M. & Högberg P. 1998. Soil chemistry and plants in Fennoscandian boreal forest as exemplified by a local gradient. *Ecology* 79: 119–137.

Grandin U. 2004. Dynamics of understorey vegetation in boreal forests: experiences from Swedish integrated monitoring sites. *For. Ecol. Manage*. 195: 45–55.

Gustavsen H.G. 1980. Site index curves for conifer stands in Finland. *Folia For.* 454: 1–31. [In Finnish with English summary].

Hägglund B. & Lundmark J.-E. 1977. Site index estimation by means of site properties, Scots pine and Norway spruce in Sweden. *Stud. For. Suec*. 138: 1–38.

Heinonen J. 1994. KPL — a computer programme package for computing stand and single tree characteristics from sample plot measurements. *The Finnish Forest Research Institute. Metsäntutkimuslaitoksen tiedonantoja* 504: 1–80. [In Finnish with English summary].

Hill M.O., Roy D.B., Mountford J.O. & Bunce R.G.H. 2000.

Extending Ellenberg's indicator values to a new area: an algorithmic approach. *J. Appl. Ecol.* 37: 3–15.

Hilli S., Stark S. & Derome J. 2008. Carbon quality and stocks in organic horizons in boreal forest soils. *Ecosystems* 11: 270–282.

Iason G.R., Lennon J.J., Pakeman R.J., Thoss V., Beaton J.K., Sim D.A. & Elston D.A. 2005. Does chemical composition of individual Scots pine trees determine the biodiversity of their associated ground vegetation? *Ecology Letters* 8: 364–369.

Ilvessalo Y. 1922. Vegetationsstatistische untersuchungen über die Waldtypen. *Acta For. Fenn.* 20(3): 1–73.

Jalal M.A.F., Read D.J. & Haslam E. 1982. Phenolic composition and its seasonal variation in *Calluna vulgaris*. *Phytochemistry* 21: 1397–1401.

Kallio P., Suhonen S. & Kallio H. 1972. The ecology of nitrogen fixation in *Nephroma arcticum* and *Solorina crocea*. *Rep. Kevo Subarctic Res. Stat.* 9: 7–14.

Kanerva S. & Smolander A. 2007. Microbial activities in the forest floor layers under silver birch, Norway spruce and Scots pine. *Soil Biol. Biochem.* 39: 1459–1467.

Kokko A., Mäkelä K. & Tuominen S. 2002. Understorey vegetation monitoring at Finnish Integrated Monitoring areas in 1988–1998. *The Finnish Environment* 544: 1–97. [In Finnish with English summary].

Kuusipalo J. 1984. Diversity pattern of the forest understorey vegetation in relation to some site characteristics. *Silva Fenn.* 18: 121–131.

Kuusipalo J. 1985. An ecological study of upland forest site classification in southern Finland. *Acta For. Fenn.* 192: 1–78.

Laasasenaho J. 1982. Taper curve and volume functions for pine, spruce and birch. *Comm. Inst. For. Fenn.* 108: 1–74.

Lahti T. & Väisänen R.A. 1987. Ecological gradients of boreal forests in South Finland: an ordination test of Cajander's forest site type theory. *Vegetatio* 68: 145–156.

Mäkipää R. 1999. Response patterns of *Vaccinium myrtillus* and *V. vitis-idaea* along nutrient gradients in boreal forests. *J. Veg. Sci.* 10: 17–26.

Minchin P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69: 89–107.

Näsholm T., Ekblad A., Nordin A., Giesler R., Högberg M. & Högberg P. 1998. Boreal forest plants take up organic nitrogen. *Nature* 392: 914–916.

Nieppola J. 1993. Understorey plants as indicators of site produtivity in *Pinus sylvestris* L. stands. *Scand. J. For. Res.* 8: 49–65.

Nieppola J.J. & Carleton T.J. 1991. Relations between understorey vegetation, site productivity, and environmental factors in *Pinus sylvestris* L. stands in southern Finland. *Vegetatio* 93: 57–72.

Nilsson M.-C. & Wardle D.A. 2005. Understorey vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Front. Ecol. Environ.* 3: 421–428.

Ojansuu R. & Henttonen H. 1983. Estimation of local values of monthly mean temperature, effective temperature sum and precipitation sum from the measurements made by the Finnish meteorological office. *Silva Fenn.* 17(2): 142–160. [In Finnish with English summary].

Oksanen, J. 2007. *'Vegan' Community Ecology Package: ordination methods, diversity analysis and other functions for community and vegetation ecologists. University of Oulu, Finland.* Available at http://vegan.r-forge.r-project.org/.

Økland R.H. & Eilertsen O. 1993. Vegetation-environment relationships of boreal coniferous forests in the Solhomfjell area, Gjerstad, S Norway. *Sommerfeltia* 16: 1–254.

Read D.J. 1991. Mycorrhizas in ecosystems. *Experientia* 47: 376–391.

Read D.J. & Perez-Moreno J. 2003. Mycorrhizas and nutrient cycling in ecosystems — a journey towards relevance? *New Phytol.* 157: 475–492.

Rydgren K. 1996. Vegetation-environment relationships of old-growth spruce forest vegetation in Ostmarka Nature Reserve, SE Norway, and comparison of three ordination methods. *Nord. J. Bot.* 16: 421–439.

Saetre P. 1999. Spatial patterns of ground vegetation, soil microbial biomass and activity in a mixed spruce-birch stand. *Ecography* 22: 183–192.

Salemaa M., Mäkipää R. & Oksanen J. 2008. Differences in the growth response of three bryophyte species to nitrogen. *Environ. Pollut.* 152: 82–91.

Sepponen P. 1985. The ecological classification of sorted forest soils of varying genesis in northern Finland. *Commun. Inst. For. Fenn.* 129: 1–77.

Sepponen P., Lähde E. & Roiko-Jokela P. 1979. On the relationship of the forest vegetation and the soil physical properties in Finnish Lapland. *Folia For.* 402: 1–31. [In Finnish with English summary].

Smolander A., Loponen J., Suominen K. & Kitunen V. 2005. Organic matter characteristics and C and N transformations in the humus layer under two tree species, *Betula pendula* and *Picea abies*. *Soil Biol. Biochem.* 37: 1309–1318.

Solantie R. 1987. Maaperän kosteus. In: Alalammi, P. (ed.), *Atlas of Finland, Folio 131 — Climate*, National board of Survey & Geographical Society of Finland, Helsinki, pp. 18–19. [In Finnish, maps and figures in English].

Solantie R. 2005. Productivity of boreal forests in relation to climate and vegetation zones. *Boreal Env. Res.* 10: 275–297.

Tamm C.O. 1991. *Nitrogen in terrestrial ecosystems*. Springer Verlag, Heidelberg.

Tamminen P. 1993. Estimation of site index for Scots pine and Norway spruce stands in South Finland using site properties. *Folia For.* 819: 1–26. [In Finnish with English summary].

Tamminen P. 2000. Soil factors. In: Mälkönen E. (ed.), *Forest condition in a changing environment — the Finnish case*, Kluwer Academic Publishers, Dordrecht, pp. 72–86.

Tonteri T., Hotanen J.-P. & Kuusipalo J. 1990a. The Finnish forest site type approach: ordination and classification studies of mesic forest sites in southern Finland. *Vegetatio* 87: 85–98.

Tonteri T., Mikkola K. & Lahti T. 1990b. Compositional gradients in the forest vegetation of Finland. *J. Veg. Sci.*

1: 691–698.

Tuhkanen S. 1980. Climatic parameters and indices in plant geography. *Acta Phytogr. Suec*. 87: 1–110.

Urvas L. & Erviö R. 1974. Influence of the soil type and the chemical properties of soil on the determining of the forest type. *J. Agric. Soc. Finland* 46: 307–319. [In Finnish with English summary].

Valmari J. 1921. Beiträge zur chemischen bodenanalyse. *Acta For. Fenn*. 20(4): 1–67.

Virtanen R., Oksanen J., Oksanen L. & Razzhivin V.Y. 2006. Broad-scale vegetation–environment relationships in Eurasian high-latitude areas. *J. Veg. Sci*. 17: 519–528.

Vuokila Y. & Väliaho H. 1980. Growth and yield models for conifer cultures in Finland. *Comm. Inst. For. Fenn*. 99(2): 1–271. [In Finnish with English summary].

Wood S.N. 2000. Modelling and smoothing parameter estimation with multiple quadratic penalties. *J. R. Stat. Soc. Ser. B* 62: 413–428.

Wood S.N. 2006. *Generalized additive models. An introduction with R*. Chapman and Hall/CRC, Boca Raton.