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A. Skrindo & R.H. Økland

Fertilization effects and vegetation-environment
relationships in a boreal pine forest in
Åmli, S Norway

1998



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Species composition in 144 sample plots, each 1 m², in 35-year old pine forest in Åmli municipality in Aust-Agder, S Norway, was recorded. The plots were systematically placed within the 12 blocks in a factorial fertilization experiment [addition of nitrogen (2 levels), magnesium and phosphorus], initiated six years before our analysis was carried out. At each sample plot, 28 explanatory variables were recorded. Results obtained by parallel use of three ordination methods demonstrated existence of one main coenocline from lichen-rich sites to sites rich in mosses and ericaceous species. The coenocline was interpreted by analysis of correlations between plot positions and explanatory variables, and by analysis of spatial structure using geostatistical methods, as a fine-scale moisture complex-gradient. Important correlated variables were: humus depth, tree density and canopy closure, and microtopography.

Small, but significant effects of fertilization by nitrogen and phosphorus on the vegetation was demonstrated and discussed.

Keywords: Boreal pine forest, CCA, DCA, Ecology, Environment, Fertilization, Gradient, LNMDS, Magnesium, Nitrogen, Norway, Ordination, PCA, Phosphorus, Vegetation.

Astrid Skrindo, Botanical Garden and Museum, Univ. of Oslo, Trondheimsvn. 23B, N-0562 Oslo, Norway. Present address: Department of Horticulture and Crop science, Agricultural Univ. of Oslo, P.O. Box 5022, N-1432 Ås, Norway.

Rune Halvorsen Økland, Botanical Garden and Museum, Univ. of Oslo, Trondheimsvn. 23B, N-0562 Oslo, Norway.

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INTRODUCTION

Boreal coniferous forests, covering 27 % of the land area (Anonymous 1992a), are the economically most important among terrestrial ecosystems.

Knowledge of vegetation-environment relationships in these forests is therefore important. Norwegian spruce-dominated forests have recently been subjected to several detailed studies (e.g. T. Økland 1996), while the number of studies on vegetation-environment relationships in Fennoscandian pine forest is low. Typically, pine forests have been included in studies of boreal forests covering the whole range of variation from pine- to spruce-dominated stands (e.g. Malmström 1949, Kuusipalo 1985, Lahti & Väisänen 1987, R. Økland & Eilertsen 1993). Most of these studies address broad-scale patterns of variation.

The ground vegetation is an important part of the forest ecosystem, both in terms of biomass and function (e.g. Stålfelt 1937, Oechel & van Cleve 1986, Mäkipää 1994).

Deposition of airborne pollutants increased strongly from 1950 to 1980 (Anonymous 1997a). Since 1980, sulphur deposition has decreased, while nitrogen deposition has remained at the same level (Anonymous 1997a). Accordingly, there has been a shift of focus from effects of acidification and forest decline to effects of nitrogen enrichment and fertilization. Nitrogen is known to be a growth-limiting factor in Scandinavian boreal forests (e.g. Aaltonen 1926, Tamm 1991, Binkley & Högberg 1997). Even though forest soils can accumulate large amounts of inorganic nitrogen, there is an increasing concern that forest soils will become nitrogen-saturated, especially in S Norway and S Sweden where much inorganic nitrogen is deposited compared to the rest of the country (Anonymous 1997b). An ecosystem is considered as nitrogen-saturated if the availability of inorganic nitrogen exceeds the demand of the organisms inhabiting that ecosystem (Aber et al. 1989). Soil saturation by nitrogen implies lowered net uptake of nitrogen by plants and increased NO_3^- -leaching, whereas an equivalent increase in the leaching of nitrogen and cations, and a decrease in soil pH, occurs (e.g. Aber et al. 1989). Some stands near the southwest coast of Sweden now show leaching losses of nitrogen that rival nitrogen deposition rates (Binkley & Högberg 1997).

Documented changes in forest vegetation that may be attributed to pollution are reported by, e.g. Falkengren-Grerup (1989) from S Sweden and R. Økland (1995) and R. Økland & Eilertsen (1996) from S Norway. Long records of abundance data from permanent plots in the Scandinavian countries are, however, almost completely lacking, as pointed out by T. Økland (1990) and Mäkipää (1994). Effects of pollution on forests have therefore mostly been addressed by less optimal strategies such as re-analysis of non-permanent plots (Niippola 1992 cf. also Falkengren-Grerup 1989).

The most serious long-term effect of acid rain on Norwegian terrestrial ecosystems is considered to be the reduced availability of important plant nutrients (Abrahamsen 1984, Abrahamsen et al. 1994). Deposition of acidifying sulphuric compounds increases the leaching of cations such as magnesium, and may also strengthen the absorption of anions from the colloids, and thereby reduce the availability of phosphorus to plants. With the aim of investigating relationships between nitrogen addition and nutrient balance of soil and trees, nitrogen, magnesium and phosphorus was applied to a pine forest in an experimental, factorial design in S Norway in 1990 (Abrahamsen & Erstad 1995). Due to lack of knowledge of vegetational responses to fertilization, the present study of ground vegetation was carried out in this fertilization experiment, six years after fertilization started. As vegetation was not

recorded prior to the start the experiment, the scope of the present study is restricted to comparison of unfertilized control plots and plots with different fertilizations, in 1996.

Effects of (nitrogen) fertilization on pine-forest understory vegetation have been studied by several authors, using different experimental designs. Persson (1981) studied changes in vegetation during a six-year period, using 0.25-m² plots subjected to NH₄NO₃-pellet fertilization and irrigation treatments; Kellner (1993) studied vegetational change in 400-m² plots at several occasions after fertilization; Nygaard & Ødegaard (1993) studied vegetation in 1-m² plots eight years after the they received fertilizer for the last time; and van Dobben et al. (1993) studied vegetation in 400-m² plots 15 years after they were last fertilized. These, and other studies, demonstrate a wide variety of effects on different species. Despite considerable inconsistencies between them, most authors have found negative effects of fertilization on bryophytes and a change in vascular plant species composition. The response of vegetation to fertilization has not yet been found to vary according to variation in natural environmental factors, although such interactions are likely to occur (cf. Tamm 1991).

The structure of the ground vegetation and the relationship between vegetation and environmental factors can be analysed by many different methods. During the last 40 years, there has been a proliferation of numerical techniques (Kent & Ballard 1988). The choice of method, e.g. for ordination, still remains a controversial issue. Of the most frequently used ordination techniques, PCA shows best gradient recovery when species abundance are linear with respect to the important environmental complex-gradients, i.e. when compositional turnover (β -diversity) is low, otherwise DCA and LNMDS perform the best (Minchin 1987). Comparisons by means of simulated data sets have led to the conclusion that LNMDS is more robust than DCA and that DCA performs best only when species responses are Gaussian, which is rarely the case in field situations (Minchin 1987). However, simulated data sets are criticised for lack of the realism of field data, making comparisons on field data sets a necessary supplement (Oksanen 1983, R. Økland 1990a). Some authors find that DCA performs better than LNMDS for field data (e.g. T. Økland 1996), while others reach the opposite conclusion for other field data sets (e.g. Rydgren 1996). Because all ordination methods may distort the underlying true gradient structure, parallel use of several different ordination methods is strongly recommended (R. Økland 1990a, 1996). Nevertheless, further comparisons of the performance of ordination methods are needed.

The aims of this study are (1) to compare three ordination techniques (PCA, DCA and LNMDS) on a field data set from pine forest, (2) to relate the vegetational variation in this data set to environmental factors, and (3) to test for effects of fertilization by nitrogen, magnesium and phosphorus on the vegetation composition in a pine forest. Effects of fertilization on the individual species will be treated a separate paper.

THE INVESTIGATION AREA, MATERIALS AND METHODS

THE INVESTIGATION AREA

The investigation area was selected by Gunnar Abrahamsen in 1990 (Abrahamsen & Erstad 1995). It is situated in a Scots pine (*Pinus sylvestris*) forest on a flat, fluvial deposit with weakly podzolized soil at Øy in Åmli municipality (8°34'E.Gr. 59°54'N, 160 m.a.s.l.), Aust-Agder county, S Norway (Fig. 1). The forest was clear-felled and non-systematically re-planted 35 years ago.

The climate is suboceanic. The estimated annual mean (normal) temperature (1961–1990) at the nearest meteorological station, Tveitsund (25 km N of the study area, 252 m.a.s.l.), was 5.0 °C (Aune 1993). The mean temperatures of the warmest and coldest months (July and February, respectively) during the same period, were 15.1 and –4.8 °C. Annual mean precipitation during the same period was 994 mm (Førland 1993), the driest month was April (48 mm) and October received most precipitation (127 mm). The ground is covered by snow from December to April in average years. Nitrogen deposition close to the meteorological station was 3.35 kg NO₃⁻ ha⁻¹ and 3.12 kg NH₄⁺ ha⁻¹ in 1996 (Anonymous 1997b).

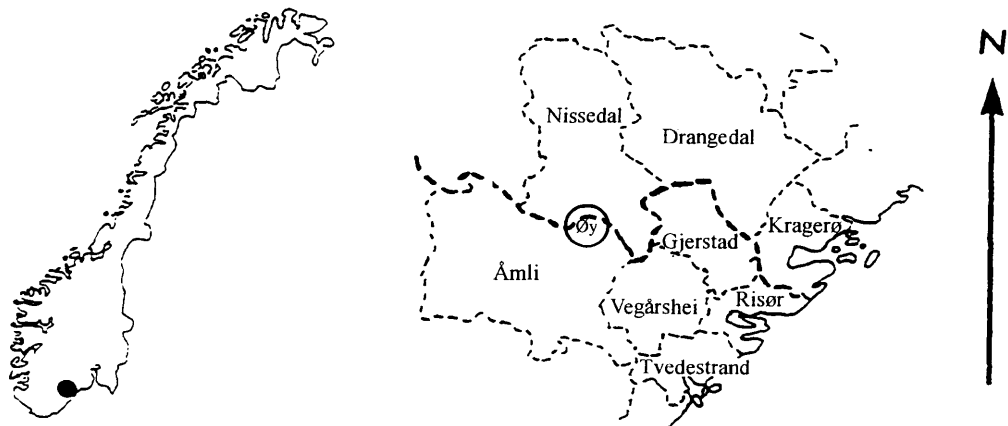


Fig. 1. Maps over Norway with insert showing several municipalities and the position of Øy, the investigation area.

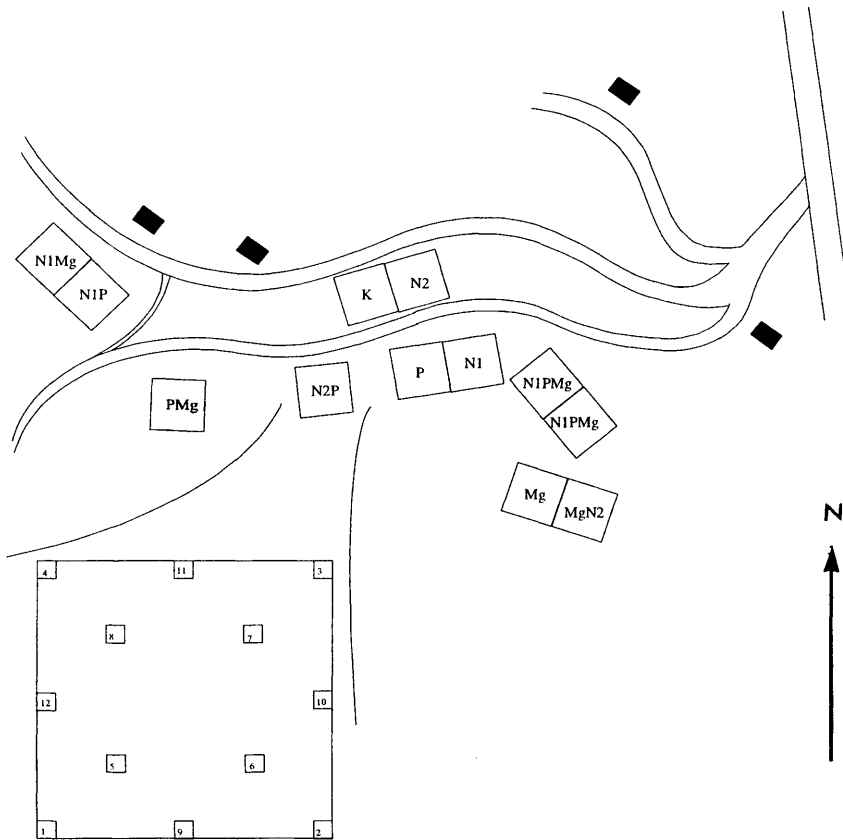


Fig. 2. Sampling design. Map of the study area with 12 macro plots and 144 meso plots.

THE SAMPLING DESIGN

A combination of random and systematic sampling techniques was used. Twelve plots, each 30×30 m, were selected by Abrahamsen & Erstad (1995). Three pellet-fertilizers, nitrogen (0, 30 and $90 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), magnesium (0 and $1.5 \text{ kg Mg ha}^{-1} \text{ yr}^{-1}$) and phosphorus (0 and $5.3 \text{ kg P ha}^{-1} \text{ yr}^{-1}$) were applied to the plots once a year (at mid-summer) from 1990 to 1996, using a random factorial design. Within each 30×30 m plot, a 7-m buffer zone along each side was left unused and the central 16×16 m was used as a macro plot. Twelve meso plots, each 1 m^2 , were systematically placed over the macro plot by grid sampling (R. Økland 1990a), see Fig. 2. Each meso plot was divided into 16 subplots, 0.0625 m^2 each. The sample set thus included 12 macro plots and 144 meso plots, numbered 1-144 and named by the combination of fertilizers the macro plot received: MN1, MN2...MN12, M1...M12, PMn1...PMn12, PMN1...PMN12, n1...n12, P1...P12, PN1...PN12, PM1...PM12, Mn1...Mn12, Pn1...Pn12, C1...C12, N1...N12 where N indicates $90 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of nitrogen, n indicates 30

yr⁻¹ of nitrogen, M indicates magnesium, P indicates phosphorus and C indicates unfertilized controls.

RECORDING AND MANIPULATION OF VEGETATION DATA

The vegetation of the field and bottom layers, which include vascular plants less than 80 cm high, and bryophytes and lichens, respectively, was recorded at the meso plot scale. Vegetation was analysed by recording species abundance in two ways: (1) by subjectively estimating percentage cover (pc) for all species in each meso plot on a 1–100 scale, and (2) by recording presence/absence of all species in each subplot for calculations of subplot frequency (sf) on a scale from 1 to 16 (T. Økland 1988). The tree layer was treated as environmental factors influencing the understorey; recordings of trees were thus used to calculate relevant explanatory variables. No shrub layer existed.

The following vegetation data sets were subjected to further analysis: ME 144sf, containing subplot frequency data for 39 species (see Appendix 1) in 144 meso plots; ME 144pc, containing percentage cover data (see Appendix 2); and ME 120sf and ME 120pc, containing ten meso plots from each macro plot (two meso plots were randomly omitted from the data set to meet the requirements for maximum data size set by the DECODA package). Omitted plots were: 7, 8, 23, 24, 26, 30, 42, 45, 57, 58, 63, 66, 75, 78, 85, 88, 103, 104, 116, 120, 123, 132, 133, 138.

Biological Data program/PC version 1.01 (Pedersen 1988) was used to edit the sample-species matrix (144 sample plots × 39 species). Weighting of each matrix element in the subplot frequency data set was performed by use of the power function (van der Maarel 1979, Clymo 1980, R. Økland 1990a):

$$y_{ij} = f(x_{ij}) = ax_{ij}^w,$$

where x_{ij} is the abundance of the species i in the sample plot j , w is a weighting parameter, a is a ranging scalar and y_{ij} the weighted abundance. The percentage scale was downweighted to range = 16 to be comparable to the subplot frequency scale, i.e. so that $x = 1 \Rightarrow y = 1$ and $x = 100 \Rightarrow y = 16$, giving $a = 1$ and $w = 0.602$ (cf. R. Økland 1990a, Rydgren 1993). In addition, species with a frequency less than the median frequency were downweighted in proportion to their frequency (Eilertsen et al. 1990).

RECORDING AND MANIPULATIONS OF EXPLANATORY VARIABLES

The following topographic variables were measured for all meso plots:

(01) *Unevenness (Uneven)*. A 1-m² metal frame with a 16-subplots grid was levelled, and the vertical distances (z_i) from the corners of each subplot to the soil surface were measured. The 25 measurements of z_i , five measurements in each row, and indexed from the bottom left side of the meso sample, were used in a bivariate regression to determine the plane

of best fit to the observed z_i 's as a function of position in the plot. Fitted values in this regression, z_i' , were used to calculate the deviation k_i of the soil surface from the plane of best fit ($i = 1, \dots, 25$). An index of unevenness (u) was calculated in accordance with R. Økland & Eilertsen (1993):

$$u = (\sum_{ij} |k_i - k_j|)/36,$$

where the sum was taken over the 36 pairs of adjacent subplot positions within each meso plot.

(02-03) *Convexity*. The deviances from the plane of best fit, k_i (see above), were used to calculate an objectivized index of convexity, *ConvObj*, in accordance with R. Økland & Eilertsen (1993). Convex and concave sample plots have k_i values that are systematically distributed over the plot. The average deviation from fitted values (the plane of best fit) near the centre of the plot, was calculated as:

$$k_0 = (k_7 + k_8 + k_9 + k_{12} + k_{13} + k_{14} + k_{17} + k_{18} + k_{19})/9,$$

where the k_i values are indexed as above. An index of convexity (c) was calculated as the mean deviation of the 16 positions not used to calculate k_0 , from k_0 :

$$c = \sum_i (k_0 - k_i)/25,$$

where $i = 1, \dots, 6, 10, 11, 15, 16, 20, \dots, 25$.

In addition, convexity was recorded subjectively as *ConvSub*, on a scale from -2 (very concave) via 0 (planar) to 2 (very convex).

(04-05) *Slope* was measured by a compass (400° scale), on the metal frame as fitted as accurately as possible to the surface topography of the meso plot. Slope on a finer scale, *SlopeFine*, was measured along the 10-cm line with steepest descent within each meso plot.

The following soil variables were measured to be representative for the meso plots:

(06) *Litter depth (LitDepth)*. The depth of the litter layer (consisting of plant remains, the origin of which was easily recognisable) was measured in four shallow pits at fixed positions 10 cm outside the plot, near the middle of each plot edge. *LitDepth* was recorded as the mean of these four measurements.

(07-09) *Humus depth* was measured in the same positions as *LitDepth*, as vertical distance from the soil surface to the eluviation layer. Three variables were derived: *HumDMin*, the minimum, *HumDMed*, the median, and *HumDMax*, the maximum of the four measurements.

Samples for determination of *pH*, *loss on ignition* and *total amount of nitrogen* in humus, were collected from all four edges of each meso plot. Care was taken to avoid inclusion of litter and the bleached sandy soil of the eluviation layer. These soil samples were air-dried and sieved (2 mm mesh width) before further analyses.

(10) *pH* was measured by a pH-meter (Ross Combination pH Electrode, 0-14 pH epoxy body with bulb guard) in the supernatant after 10 g of dry soil had been added to 75 ml of water, mixed for two hours, and left for sedimentation for 21 hours.

(11-12) *Soil moisture*. Volumetric soil moisture was determined in composite samples, one from each meso plot, made by mixing samples taken from four positions just outside each

Tab. 1. Explanatory variables; number, abbreviation, unit of measurement, range of scale, presumed statistical distribution, and transformation.

No	Abbrev.	Variable	Unit	Range	Distribution	Transform.
Topographical variables						
1	Uneven	Unevenness		0 - +∞	uniform	no
2	ConvSub	Subjective convexity		(-2,0,2)	uniform	no
3	ConvObj	Objective convexity		-∞ - +∞	uniform	no
4	Slope	Slope	g	0-100	lognormal	ln(1+x)
5	SlopeFine	Slope, fine scale	g	0-100	uniform	no
Soil variables						
6	LitDepth	Litter depth	cm	0 - ∞	lognormal	ln(1+x)
7	HumDMed	Median humus depth	cm	0 - ∞	uniform	no
8	HumDMin	Minimum humus depth	cm	0 - ∞	uniform	no
9	HumDMax	Maximum humus depth	cm	0 - ∞	uniform	no
10	pH	pH		1-14	uniform	no
11	Moist1	Soil moisture	Vol. %	0-100	uniform	no
12	Moist2	Soil moisture	Vol. %	0-100	uniform	no
13	LossIgni	Loss on ignition	%	0-1	uniform	no
14	N	Nitrogen	%	0-1	uniform	no
Tree variables						
15	LittIndex	Litter index		0 - ∞	lognormal	ln(1+x)
16	BasArea	Basal area	0 - ∞	lognormal	lnx	
17	Canopy	Canopy cover		0 - ∞	lognormal	ln(1+x)
18	CroAre5	Crown area, 5×5 m plot		0 - ∞	uniform	no
19	CroAre1	Crown area, 1×1 m plot		0 - ∞	lognormal	ln(1+x)
20	TreeStu1	Number of tree stumps, 1×1 m plot		0 - ∞	uniform	no
21	TreeStu3	Number of tree stumps, 3×3 m plot		0 - ∞	uniform	no
22	NuTree1	Numbers of trees, 1×1 m plot		0 - ∞	lognormal	ln(1+x)
23	NuTree3	Number of trees, 1×1 m plot		0 - ∞	lognormal	ln(1+x)
24	TallTree3	Tallest tree, 3×3 m plot		0 - ∞	uniform	no
25	TallTree5	Tallest tree, 5×5 m plot		0 - ∞	uniform	no
Fertilization variables						
26	FertilizN	Fertilization by nitrogen		0,1,2		no
27	FertilizMg	Fertilization by magnesium		0,1		no
28	FertilizP	Fertilization by phosphorus		0,1		no

plot. The composite samples were frozen as soon as possible after being collected, weighed in the frozen state, dried at 110 °C until constant weight, and reweighed. Two series of samples were collected: *Moist1*, collected on 14 Aug 1996, and *Moist2*, collected on 21 Aug 1996. The samples were collected 5 and 12 days after precipitation, respectively. The first series is likely to represent median soil moisture conditions (cf. R. Økland & Eilertsen 1993) while the second is considered to represent conditions drier than median.

(13) *Loss on ignition (LossIgni)* was determined by ashing a soil sample at 550 °C to

constant weight in a muffle furnace and measuring the weight loss.

(14) *Total amount of nitrogen (N)* was measured as % of *LossIgni* by the Kjeldahl method, cf. Hesse (1971): a 1 g sample was mixed with conc. H_2SO_4 , heated for 30 minutes at 440 °C, and distilled by adding NaOH. The emitted gaseous NH_3 was collected in a tube containing boric acid and an indicator, and total amount of nitrogen was measured by titration.

For recording of tree-layer variables, sketches of tree positions relative to the plots and their crown perimeters were made for each 30 × 30 m plot (Appendix 4). The following tree variables were recorded for each meso plot:

(15) *Litter index (LittIndex)*. The amount of litter falling on each meso plot was estimated by an index, derived from a similar index of by R. Økland & Eilertsen (1993). This index takes into consideration the position of the plot relative to all trees covering the plot, and characteristics of these trees. The trees in the study area were of similar age (35 years), and thus, for simplicity, considered to have the same crown density and height of the crown. The amount of litter falling on a sample plot was assumed to be proportional to (i) tree height (h) as measured by Nilsen (1995), (ii) the fraction of the plot situated within the crown perimeter (f), as measured by a planimeter (Tamaya Planix 7), and (iii) the position of the proximal end (i.e. the end closest to the tree) of the sample plot relative to the position of the stem, as given by an index v . $v = 1$ for trees rooted within the meso plot; otherwise $v = d_r/d$. d and d_r were measured on a line drawn from the stem centre through the plot centre; d was the distance along this line from stem centre to the crown perimeter, and d_r was the distance along this line from the proximal end of the sample plot to the crown perimeter. The litter index (l) was calculated as the sum of contributions l_i from all trees covering the sample plot;

$$l_i = f_i \cdot h_i \quad \text{for trees rooted within the sample plot}$$

$$l_i = (d_r/d_i) \cdot f_i \cdot h_i \quad \text{for all other trees.}$$

(16) *Basal area (BasArea)*, a measure of tree-layer density, was determined at the lower left corner of each plot by counting the number of trees at eye height that were wider than the narrow split in a relascope (Fitje & Strand 1973).

(17) *Canopy cover (Canopy)* was measured by a hand-held concave spherical densiometer (Lemmon 1956, MacAlister 1997), directed from the four edges of each plot towards the plot centre. The number of densiometer squares (out of 96) that were not covered by tree foliage was counted, and the mean of these four measurements used as the *Canopy* variable. The variable thus measure canopy openings rather than canopy cover.

(18-19) *Crown area* was measured for each tree in the 30 × 30 m plot on the sketch map by a digital planimeter. The crown area of each tree covering the meso plot and 5 × 5 m plots (the latter with the 1 × 1 m meso plot in the centre), were summed up and used as *CroAre1*, *CroAre5*, respectively.

(20-21) *Tree stumps*. The number of tree stumps in each meso plot was recorded as *TreeSu1*, and the number in the 3 × 3 m plot surrounding the meso plot was recorded as *TreeSu3*.

(22-23) The *number of trees* was counted in the meso plot (*NuTree1*) and 3 × 3 m plots, (*NuTree3*).

(24-25) The *tallest tree* in the 3 × 3 m and 5 × 5 m plots surrounding the meso plot was recorded, as *TallTree3* and *TallTree5*, respectively.

The fertilization treatments were recorded as variables as follows:

(26) (*FertilizN*): Nitrogen (0 = no N added, 1 = 30 kg ha⁻¹ yr⁻¹, 2 = 90 ha⁻¹ yr⁻¹).

(27) (*FertilizMg*): Magnesium (0 = no Mg added, 1 = 1.5 ha⁻¹ yr⁻¹).

(28) (*FertilizP*): Phosphorus (0 = no P added, 1 = 5.3 ha⁻¹ yr⁻¹).

The 28 explanatory variables, with units of measurement and frequency distributions, are summarised in Tab. 1 (data in Appendix 3). The transformations $\ln(1+x)$ and $\ln x$, whatever appropriate, was applied to the more or less lognormally or lograndomly distributed variables. After transformation, all explanatory variables were uniformly or more or less unimodally distributed with rather homogeneous variances. This set of the explanatory variables is referred to as EXV data set.

RECORDING OF SPECIES RICHNESS VARIABLES

For each plot, four species richness, or biotic, variables were recorded: *NuSpec*, the total number of species in each sample plot; *NuVasc*, the number of vascular plant species in each sample plot; *NuBryo*, the number of bryophyte species each sample plot; and *NuLich*, the number of lichen species in each sample plot.

RELATIONSHIPS BETWEEN EXPLANATORY VARIABLES AND BETWEEN SPECIES RICHNESS VARIABLES

Two different methods were used to analyse relationships between explanatory variables: PCA (Principal Component Analysis; Pearson 1901) was applied to the EXV data set using CANOCO, Version 3.12 (ter Braak 1987, 1990). Variables were centred and standardised by division by standard deviation prior to analyses. A conjugate variable was associated with each variable; thus 50 variables were included in the analysis (cf. Ponge & Ferdy 1997). Correlation biplot scaling of PCA axes was used to optimise fit of angles between variable vectors to inter-variable correlations.

Tab. 2. Biotic variables; abbreviation, range of scale, presumed statistical distribution, and transformation.

Abbreviation	Variable	Range	Distribution	Transform.
NuSpec	Number of species	0 - 39	uniform	no
NuVasc	Number of vascular plants	0 - 8	uniform	no
NuBryo	Number of bryophyte	0 - 14	uniform	no
NuLich	Number of lichens	0 - 17	uniform	no

Kendall's τ (Kendall 1938) as implemented into Statgraphics Version 5.0 (Anonymous 1992b) was calculated between all pairs of variables in each of the EXV data set and the set of species richness variables.

ORDINATION OF VEGETATION

Three ordination methods, DCA (Detrended Correspondence Analysis; Hill 1979, Hill & Gauch 1980), PCA and LNMDS (Local Non-metric Multidimensional Scaling; Kruskal 1964a, 1964b, Minchin 1987) were used in parallel to obtain robust representations of the gradient structure of the vegetation data sets (cf. R. Økland 1996), and for comparison of methods.

DCA, as implemented into CANOCO, Version 3.12 (ter Braak 1987, 1990) and a new, debugged version of Hill's original DECORANA program (cf. Oksanen and Minchin 1997), were applied to the ME 144sf and ME 144pc data sets. Corresponding first and second DCA axes obtained by the two versions were strongly correlated ($|r| > 0.97$, $P \ll 0.0001$). This demonstrated that the axes obtained by CANOCO version 3.12 were not influenced by bugs or instability (cf. Tausch et al. 1995, Oksanen & Minchin 1997), and results obtained by this version was therefore used. Standard options were used, including detrending by segments. Ordination axes are referred to as follows: DCA1 – the first axes in the DCA ordinations of the ME 144sf and ME 144pc data sets; DCA1sf – the first axis in the ordination of the ME 144sf data set, etc.

PCA was applied to the ME 144sf and ME 144pc data sets of centred and standardised species abundances, as recommended by R. Økland (1990a). Euclidean distance biplot scaling of axes was used, other options were standard. Axes were linearly rescaled in S.D. units by DCCA (Detrended Canonical Correspondence Analysis) as implemented in CANOCO, Version 3.12, using the PCA-axes as constraining variables, one at a time. In this way, the PCA axes were made comparable to the corresponding DCA and LNMDS axes (cf. R. Økland 1990a, T. Økland 1996).

The third and fourth DCA and PCA axes were not interpreted, but their gradient lengths and eigenvalues were presented for comparison with the first and second axes.

LNMDS was applied to the ME 120sf and ME 120pc data sets by use of the modified KYST program (Kruskal 1964a, 1964b, Minchin 1987) as implemented into the DECODA program package, version 2.0 (Minchin 1986, 1990). Percentage dissimilarity (Bray-Curtis, or Czekanowski measure; Czekanowski 1909), standardised by division with species maxima, was used as between-plot dissimilarity measure, as recommended by Faith et al. (1987) and R. Økland (1990a). Two-dimensional LNMDS solutions were found, using the following parameter settings: 300 initial, random, configurations; maximum iterations = 1000; stress reduction ratio for stopping iteration procedure = 0.9999 (stress is a measure of correspondence between between-plot floristic dissimilarities and the corresponding distances in the ordination diagram). As the lowest stress was still only obtained from one starting configuration, the six solutions with lowest stress were tested for equality by Procrustes analysis (Minchin 1987). The six solutions made up five different groups that were compared axis by axis using Kendall's τ . Correlations were significant at $P < 0.0001$ in all cases. The solution with lowest stress was therefore used for further interpretation. LNMDS axes were linearly rescaled in S.D. units by DCCA (see above), in order to obtain comparable scalings

for all ordination axes regardless of method.

To compare the ordinations, a PCA ordination was applied to centred and standardised ordination scores for the 120 plots subjected to LNMDS, and their conjugate variables. The fit between angles between ordination axis vectors and correlations between axes, was optimised by use of Euclidean distance biplot scaling of axes. Other options were standard. Pair-wise correlations among ordination axes were calculated as Kendall's τ .

As a measure of the influence of an ordination axis by outliers, the core of each ordination axis was calculated as the largest interval containing 90% of the plots (R. Økland 1990b), divided by the length of the axis (in S.D. units). A low core length indicated high influence by outliers.

RELATIONSHIPS BETWEEN VEGETATION AND EXPLANATORY VARIABLES

Kendall's τ was calculated between explanatory variables and the ordination axes (plot scores), and between the species richness variables and the ordination axes.

The constrained variant of correspondence analysis; CCA (Canonical Correspondence Analysis; ter Braak 1986) and the constrained variation of PCA; RDA (Redundancy Analysis; Rao 1964), as implemented into CANOCO Version 3.12, were used to assess the variation explained by each of the fertilization variables (fMg, fN, fP), see R. Økland and Eilertsen (1994). All CCAs and RDAs were run with the fertilization variables as the only constraining variable, one variable at a time. The ratio of the eigenvalue of a constrained axis and the total inertia (the sum of eigenvalues of all extractable CA or PCA axes, cf. Greenacre (1984), Borcard et al. (1992) and R. Økland & Eilertsen (1994)), the "fraction of variation explained", was calculated as a standard measure of variation, comparable between CCA and RDA. The resulting figures were, however, used with caution because this measure of variation is likely to underestimate strongly the amount of compositional variation that is actually explained by a variable (R. Økland in press). The significance of the explained variation was tested by the Monte Carlo simulation test (ter Braak 1990) in CANOCO, using 999 unrestricted permutations. The test statistic was the partial F-statistic, with model and residual sums of squares totalled across species (ter Braak & Wiertz 1994). CCA and RDA were also performed with humus depth variables (HumDMin, HumDMed and HumDMax) as covariables, to test the significance of the variation remaining after the variation due to the humus depth variables had been accounted for.

One-way Analysis of Variance (ANOVA; cf. Sokal & Rohlf 1995), as implemented in Statgraphics version 5.0, was applied separately to plot scores along each ordination axis, using the fertilization variables (*FertilizMg*, *FertilizN*, *FertilizP*) as grouping variables, one at a time.

Kruskal-Wallis One-Way Analysis by Ranks (cf. Sokal & Rohlf 1995), as implemented in Statgraphics version 5.0, was applied to abundances (percentage cover and subplot frequency) of each species, using the fertilization variables as grouping variables, one at a time. Only species that occurred in $\geq 5\%$ of the meso samples were tested.

SPATIAL STRUCTURE

The semivariance was calculated as a means of investigating the spatial structure of the explanatory variables and the ordination axes. Semivariance is a statistic that expresses the variation in a variable of interest as a function of spatial scale (Phillips 1985, Palmer 1990, Rossi et al. 1992). Fractal dimension (or Hausdorff-Besicovitch dimension) was derived from semivariance as a measure of the degree of spatial structuring of a variable (Phillips 1985, Palmer 1988).

Semivariance as a fraction of sample variance (standardized semivariance (γ_s ; Rossi et al. 1992) was calculated for all variables in the EXV data set and each ordination axis, using the program GS+ (Geostatistics for the Environmental Sciences), Version 2.01 (Anonymous 1990, 1994). From a map of the 144 meso plots (Fig. 2), the pairwise Euclidean distances between all meso plots were used to make 16 lag classes: 0-5 m, 5-10 m, 10-15 m, 15-20 m, 20-30 m, 30-40 m, 40-50 m, 50-60 m, 60-70 m, 70-80 m, 80-100 m, 100-120 m, 120-140 m, 140-160 m, 160-180 m, 180-200 m. The semivariance (γ) was calculated for each lag class as:

$$\gamma(f) = 0.5 \cdot N_f^{-1} \cdot [\sum_{j,l: d_{j,l} < d_{f-1} \leq d_f} (x_j - x_l)^2],$$

where N_f is the number of pairs in the lag class f , $d_{j,l}$ is the distance between observations j and l , d_f is the upper limit of lag class f , x_j and x_l are the values for the regionalized variable for locations j and l respectively, and 0.5 is a scaling factor that adjusts the estimated semivariance to the same scale as the sample variance.

Fractal dimensions (D) were calculated for the same variables and the same lag classes as above:

$$D = 3 - [\ln \gamma(2d) - \ln \gamma(d)] / (\ln 2d - \ln d),$$

where $\gamma(d)$ is the semivariance of the lag class with upper limit d . The fractal dimension normally lies between two (maximum spatial structure) and three (no spatial structure). Fractal dimensions > 3 may indicate periodicity in a variable.

NOMENCLATURE

The nomenclature of vascular plants, mosses and lichens follows Lid & Lid (1994), Frisvoll et al. (1995) and Krog et al. (1994), respectively. *Cladonia chlorophaea* agg. may include *Cladonia chlorophaea* (Flörke ex Sommerf.) Spreng., *Cladonia merochlorophaea* Asah., *Cladonia cryptochlorophaea* Asah., *Cladonia grayi* Merr. ex Sandst. and *Cladonia pyxidata* (L.) Hoffm.

RESULTS

RELATIONSHIPS BETWEEN EXPLANATORY VARIABLES

The first PCA axis accounted for 15.2 % of the total inertia in the EXV data set and the second principal component accounted for 12.5 % of the variation. The variables did not segregate into distinct groups along the axes, but made up a more or less continuous cloud of points (Fig. 3). Fertilization with magnesium and phosphorus and the soil moisture variables had short vectors, indicating weak relationships with the axes. The topography, humus depth and tree stump variables were closely related to loss on ignition and total amount of nitrogen.

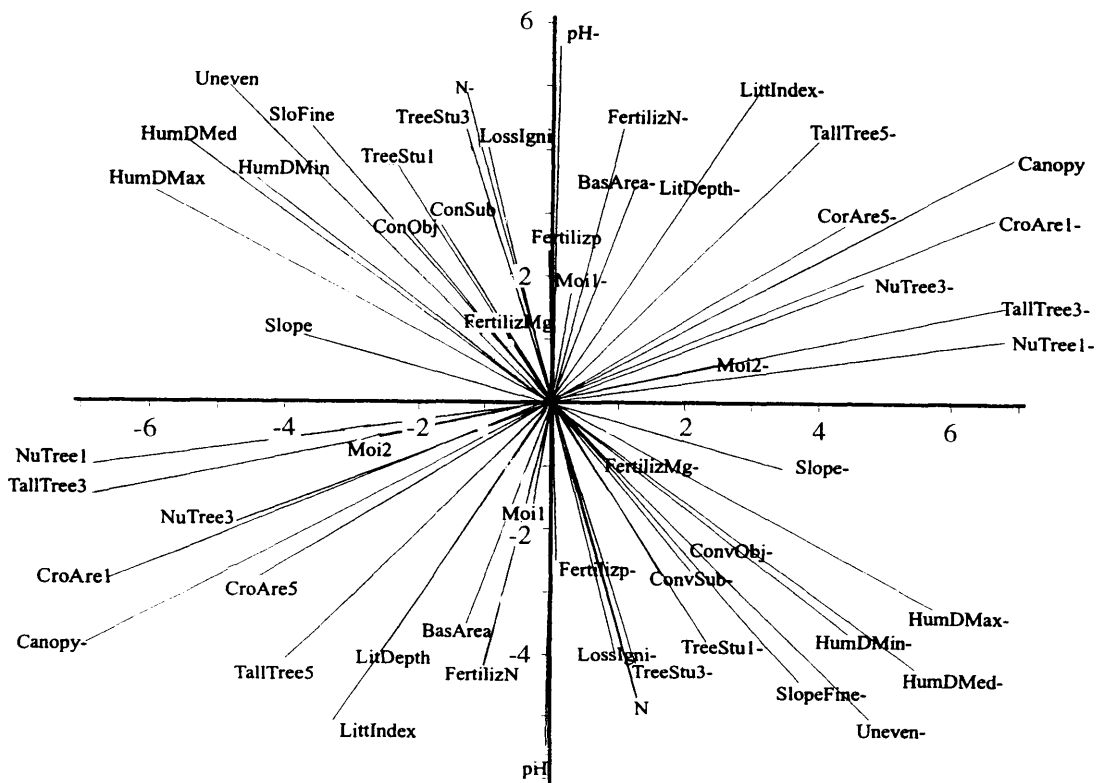


Fig. 3. PCA ordination of 28 explanatory variables (and their conjugate variables) in the EXV data set, axes 1 (horizontal) and 2 (vertical). Names of explanatory variables abbreviated in accordance with Tab. 1.

Tab. 4. Standardized semivariance (γ_s) of the explanatory variables. $\gamma_s < 0.8$ in bold face.

Variable	Sample variance	Lag class (No., upper bound (m), and No. of observation pairs)															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
		5 239	10 249	15 259	20 239	30 431	40 381	50 545	60 533	70 565	80 569	100 873	120 761	140 929	160 918	180 673	200 502
Uneven	1.040	0.848	0.852	0.778	0.848	0.863	0.965	1.093	1.345	1.230	0.965	0.957	1.137	1.121	0.853	0.709	1.037
ConvSub	3.534	1.056	0.936	1.032	1.080	1.138	1.063	1.113	1.264	1.095	0.931	0.920	1.163	0.996	0.671	0.820	1.028
ConvObj	0.774	0.940	0.908	1.129	1.083	1.095	1.085	1.035	1.273	1.080	0.928	1.013	1.134	1.010	0.796	0.952	1.016
Slope	1.082	1.026	0.917	0.930	1.031	1.007	1.006	0.985	1.137	1.063	0.970	0.953	1.046	1.057	0.946	0.857	1.007
SlopeFine	220.820	0.928	0.965	0.997	1.065	1.067	0.927	1.134	1.028	1.022	0.880	0.927	1.017	0.873	1.021	1.111	1.007
LitDepth	0.144	0.637	0.710	0.829	1.039	1.115	1.267	1.256	1.365	1.306	0.914	0.827	1.053	1.441	1.232	1.073	0.904
HumDMed	2.993	0.912	0.974	0.948	1.026	0.944	0.958	0.784	0.935	0.918	0.887	1.036	1.046	1.005	1.069	0.976	0.942
HumDMin	3.098	0.948	1.088	0.961	1.107	1.033	0.841	0.889	1.083	1.010	0.941	0.981	1.014	1.169	1.113	0.943	0.886
HumDMax	7.508	1.026	0.868	1.027	0.964	1.006	1.008	0.879	0.959	0.897	0.952	0.966	1.049	1.032	1.130	0.918	0.966
pH	0.048	0.520	0.622	0.663	0.734	0.847	1.203	1.268	1.345	1.101	0.939	0.823	1.029	1.088	1.028	1.115	1.136
Moist1	39.564	0.881	0.868	0.827	0.982	1.041	1.106	1.167	1.137	1.032	0.955	0.835	1.176	1.097	1.124	1.201	0.808
Moist2	41.732	0.887	0.940	0.881	1.029	1.051	1.058	0.997	0.955	0.957	1.103	0.936	1.033	1.012	1.079	1.175	0.869
LossIgni	0.023	0.922	1.124	0.859	1.056	1.044	0.820	0.835	0.755	0.843	0.794	0.937	0.813	0.947	1.051	1.046	1.188
N	0.053	0.892	1.112	0.928	0.858	0.940	1.152	1.160	1.089	0.887	0.874	1.043	1.135	1.024	1.154	0.866	1.054
LittIndex	0.846	0.849	1.161	0.996	0.979	0.991	1.158	1.083	0.868	1.115	0.982	0.943	1.070	1.053	1.129	1.097	0.861
BasArea	0.063	0.507	0.652	0.583	0.601	0.654	1.157	1.300	1.236	1.167	1.054	1.249	1.249	0.977	0.890	0.860	1.095
Canopy	0.757	0.789	0.926	0.930	1.023	1.022	1.194	0.958	0.991	0.985	0.973	1.001	0.899	0.863	0.890	1.095	1.171
CroAre5	13.469	0.403	0.808	0.789	0.730	0.795	1.057	1.186	1.180	1.188	1.043	1.066	1.175	1.003	0.911	0.852	0.898
CroAre1	0.058	0.923	0.948	0.976	1.088	1.086	1.143	1.070	1.080	1.188	0.988	0.997	1.057	0.972	0.970	1.053	1.043
TreeStu1	0.176	0.913	1.047	0.985	1.091	1.098	1.153	1.168	1.096	0.948	0.917	0.925	0.872	1.007	1.000	0.872	0.915
TreeStu3	0.314	0.952	0.955	1.033	1.044	0.959	0.966	1.007	0.973	0.961	1.019	0.914	0.950	1.034	1.057	1.080	0.936
NuTree1	0.314	1.001	0.952	1.150	1.021	1.030	1.118	1.042	1.115	1.059	1.123	1.054	1.017	0.967	0.828	0.920	0.981
NuTree3	0.221	0.935	0.893	1.014	0.868	0.961	0.983	0.991	1.127	1.149	1.281	1.004	1.000	1.101	0.954	0.945	0.893
TallTree3	26.523	0.964	1.080	1.112	0.886	0.899	1.168	1.048	1.081	1.091	1.162	1.077	1.091	1.056	0.983	0.842	1.007
TallTree5	4.410	0.837	1.075	1.098	0.823	0.836	0.587	0.665	1.061	1.417	1.648	1.062	1.059	0.972	1.155	0.722	1.326

Nitrogen-fertilization, pH, litter depth and the litter index were related to each other, as were also the tree variables.

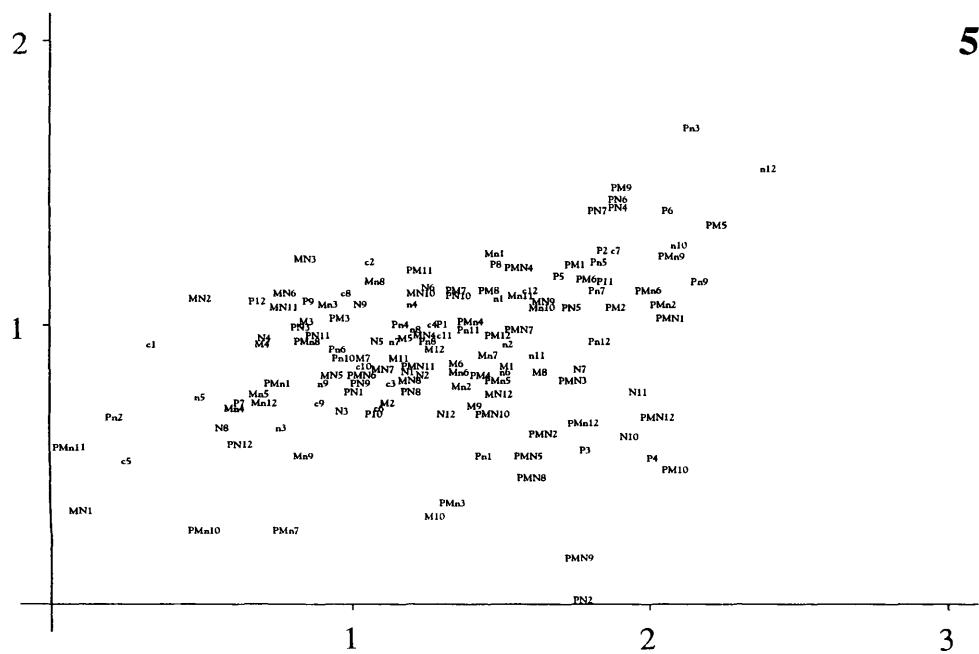
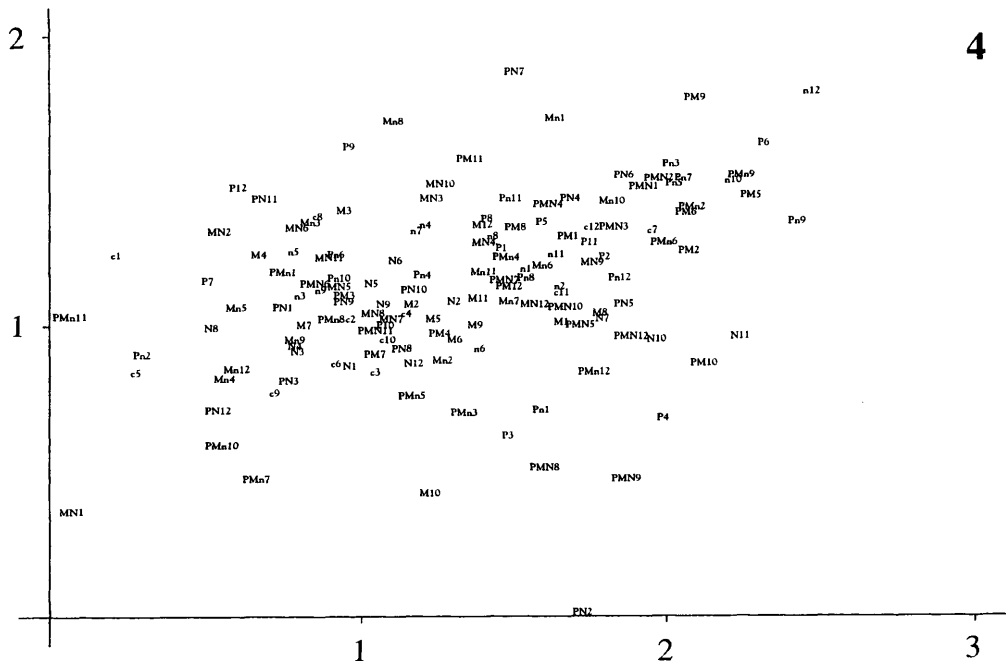
The third and fourth PCA axes accounted for 9.3 % and 8.1 % of the variation, respectively, but were not considered further because of low interpretability.

According to the correlation analysis, explanatory variables segregated into two groups of internally strongly correlated variables (Tab. 3). The humus-depth variables, loss on ignition and nitrogen made up the first group. Some of the tree variables (canopy cover, crown area in the 1 × 1 m plot, number of trees in the 3 × 3 m plot, and tallest tree in the 5 × 5 m plot), made up the second group. The other variables were correlated with variables in one or both groups and/or with other variables, without fitting into a two-group pattern or making up additional, distinct, groups.

Standardized semivariance (γ_s) and the fractal dimensions (D) for some soil variables (see Tabs 4-5) indicated spatial structuring of several soil variables at scales larger than 1 m:

Tab. 5. Fractal dimension (D) of the explanatory variables, calculated for lag intervals [d,2d] (see text). D < 2.8 in bold.

Variable	Lag class (No., upper bound d)										
	1 5	2 10	3 15	4 20	5 30	6 40	7 50	8 60	9 70	10 80	11 100
Uneven	2.995	3.006	2.849	2.814	2.360	3.000	3.190	3.242	3.134	3.177	2.884
ConvSub	3.173	2.794	2.858	3.023	2.848	3.190	3.274	3.121	3.137	3.473	2.840
ConvObj	3.051	2.745	3.044	2.998	2.783	3.225	3.031	3.167	3.097	3.221	2.996
Slope	3.162	2.831	2.885	3.036	2.825	3.053	3.047	3.121	3.008	3.035	2.922
SlopeFine	2.984	2.968	2.981	3.036	3.009	3.012	3.045	3.002	3.033	2.971	2.984
LitDepth	2.844	2.451	2.571	2.714	2.708	2.815	3.678	3.982	3.400	3.186	2.872
HumDMed	2.905	2.925	3.006	3.099	3.014	3.112	2.598	2.838	2.869	2.730	3.138
HumDMin	2.801	2.976	2.896	3.397	2.931	2.838	2.857	3.096	2.789	2.758	3.147
HumDMax	3.241	2.848	3.030	2.936	3.068	3.083	2.865	2.871	2.797	2.752	2.999
pH	2.741	2.761	2.647	2.288	2.333	3.358	3.625	3.386	3.017	2.869	2.535
Moist1	3.022	2.822	2.669	2.829	2.873	3.211	3.482	2.951	2.912	2.765	3.048
Moist2	2.916	2.869	2.745	2.960	3.139	2.939	3.091	2.886	2.920	3.032	3.108
LossIgni	2.715	3.089	2.720	3.366	3.466	3.046	2.833	2.894	2.831	2.596	2.658
N	2.682	3.373	2.981	2.575	2.787	3.397	3.154	2.941	2.791	2.600	2.985
LittIndex	2.548	3.246	3.006	2.758	3.192	3.238	3.200	2.698	3.082	2.799	3.130
BasArea	2.638	3.116	2.835	2.056	2.080	3.134	3.058	2.985	3.257	3.245	3.190
Canopy	2.769	2.856	2.864	2.777	3.045	3.295	2.937	3.140	3.191	3.128	2.774
CroAre5	2.997	3.147	2.989	2.466	2.431	3.019	3.153	3.006	3.244	3.196	3.248
CroAre1	2.962	2.801	2.845	2.928	3.009	3.210	3.102	3.030	3.289	3.026	2.935
TreeStu1	2.802	2.941	2.843	2.920	2.880	3.331	3.335	3.330	2.913	2.874	3.017
TreeStu3	2.994	2.872	3.108	3.113	2.979	2.922	3.139	3.034	2.894	2.948	2.966
NuTree1	3.071	2.899	3.160	2.870	2.885	2.993	2.984	3.132	3.131	3.440	3.104
NuTree3	3.066	3.040	3.077	2.821	2.770	2.618	2.918	3.172	3.062	3.426	3.169
TallTree3	2.835	3.286	3.306	2.600	2.734	3.008	2.961	2.987	3.048	3.241	3.096
TallTree5	2.638	3.385	3.392	3.488	2.656	2.511	2.326	3.003	3.543	3.513	2.680



Figs 4-5. DCA ordinations, axes 1 and 2. Scaling of axes in S.D. units. Meso plot names (see text) are plotted onto the meso plot positions. Fig. 4. The ME 144pc data set. Fig. 5. The ME 144sf data set.

loss on ignition was spatially structured up to 10 m, litter depth was spatially structured up to 10-40 m and pH was spatially structured up to 20-40 m. Some of the tree variables were also spatially structured: canopy cover and the tallest tree in the 5 × 5 m plot up to 10 m, basal area and the crown area in the 5 × 5 m plot up to 40 m.

Some variables (total amount of nitrogen, the litter index, canopy cover, and tallest tree in the 5 × 5 m plot) showed increasing semivariance and $D < 2.8$ at all scales (see Tabs 4-5).

Tab. 6. Characteristics of vegetational ordination axes. E/TI - eigenvalue as % of total inertia ("fraction of variance explained by axis"). Gradient lengths of PCA and LNMDs axes in S.D. units comparable to those of DCA were estimated by use of DCCA (see text). Relative core length is the ratio between the length (in S.D. units) of the largest interval containing 90% of the plots divided by the gradient length.

Ordination method	Number of plots	Characteristics of axes				
		Axis No.	Gradient length (S.D. units)	Eigenvalue	E/TI (%)	Relative core length (%)
DCApC	144	1	2.439	0.248	17.4	0.65
		2	1.856	0.158	11.0	
		3	1.754	0.085	5.9	
		4	1.503	0.068	4.8	
DCAsf	144	1	2.361	0.230	16.7	0.62
		2	1.678	0.125	9.1	
		3	1.476	0.083	6.1	
		4	1.801	0.065	4.7	
PCApC	144	1	2.129	0.134	13.4	0.56
		2	1.767	0.064	6.5	
		3	2.038	0.061	6.1	
		4	1.941	0.057	5.7	
PCAsf	144	1	1.876	0.137	13.7	0.42
		2	1.992	0.071	7.1	
		3	1.632	0.062	6.2	
		4	1.531	0.055	5.5	
LNMDSpC	120	1	2.090			0.71
		2	1.007			
LNMDsSf	120	1	2.610			0.61
		2	1.108			

ORDINATION OF VEGETATION

DCA

The gradient lengths of the first axes of the DCApc and DCAsf ordinations were 2.44 and 2.36 S.D. units, respectively (Tab. 6). The first axes differed from the second by factors of 1.3 and 1.4 with respect to gradient length, and 1.6 and 1.8 with respect to eigenvalues. The third axes were slightly shorter (in S.D. units) than the second axes, and DCA4sf was shorter than DCA3sf, while DCA4pc was longer than DCA2pc.

Plot scores made up a continuous cloud of points in a two-dimensional representation of DCA axes 1 and 2, although with somewhat lower density towards the periphery (Figs 4-5),

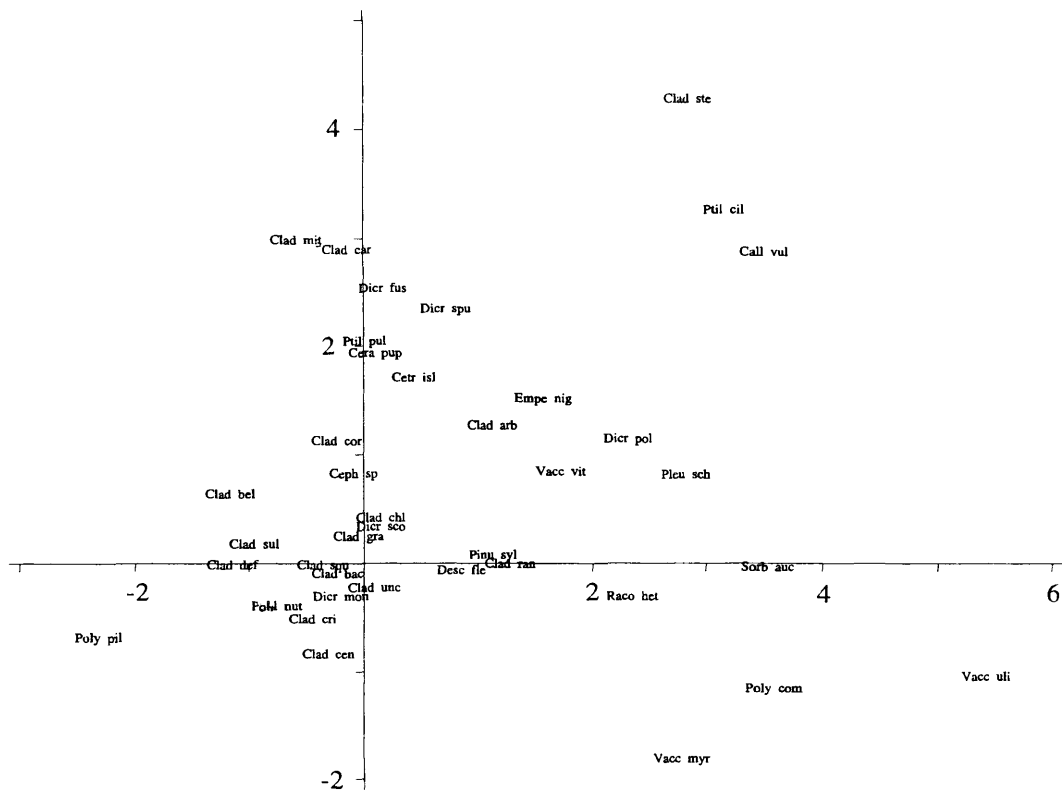
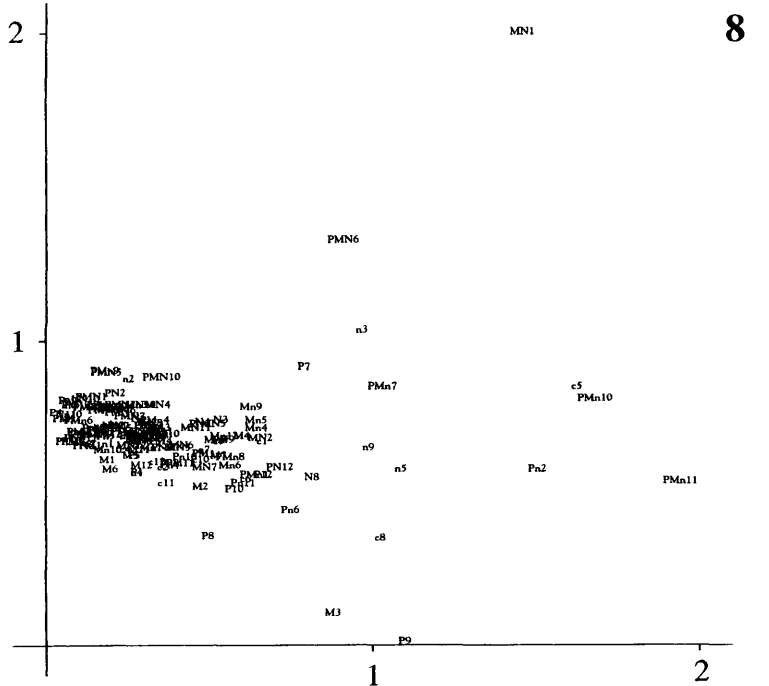
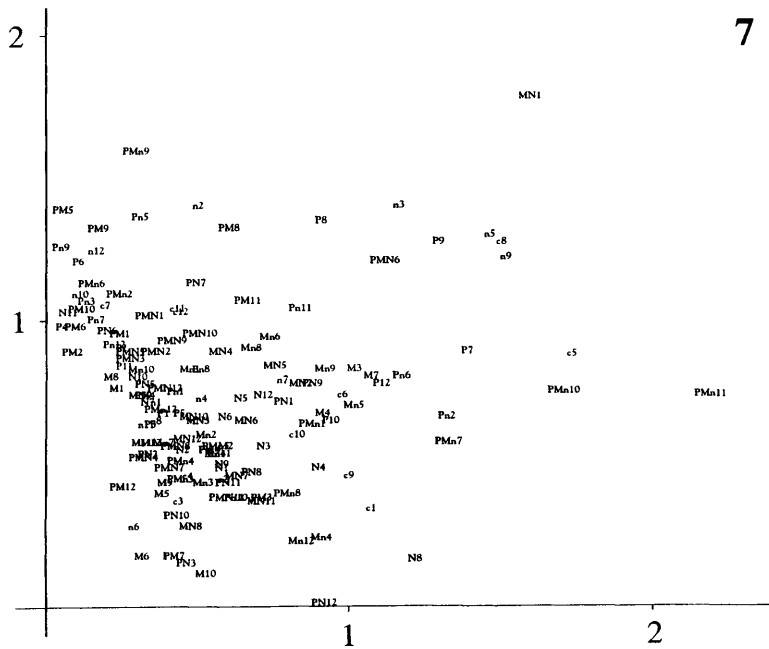
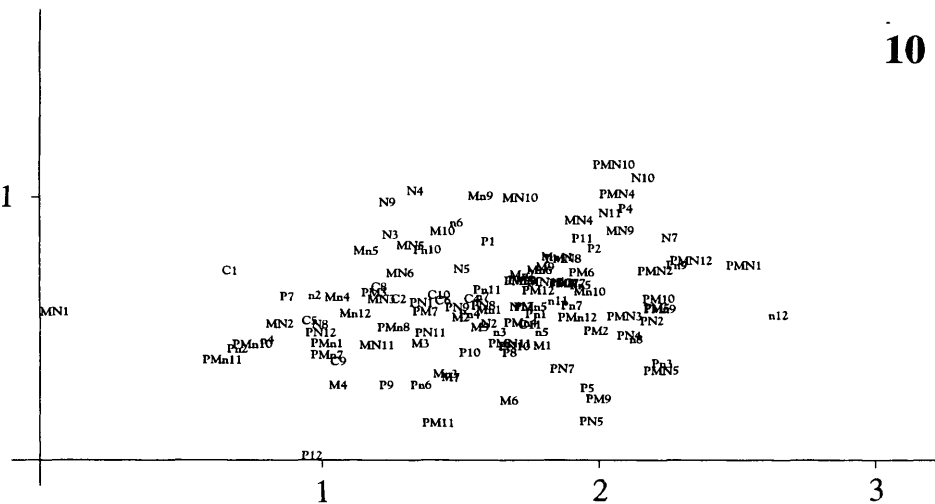
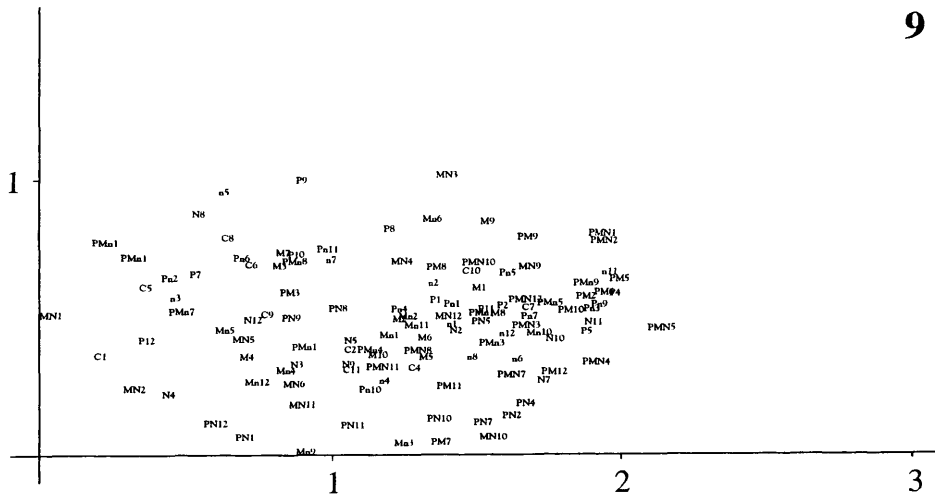


Fig. 6. DCA species ordination, axes 1 and 2. Scaling of axes in S.D. units. Abbreviated species names (see Appendix 1 for explanation) are plotted onto positions of species optima.



Figs 7-8. PCA ordinations, axes 1 and 2. Axes (linearly) rescaled in S.D. units (see text). Meso plot names (see text) are plotted onto the meso plot positions. Fig. 7. The ME 144pc data set. Fig. 8. The ME 144sf data set.



Figs 9-10. LNMSD ordinations, axes 1 and 2. Axes (linearly) rescaled in S.D. units. Meso plot names (see text) are plotted onto the meso plot positions. Fig. 9. The ME 144pc data set. Fig. 10. The ME 144sf data set.

which indicated that the mesoplots made up a continuum along a complex-gradient rather than distinct groups.

Species optima made up a gradient from lichens to ericaceous species along DCA1 (Fig. 6).

Tab. 7. Kendall's nonparametric correlation coefficients (τ) between plot scores along axes 1 and 2 of the six vegetation ordinations (lower triangle), with significance probabilities (upper triangle). Correlations significant at level $P < 0.001$ in bold face, ns - $P > 0.1$.

Ordination axes	DCA 1pc	DCA 1sf	PCA 1pc	PCA 1sf	MDS 1pc	MDS 1sf	DCA 2pc	DCA 2sf	PCA 2pc	PCA 2sf	MDS 2pc	MDS 2sf
DCA1pc	*	.0000	ns	ns	.0000	.0000	.0003	.0001	.0000	.0034	.0757	.0106
DCA1sf	.8453	*	ns	ns	.0000	.0000	.0049	.0001	.0000	.0008	ns	.0111
PCA1pc	-.0344	.0035	*	.0000	ns	ns	ns	ns	ns	ns	ns	ns
PCA1sf	-.0054	.0448	.8585	*	ns	ns	.0976	ns	ns	ns	ns	ns
LNMSD1pc	.7265	.7267	-.0141	.0257	*	.0000	.0038	.0003	.0122	.0004	ns	.0076
LNMSD1sf	.7388	.7631	-.0084	.0234	.6738	*	.0047	.0146	.0000	.0000	ns	.0070
DCA2pc	.2249	.1747	-.0846	-.1034	.1793	.1753	*	.0000	.0000	.0592	ns	ns
DCA2sf	.2430	.2359	-.0962	-.0970	.2223	.1515	.6327	*	.0155	.0107	ns	ns
PCA2pc	.3204	.2649	.0609	.0387	.1557	.2605	.3173	.1512	*	.0551	.0000	ns
PCA2sf	.1830	.2089	.0511	.0535	.2194	.2527	-.1180	-.1598	.1202	*	.0333	.0001
LNMSD2pc	.1099	.0647	.0933	.0815	.0261	.0723	.0715	-.0558	.3366	-.1326	*	ns
LNMSD2sf	.1583	.1570	.0017	.0364	.1647	.1664	-.0692	-.0501	-.0123	.2496	-.0185	*

PCA

The gradient lengths of the first rescaled PCApc and PCAsf ordination axes were 2.13 and 1.89 S.D. units, respectively (Tab. 6). Plot scores made up a continuous cloud of points along the two PCA axes, with lower density towards high plot scores along both axes (Figs 7-8).

LNMSD

The gradient lengths of the first rescaled axes of the LNMSDpc and LNMSDsf ordinations were 2.09 and 2.61 S.D. units, respectively (Tab. 6). Gradient lengths of the first axes differed from the second by factors of 2.07 for LNMSDpc and 2.35 for LNMSDsf. Plot scores made up a continuous cloud of points along two LNMSD axes, with somewhat lower density towards the periphery (Figs 9-10).

Tab. 8. Kendall's nonparametric nonparametric correlation (τ) coefficients between biotic variables (lower triangle), with significance probabilities (upper triangle). Correlations significant at level $P < 0.0001$ in bold face. ns - $P > 0.1$. Abbreviations for names of biotic variables in accordance with Tab. 2.

Variable	NuSpec	NuVasc	NyBryo	NuLich
NuSpec	*	0.1545	0.0000	0.0000
NuVasc	0.1033	*	ns	0.1000
NyBryo	0.5878	0.0097	*	0.0002
NuLich	0.6936	-0.1210	0.2590	*

Tab. 9. Kendall's nonparametric correlation coefficients (τ) between sample plot scores along ordination axes and explanatory variables (lower triangle), with significance probabilities (upper triangle). Correlations significant at level $P < 0.0001$ in bold face. ns – $P > 0.1$. Abbreviations for names of explanatory variables in accordance with Tab. 1.

Variable	DCA1pc		DCA1sf		PCA1pc		PCA1sf		LNMDS1pc		LNMDS1sf	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
Uneven	.1632	.0044	.1677	.0034	.1024	.0745	.1040	.0706	.1111	.0772	.1329	.0344
ConvSub	-.0102	ns	.0154	ns	-.0478	ns	-.0302	ns	-.0335	ns	-.0943	ns
ConvObj	.0482	ns	.0524	ns	-.0343	ns	-.0420	ns	.0182	ns	-.0003	ns
Slope	.0016	ns	.0044	ns	.0161	ns	-.0030	ns	-.0110	ns	-.0017	ns
SlopeFine	.0401	ns	.0401	ns	-.0246	ns	-.0096	ns	.0003	ns	.0524	ns
LitDepth	.0596	ns	.0820	ns	.0926	ns	.1257	ns	.0930	ns	.1390	.0335
HumDMed	.3835	.0000	.3631	.0000	.3779	.0000	.3570	.0000	.4014	.0000	.3790	.0000
HumDMin	.3738	.0000	.2954	.0000	.3590	.0000	.2946	.0000	.3551	.0000	.3451	.0000
HumDMax	.3001	.0000	.2954	.0000	.3071	.0000	.0327	ns	.3043	.0000	.2560	.0001
pH	-.1505	.0118	-.1333	.0257	-.1430	.0169	-.1091	.0690	-.0995	ns	-.1271	.0519
Moist1	-.0968	.0860	-.0658	ns	-.0456	ns	-.0184	ns	-.0157	ns	.0115	ns
Moist2	-.0542	ns	-.1326	ns	-.0176	ns	-.0100	ns	.0308	ns	.0115	ns
LossIgni	.2392	.0000	.2205	.0001	.2018	.0003	.1855	.0010	.1398	.0236	.1908	.0020
N	-.2993	.0000	-.2939	.0000	-.2574	.0000	-.2389	.0000	-.2381	.0001	-.2894	.0000
LittIndex	.0243	ns	.0204	ns	.0299	ns	.0394	ns	.0553	ns	.0682	ns
BasArea	-.0427	ns	-.0485	ns	.0221	ns	.1974	.0006	-.0442	ns	-.0600	ns
Canopy	-.1216	.0327	-.1426	.0123	-.1973	.0005	.0891	ns	-.1676	.0072	-.1390	.0258
CroAre5	.0700	ns	.1015	.0719	.0639	ns	.0891	ns	.1112	.0720	.1510	.0146
CroAre1	.1443	.0115	.1568	.0060	.2275	.0001	.2129	.0002	.1843	.0032	.1259	.0440
TreeStu1	-.0366	ns	-.0518	ns	-.1310	.0567	-.1509	.0286	-.1235	ns	-.1111	ns
TreeStu3	.0258	ns	.0182	ns	-.0630	ns	-.0419	ns	-.0234	ns	-.0111	ns
NuTree1	.1729	.0050	.1831	.0029	.2163	.0005	.2017	.0011	.2056	.0024	.1553	.0218
NuTree3	.0880	ns	.0914	ns	.1164	.0498	-.1179	.0474	.0970	ns	.0619	ns
TallTree3	.1177	.0414	.1502	.0092	.1858	.0013	.1918	.0009	.1663	.0085	.1161	.0663
TallTree5	.0283	ns	.0666	ns	.0422	ns	.0834	ns	.0854	ns	.0496	ns
FertilizN	-.0429	ns	-.0309	ns	-.0311	ns	.0179	ns	.0121	ns	.0888	ns
FertilizMg	.0169	ns	-.0074	ns	.0574	ns	.0328	ns	.0783	ns	.0323	ns
FertilizP	.2091	.0023	.2479	.0003	.1741	.0114	.1652	.0166	.1985	.0083	.1901	.0114

COMPARISON OF ORDINATIONS

The PCA ordination of plot positions along 12 ordination axes revealed high similarity between axes. The first principal component accounted for 60.4 %, and the first two components accounted for 74.2 % of the variation. Axes obtained by use of percentage cover and by use of frequency in subplots (sf) were closely similar for DCA1, DCA2, PCA1, PCA2 and LNMDS1 (Fig. 11), which indicated that both abundance measures appropriately expressed quantitative variation in the data. Furthermore, correspondence between DCA1 and LNMDS1 was demonstrated, while all other ordination axes differed considerably from these two axes. The third and fourth principal component accounted for 12.2 % of the variation, but

Variable	DCA2pc		DCA2sf		PCA2pc		PCA2sf		LNMDS2pc		LNMDS2sf	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
Uneven	-.0949	.0986	-.1624	.0047	.0956	.0964	.1618	.0051	.2202	.0005	.1344	.0941
ConvSub	-.0266	ns	-.0583	ns	-.0127	ns	.0315	ns	.0584	ns	.5476	.0375
ConvObj	-.0185	ns	-.0540	ns	.1048	ns	.0482	ns	.1501	.0318	.0160	ns
Slope	-.0480	ns	-.1051	.0845	-.0306	ns	.0410	ns	.0178	ns	-.0130	ns
SlopeFine	-.1376	.0191	-.1933	.0010	.1429	.0151	.1359	.0213	.1729	.0071	.0388	ns
LitDepth	-.0137	ns	.0457	ns	-.0612	ns	.1518	.0115	-.1896	.0037	.1033	ns
HumDMed	.0735	ns	.529	ns	.1325	.0238	.1122	.0566	.1052	.0999	.0443	ns
HumDMin	.0795	ns	.0608	ns	.1651	.0065	.1582	.0094	.1622	.0143	.0950	ns
HumDMax	.0123	ns	.0281	ns	.0797	ns	.0675	ns	.1712	.0083	.0077	ns
pH	-.1052	.0789	-.0907	ns	-.1524	.0110	.1308	.0297	-.1859	.0045	.1976	.0025
Moi1	-.1240	.0281	-.1036	ns	-.1277	.0239	.0353	ns	-.0583	ns	-.0034	ns
Moi2	-.1058	.0611	-.0460	ns	-.1198	.0342	.0268	ns	-.1454	.0185	.0555	ns
LossIgni	.0931	.0993	.0599	ns	.1510	.0076	.0827	ns	.0300	ns	-.0148	ns
N	-.0133	ns	-.0036	ns	-.1852	.0011	-.1120	.0484	-.0983	ns	-.0832	ns
LittIndex	-.0324	ns	.0306	ns	-.0788	ns	.0345	ns	-.0839	ns	.0233	ns
BasArea	-.0047	ns	.0635	ns	-.1106	.0564	-.0795	ns	-.0716	ns	.0580	ns
Canopy	.0127	ns	-.0913	ns	.1472	.0100	-.0329	ns	.1749	.0050	-.0156	ns
CroAre5	.0126	ns	.0145	ns	-.0294	ns	.0830	ns	-.0624	ns	-.0041	ns
CroAre1	-.0304	ns	.0233	ns	-.1073	.0608	.0819	ns	-.1329	.0334	.0319	ns
TreeStu1	-.0587	ns	-.1073	ns	.1367	.0472	.0140	ns	.1163	ns	-.0345	ns
TreeStu3	-.0864	ns	-.1217	.0516	.1631	.0091	-.0226	ns	.1074	ns	-.0159	ns
NuTree1	.0180	ns	.0723	ns	-.0857	ns	.0178	ns	-.0669	ns	.1299	.0548
NuTree3	.0580	ns	.1196	.0442	-.0264	ns	-.0011	ns	.0068	ns	.0776	ns
TallTree3	-.0789	ns	.0312	ns	-.1336	.0210	.0495	ns	-.1329	.0357	-.0025	ns
TallTree5	-.1164	.0415	.0122	ns	-.1579	.0057	-.0437	ns	-.1364	.0290	.0576	ns
FertilizN	-.0568	ns	-.1179	ns	-.0889	ns	.2983	.0000	-.2248	.0015	.1582	.0257
FertilizMg	-.0272	ns	-.0831	ns	-.0775	ns	.1129	ns	.0107	ns	.0323	ns
FertilizP	.0808	ns	.0545	ns	.1411	.0406	.0945	ns	.0943	ns	-.1755	.0195

did not contribute new insights into relationships among ordination axes.

The first axes obtained by a given ordination method, differing only with respect to abundance measure, were strongly correlated (Tab. 7). The correlations between DCA1 and LNMDS1 were strong, while PCA1 differed from axes obtained by the other methods. The corresponding second axes obtained by pc and sf were strongly correlated for DCA only. DCA2pc was correlated at the $P < 0.0001$ level with PCA2sf and PCA2pc, while PCA2pc was correlated with LNMDS2pc as well. Other correlations were less strong.

DCA and LNMDS had longer core lengths than PCA (the longest was observed for LNMDSpc; Tab. 6), suggesting that PCA was more strongly influenced by outliers and indicating that PCA provided a representation of the gradient structure in the data set that was inferior to DCA and LNMDS.

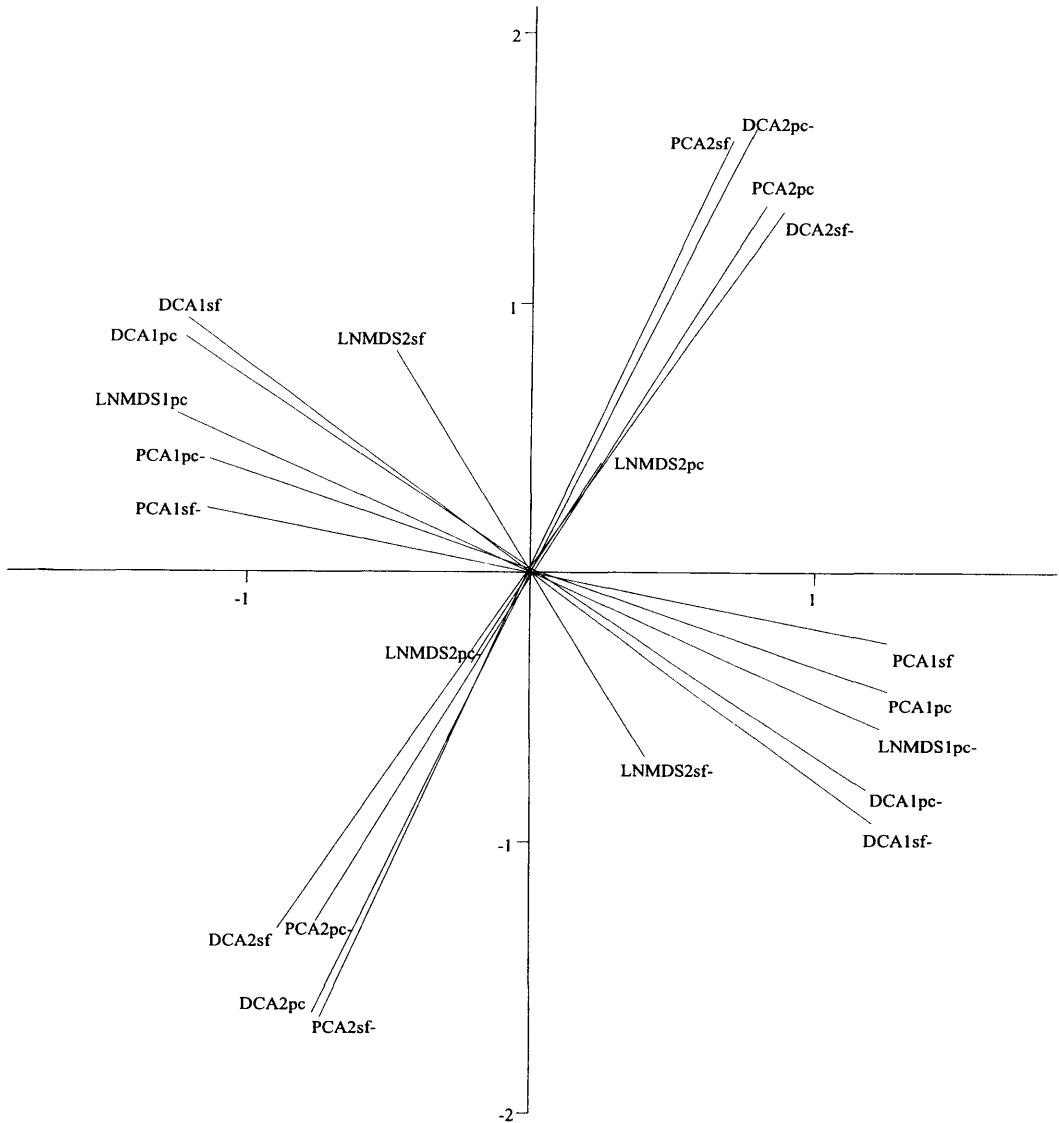


Fig. 11. PCA ordination of plot positions along axes 1 and 2 in six ordinations, and their conjugate variables; axes 1 and 2.

RELATIONSHIPS BETWEEN SPECIES RICHNESS VARIABLES

The total number of species was most strongly influenced by the number of bryophytes and the number of lichens (Tab. 8). The number of lichens and the number of bryophytes were not

Tab. 10. Standardized semivariance (γ_s) of the DCA and PCA ordination scores. $\gamma_s < 0.8$ in bold face.

Variable	Sample variance	Lag class (No., upper bound (m), and No. of observation pairs)															
		1 5 239	2 10 249	3 15 259	4 20 239	5 30 431	6 40 381	7 50 545	8 60 533	9 70 565	10 80 569	11 100 873	12 120 761	13 140 929	14 160 918	15 180 673	16 200 502
DCA1pc	2735.29	0.897	0.984	1.031	0.980	1.074	0.905	0.893	1.033	0.997	1.019	1.075	1.026	1.099	0.950	0.963	0.895
DCA2pc	870.25	0.870	1.095	0.874	0.905	0.903	0.803	0.963	1.094	1.202	1.197	1.082	0.968	1.088	0.977	0.927	0.941
DCA1sf	2313.61	0.881	0.961	1.065	0.969	1.079	0.880	0.904	1.048	1.073	1.057	1.064	1.053	1.050	0.943	0.922	0.890
DCA2sf	767.29	0.800	1.050	0.975	0.858	0.928	0.845	0.938	1.093	1.111	1.181	1.055	1.032	1.134	0.891	0.829	1.078
PCA1pc	1346.89	0.965	0.989	1.193	1.022	1.137	1.157	1.148	1.160	1.035	0.998	0.994	1.031	1.133	0.876	0.878	0.865
PCA2pc	870.25	0.870	1.095	0.874	0.905	0.903	0.803	0.963	1.094	1.202	1.197	1.082	0.968	1.088	0.977	0.927	0.941
PCA1sf	1361.61	0.901	0.978	1.347	1.110	1.227	1.160	1.101	1.130	1.018	1.006	0.864	1.022	1.146	0.809	0.891	0.848
PCA2sf	707.56	0.771	0.791	1.069	0.708	0.783	1.477	1.592	0.925	1.115	0.991	0.891	1.115	0.914	0.689	1.357	0.737

Tab. 12. Kendall's nonparametric correlation coefficients (τ) between sample plot scores along ordination axes and biotic variables (lower triangle), with significance probabilities (upper triangle). Correlations significant at level $P < 0.0001$ in bold face. ns - $P > 0.1$. Abbreviations for names of biotic variables in accordance with Tab. 1.

Variable	DCA1pc		DCA1sf		PCA1pc		PCA1sf		LNMDS1pc		LNMDS1sf	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
NuSpes	-.3384	.0000	-.3443	.0000	.0986	ns	.0674	ns	-.5076	.0000	-.4000	.0000
NuVasc	.2224	.0015	.2019	.0039	.0178	ns	.0269	ns	.2234	.0014	.2745	.0001
NuBryo	-.1780	.0073	-.1704	.0102	.0912	ns	.0671	ns	-.3079	.0000	-.2245	.0007
NuLich	-.4549	.0000	-.4704	.0000	.0749	ns	.0322	ns	-.6161	.0000	-.5388	.0000

correlated with each other, nor with the number of vascular plants (Tab. 8).

ENVIRONMENTAL INTERPRETATION OF ORDINATIONS

The humus depth variables and loss on ignition increased along the first axes (significantly at the $P < 0.0001$ level), and the amount of nitrogen decreased along the same axes (Tab. 9). Unevenness, the number of trees in the meso plot and fertilization with phosphorus increased along DCA1 at $P < 0.005$. At the same level, crown area and number of trees in the sample

Tab. 11. Fractal dimension (D) of the DCA and PCA ordination scores, calculated for lag intervals [d,2d] (see text). $D < 2.8$ in bold.

Variable	Lag class (No., upper bound d)										
	1 5	2 10	3 15	4 20	5 30	6 40	7 50	8 60	9 70	10 80	11 100
DCA1pc	2.866	3.006	2.940	3.115	3.057	2.829	2.734	3.009	2.859	3.101	3.263
DCA2pc	2.668	3.276	2.953	3.172	2.753	2.425	2.832	3.177	3.144	3.292	3.201
DCA1sf	2.875	2.988	2.981	3.140	3.042	2.736	2.765	2.994	3.030	3.164	3.258
DCA2sf	2.608	3.291	3.071	3.023	2.764	2.516	2.829	3.082	2.971	3.407	2.969
PCA1pc	2.965	2.953	3.069	2.821	2.971	3.214	3.207	3.170	2.870	3.188	3.201
PCA2pc	2.668	3.276	2.953	3.172	2.723	2.425	2.832	3.177	3.144	3.292	3.201
PCA1sf	2.882	2.817	3.135	2.936	3.119	3.206	3.350	3.145	2.829	3.314	3.026
PCA2sf	2.962	3.161	3.450	2.939	2.758	3.576	3.837	2.731	3.287	3.524	3.273

Variable	DCA2pc		DCA2sf		PCA2pc		PCA2sf		LNMDS2pc		LNMDS2sf	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
NuSpes	-.1123	.0813	-.2088	.0012	-.0986	ns	-.4800	.0000	.2674	.0000	-.1722	.0073
NuVasc	.1228	.0796	.0206	ns	-.0178	ns	.0939	ns	.1785	.0105	.0074	ns
NuBryo	.0134	ns	-.0527	ns	-.0912	ns	-.2694	.0001	.2033	.0021	-.2048	.0020
NuLich	-.1827	.0051	-.2289	.0005	-.0749	ns	-.5432	.0000	.1882	.0038	-.1048	ns

plot, height of the tallest tree in the 3 × 3 m plot, basal area and canopy cover increased along one or both PCA1 axes. LNMDS1pc was correlated with crown area and number of trees in the meso plot at the P < 0.005 level.

There were fewer significant correlations at the P < 0.0001 level with the second axes than with the first axes. Fertilization with nitrogen was correlated with PCA2sf (Tab. 9). Weaker correlations with one or more of DCA2pc, DCA2sf, PCA2pc and LNMDS2pc showed that unevenness, fine-scale slope and humus depth increased along the ordination axes, while

Tab. 13. Constrained ordination (CCA and RDA) of the ME 144pc and ME 144sf data sets with the fertilization variables (fN, fMg and fP) as constraining variables, one at a time. CCAcov and RDAcov are constrained ordination with the humus-depth variables as covariables. E/TI is the ratio of the eigenvalue of the constrained ordination axis and total inertia, expressed as % ("percentage variation explained" by the fertilisation variables). P – significance level as tested by a Monte Carlo permutation test (999 permutations).

Constrained ordination method	Fertilization variable											
	fN				fMg				fP			
	pc		sf		pc		sf		pc		sf	
	E/TI (%)	P	E/TI (%)	P	E/TI (%)	P	E/TI (%)	P	E/TI (%)	P	E/TI (%)	P
CCA	1.1	0.061	1.3	0.031	0.9	0.162	1.0	0.065	1.8	0.003	2.0	0.001
RDA	0.9	0.200	1.8	0.200	0.9	0.152	0.9	0.082	1.4	0.005	1.4	0.016
CCAcov	1.2	0.033	1.4	0.009	1.0	0.117	1.3	0.021	1.5	0.001	1.8	0.001
RDAcov	4.3	0.001	3.5	0.001	2.0	0.011	1.6	0.017	3.4	0.001	2.7	0.001

Tab. 14. One-way ANOVA for plot scores along ordination axes (dependent variables) with fertilization variables as independent variables. df – Degrees of freedom, F – F-ratio, P – significance level.

Ordination axis	Fertilization variable					
	fN (df = 2)		fMg (DF = 1)		fP (df = 1)	
	F	P	F	P	F	P
DCA1pc	0.269	0.7643	0.007	0.9354	8.529	0.0041
DCA2pc	1.116	0.3306	0.260	0.6128	0.265	0.6128
DCA1sf	0.178	0.8373	0.064	0.8039	12.325	0.0006
DCA2sf	1.487	0.2296	2.579	0.1106	0.129	0.7243
PCA1pc	0.700	0.4981	0.830	0.3735	2.927	0.0893
PCA2pc	2.074	0.1295	1.074	0.3018	3.371	0.0685
PCA1sf	1.471	0.2332	0.108	0.7463	1.268	0.2622
PCA2sf	8.762	0.0003	3.972	0.0482	0.038	0.8477
LNMSD1pc	0.235	0.7912	1.081	0.3006	6.554	0.0118
LNMSD2pc	4.865	0.0094	0.034	0.8555	0.450	0.5110
LNMSD1sf	0.711	0.4931	0.019	0.8911	5.015	0.0271
LNMSD2sf	6.597	0.0019	10.929	0.0013	6.430	0.0126

soil moisture, pH and the height of the tallest tree in the 3×3 and 5×5 m plot decreased. PCA2sf and LNMSD2sf were correlated with unevenness and pH; unevenness decreased and pH increased along these axes.

Standardized semivariance (Tab. 10) and fractal dimension (D) as function of lag distance (Tab. 11) showed that the ordination axes DCA2pc, DCA2sf and PCA2pc were weakly spatially structured at the finest scale (up to 5 m), while the first axes showed no fine-scale spatial structure. The drop in fractal dimension for most axes (except PCA2) in the interval 30-100 m might suggest spatial structure at the between 30×30 m-plot scale.

VARIATION IN SPECIES RICHNESS ALONG ORDINATION AXES

The total number of species and the number of lichen species decreased along the first DCA and LNMSD axes and along PCA2sf (Tab. 12). The relationships between species richness variables was particularly strong for LNMSD based upon percentage cover. In addition, the total number of species increased along LNMSD 2pc. The total number of bryophytes decreased along LNMSD 1pc but not along the other corresponding axes.

EFFECTS OF FERTILIZATION ON VEGETATION

The constrained ordination methods, CCA and RDA, with the fertilization variables (fN, fMg and fP) as explanatory variables, gave inconsistent results (Tab. 13): using CCA, fertilization with phosphorus accounted for a significant "fraction of the variation" (1.8-2.0 %) in the ME 144pc and ME 144sf data sets. When the variation "accounted for" by the humus depth variables was removed, fertilization with nitrogen "accounted for" 1.4 % of the remaining variation in the ME 144sf data set while 1.5-1.8 % of the remaining variation in both data sets was accounted for by fertilization with phosphorus. RDA did not show any significant effect of fertilization, but after removal of the variation accounted for by humus depth, fertilization with nitrogen accounted for 3.5-4.3 %, and phosphorus fertilization accounted for 2.7-3.4 % of the remaining variation in both data sets. Fertilization by magnesium did not "account for" any of the variation by any of the methods.

ANOVA of plot scores, grouped defined by the fertilization variables, showed a significant effect of fertilization by nitrogen along PCA2sf ($P < 0.001$) and along LNMDS2 ($P < 0.01$). Fertilization by magnesium showed no significant effect, and fertilization by phosphorus showed significant effects along DCA1sf ($P < 0.001$) and DCA1pc only ($P < 0.01$; Tab. 14).

DISCUSSION

EVALUATION OF THE RELATIVE PERFORMANCE OF ORDINATION TECHNIQUES

Results obtained by the three ordination methods differ in several respects. To decide which is the best method for this particular data set, the following properties are important (cf. R. Økland 1990a): (i) clumping of plot scores, (ii) influence of sample plots with rare species which makes these plots act as outliers, and (iii) interpretability in ecological terms, i.e. correlations with explanatory variables.

PCA is more strongly influenced by outliers than DCA and LNMDS, as indicated by the clumping of plots in Figs 7-8 and the short core lengths of PCA. The environmental interpretability is stronger for DCA and LNMDS, as indicated by higher significance levels of correlations and the higher number of correlated variables. For these reasons, we conclude that PCA perform poorer than DCA and LNMDS. This was unexpected, as the compositional turnover in the data set is low with β -diversities of the first axes close to 2 S.D. units. PCA is often reported to perform well with such data sets (e.g. Oksanen 1983, Minchin 1987, R. Økland 1990a), but also Rydgren (1996) found PCA to perform less well than DCA and LNMDS on a data set with low compositional turnover. Our results thus support the views of Minchin (1987) and R. Økland (1990a) that even though PCA may show good recovery of short gradients, non-linear techniques such as LNMDS will usually perform at least equally well with such data.

The two DCA diagrams (Figs 4-5) are more similar to each other than the two LNMDS diagrams (Figs. 9-10), indicating that DCA is less sensitive than LNMDS to the choice of abundance measure. Whereas DCA plot scores are the weighted averages of species optima (Hill & Gauch 1980, ter Braak & Prentice 1988), and the spread of plots and species optima are optimized in DCA, maintenance of the rank order of floristic dissimilarities between plots in the ordination diagram is optimised in LNMDS (Minchin 1987). Two plots from the same site containing the same species but differing in all species' abundances (low abundance for all species in one, and high for all species in the other), will obtain the same positions along DCA-axes, while LNMDS will treat the plots as floristically dissimilar and separate them more or less strongly (T. Økland 1996).

DCA and LNMDS are almost equally strongly influenced by outliers: the cores have nearly the same lengths and neither method aggregate plots like PCA does. Most explanatory variables that are correlated with the first DCA and LNMDS axes have higher correlation coefficients with the former. Among the second axes, LNMDSpc is more strongly correlated with explanatory variables than LNMDSsf and DCA, probably because of the different ways plot positions are obtained by the two methods: in DCA, by first optimising the dispersion of the plot scores (the variation explained) along one axis, then repeating the process to obtain the next axis, and so on (R. Økland 1990a); while in LNMDS, on the contrary, by maximizing the rank order agreement between the inter-plot distances in the specified number of dimensions (here: 2; see Minchin 1987).

We cannot rank DCA or LNMDS above the other for this particularly data set by means of the criteria listed above. Instead, we consider the two methods as complementary and interpret the results in parallel. Our results thus support the suggestion by R. Økland (1990a, 1996) that DCA and LNMDS should be used in parallel.

EFFECTS OF FERTILIZATION

Fertilization method and sampling design

As the design of fertilization experiments is known to affect the outcome of such experiments strongly, a discussion of the design used in the present study is needed prior to interpretation of the results.

No opportunities existed for studying the change of the vegetation during the fertilization period, since the understory vegetation was not investigated before fertilization started. In principle, experimental studies without long-term repeated observations over a considerable time span, may be insufficient or even misleading (Bakker et al. 1996). Interesting results have, however, been obtained by other post-fertilization studies (e.g. Nygaard & Ødegaard 1993, van Dobben et al. 1993). Furthermore, there are reasons to believe that the variation in vegetation in the investigation area was rather small before fertilization, since the area is flat and the tree stand is even-aged (Abrahamsen & Erstad 1995). We therefore assume that the comparability of treatments is acceptable, although not optimal.

In most other comparable studies, fertilization proceeded for longer periods, or more years passed from fertilizer was applied for the last time until vegetation was analysed: Nygaard & Ødegaard (1993) performed their field recordings 8 years after fertilization, van Dobben et al. (1993) 15 years after, and Mäkipää (1994) 30 years after fertilization. The effects of fertilization would probably have been stronger, perhaps also qualitatively different, if the period since the last fertilization had been extended.

Fertilization with NH_4NO_3 pellets causes an increase in the total amount of nitrogen in previously unsaturated soil (Nygaard & Ødegaard 1993). This increase is likely to affect vascular plants and some endohydric bryophytes that absorb nutrients from the soil (e.g. Persson 1981, Proctor 1982, Nilsen & Abrahamsen 1995). Most bryophytes and lichens are ectohydric, and absorb water and nutrients through their entire surface, from precipitation, moist air and by uptake from the transpiration current from the soil (Stålfelt 1937, Tamm 1953, Blum 1974, van Tooren et al. 1990). Irrigation of the forest floor with fertilizer dissolved in water would therefore probably have been more appropriate if effects of deposition of airborne pollutants on the bottom layer was to be simulated. However, there is increasing evidence that even ectohydric bryophytes are supplied with water and nutrients that have been in contact with the soil. Skre & Oechel (1979) demonstrated, in a fertilization experiment in a spruce forest, that *Hylocomium splendens* and *Pleurozium schreberi* were not nutrient-limited, and suggested that uptake from the soil is also important (also see Bates & Farmer 1990). Callaghan et al. (1978), Wells & Brown (1996), Brümelis & Brown (1997), T. Økland et al. (in prep.) indicate that dissolved ions move upwards through the moss layer with the transpiration current. Fertilization was performed once a year at mid-summer, but since bryophytes are most vigorously growing in spring and autumn (Hagerup 1935, Stålfelt 1937,

Tamm 1953, R. Økland 1995), application of fertilizer at other times of the year is likely to influence bryophytes more strongly.

Variation in vegetation due to nutrient availability and the effects of fertilization

In the present study pH is only weakly related to LNMDS2pc, while nitrogen (as percentage of loss on ignition) decreases significantly along the main coenocline from the lichen-rich sites to sites rich in ericaceous species (the first ordination axes). This contrasts with the findings of, e.g. Dahl et al. (1967) and Moore (1984), but is in accordance with results of R. Økland & Eilertsen (1993) for a similar coenocline in the nearby Solhomfjell area. Our results indicate that nutrient availability is not important in the study area or that fertilization with nitrogen, magnesium and phosphorus has modified the relationship between nutrient availability and species composition.

Fertilization with nitrogen

The total amount of nitrogen in humus is only weakly correlated with the nitrogen fertilization variable ($\tau = 0.1905$ at significance level $P = 0.004$). Nilsen & Abrahamsen (1995) recorded more rapid increase in tree volume at sites fertilized with nitrogen for the three first years after fertilization started, but G. Abrahamsen (pers. comm.) found reduced effects of nitrogen fertilization after six years of fertilization, and concluded that the soil was nitrogen-saturated. Leaching from saturated soils or leakage from the thin humus layer because of high concentration and large doses of fertilizer are possible reasons why the correlation between the total amount of nitrogen and nitrogen fertilization is not stronger than observed.

In this study, small but yet significant effects of fertilization with nitrogen on vegetation are demonstrated by several methods, after only six years of fertilization. The highly significant correlations between the nitrogen fertilization variable and litter depth, as well as this variable's significant correlations with some tree variables, indicate that the effect of fertilization is partly via increased tree growth (shading, litterfall etc.). This also accords with the results of Nilsen & Abrahamsen (1995), demonstrating higher incremental tree growth in fertilized plots than in unfertilized plots. Furthermore, the spatial structuring of several tree variables at scales of 30-60 (the inter-block distance), is likely to represent fertilization effects.

Fertilization with phosphorus

Phosphorus fertilization is correlated with plot position along the main coenocline, indicating that phosphorus-fertilized plots are more frequent near the coenocline end with dominance of ericaceous species, while phosphorus-unfertilized plots are more frequent near the lichen-rich end. Variation along the main coenocline is interpreted to be due to environmental variables on a fine scale, as no spatial structure is found along the first axes, while fertilization with phosphorus gives rise to effects on a broader scale because of the sampling design. This suggests that the correlation between phosphorus fertilization and the main coenocline does not represent a causal relationship.

INTERPRETATION OF VARIATION IN VEGETATION

The main coenocline

The similarity of the first axes obtained by DCA and LNMDS indicates existence of one major coenocline in the study area.

Most lichen species have their optima close to the low-score end of the first axes and the number of lichen species decreases along these axes. Ericaceous species and some bryophytes, on the other hand, have optima near the high-score end (see DCA species plot, Fig. 6). This indicates existence of a coenocline from lichen-rich sites to sites rich in ericaceous species. We interpret this coenocline as a part of the well-known coenocline from spruce forest via pine forest dominated by ericaceous species to pine forest dominated by lichens. This gradient has been recognised as a major compositional gradient for decades (Malmström 1949, Kuusipalo 1985) and has also been identified by ordination (Kuusipalo 1985, R. Økland & Eilertsen 1993). R. Økland & Eilertsen (1993) show that this coenocline remains the most important in a set of vegetation plots from pine forest, when analysed separately.

The main vegetation gradient shows no obvious spatial structuring in the study area, indicating that this coenocline represents variation in vegetation on a scale finer than 5 m, caused by factors other than fertilization. There is, however, also a tendency for vegetation to be spatially structured at scales of 30–100 m, i.e. at the between-macro plot scale.

The main coenocline is more strongly correlated with explanatory variables than are the second axes of the ordinations, but most of the correlations between explanatory variables and ordination axes in this study are low. Nevertheless, the consistent pattern of correlations obtained for ordination axes derived by different methods gives strong support for our interpretation of one main coenocline. At sites dominated by lichens (low-score end of our first axes), the humus is shallow, soil organic content is low, the terrain is rather flat and the tree canopy is rather open (fewer trees per unit area). Malmström (1949), Kuusipalo (1985) and R. Økland & Eilertsen (1993) found the same patterns of environmental variables along corresponding coenoclines in other parts of Fennoscandia.

Broad-scale topographic variation is often claimed to be a major determinant of the main coenocline in coniferous forests (Malmström 1949, Kuusipalo 1985, R. Økland & Eilertsen 1993). In the present study, however, sites rich in ericaceous species segregate from the lichen-rich sites without differences in broad-scale topography. The study area is flat and topographic variation occurs on fine scales only. The increase in unevenness along the first ordination axes suggests that a microtopographic gradient is part of the complex-gradient underlying this coenocline.

Soil moisture is claimed to be governed by broad-scale topography (Malmström 1949, Kuusipalo 1985, van Cleve & Yarie 1986). In this study, there is no broad-scale topographic gradient and the lack of spatial structure of soil moisture variables indicates variation mostly on a fine scale. No relationship is found between volumetric soil moisture variables and the first ordination axes in this study, even though availability of water is one of the fundamental limiting factors for plant growth and often believed to be a major determinant of species distribution along this gradient (R. Økland & Eilertsen 1994). This apparent paradox may be due to several reasons: (1) Difficulties with soil sampling; the humus layer is often less than 5 cm, in some places almost non-existent. The samples were taken from the upper 5 cm of

the humus layer which may not be the optimal method to measure the actual moisture conditions for the vascular plants, in as much as they also absorb water from deeper layers (e.g. Stålfelt 1937, Björkman & Lundberg 1971). (2) Soil moisture varies in time and space. The moisture measurements were taken 5 and 12 days after the last rainfall, which may not be the representative of the conditions under which the composition of vegetation is affected by soil moisture. R. Økland & Eliertsen (1993) forward the soil moisture deficiency hypothesis which suggests that the main coenocline in pine forests is the response to a gradient in soil moisture deficiency, i.e. a gradient in the possibility of becoming affected negatively by drought. Although our results apparently do not seem to support this hypothesis, we cannot conclude that this hypothesis does not apply to the investigation area. The reasons for this are: (i) Too few replicates of soil measurements were collected to be sure that the measurements reflect the moisture deficiency situation. (ii) Moisture may be an important factor in the investigation area even though the soil moisture variables are not correlated with the first ordination axes. Cryptogams absorb most water and nutrients directly from precipitation, moist air and transpiration from the soil (Stålfelt 1937, Tamm 1953, Blum 1974). These aspects of water supply are not likely to be reflected in the soil moisture measurements. (3) There is no broad-scale topographic variation in the study area, but other factors that are correlated with the axes are likely to influence moisture conditions on a finer scale: depth of the humus layer, drainage regimes, aspect, canopy closure and density of trees, litterfall, and plant cover in the field and bottom layers. In the study area, the depth of the humus layer increases along the coenocline, indicating that there is more moisture available near the ericacean-rich end of the coenocline. At the lichen-rich end of the coenocline, the canopy is rather open and the humus layer is shallow. Thus, this end of the coenocline is likely to experience higher water run-off, and be more strongly exposed to desiccating winds and radiation which further increases water loss. This is in accordance with Ipatov & Tarkhova (1980), who did not find any distinct microclimatic (including soil moisture) differences between pine forest sites dominated by lichens and sites dominated by bryophytes, although lichens were restricted to open sites. The tree variables in this study are not all significantly correlated with the first ordination axes, but their affiliation to one group of internally correlated variables confirm a tendency towards increasing tree density and canopy closure along the coenocline. The tree canopies intercept precipitation by leading the run-off water along branches and stem, giving rise to a gradient in throughfall quantities from gap to stem, and from between canopies to under canopies (cf. Lukkala 1942, R. Økland & Eilertsen 1993). At sites crowded with trees, root uptake of water increases due to increasing total transpiration (cf. Taylor et al. 1987, T. Økland 1990) and the soil is generally drier (Schaetzl et al. 1989). Bryophytes dominate at sites with a rather dense tree layer. They retain moisture better than lichens and litter (Stålfelt 1937), and prevent the soil from desiccation.

The importance of different environmental factors for the corresponding coenocline, seemingly differs between study areas: in this investigation, the humus depth-variables are most strongly correlated with the gradient. However, we cannot from these results conclude that different underlying factors responsible for similar vegetational responses in different areas.

Interpretation of the second ordination axes

The differences between the second ordination axes obtained by DCA and LNMS indicate

that the second axes do not represent independent, new, gradients in the vegetation, although all second axes are correlated with explanatory variables. The second axes are spatially structured, both a fine scale (5 m) and at scales of 30 to 50 m, indicating that the variation along the second axes is mainly on the between-macro plot scale, in contrast to the first ordination axes. There is a tendency for decreasing soil moisture and fine-scale slope along the second DCA axes, while the directions of variation in tree density are inconsistent between DCA2pc and DCA2sf, and between the different tree variables. On the other hand, the second LMNDS axes, especially LNMDS2pc, are correlated with more environmental variables than DCA and LNMDS2sf. The correlations between the explanatory variables and LNMDS2pc are mostly weak, but unevenness, fine-scale slope and humus depth increase, while soil moisture and litter depth decrease, and tree density varies in an inconsistent manner along this axis.

Even though the second axes may seem to represent a topographic-soil moisture complex gradient, the difference between results obtained by DCA and by LNMDS, and the weak and inconsistent correlations with the explanatory variables, make the interpretation of these ordination axes uncertain.

CONCLUSION

Fertilization by nitrogen and phosphorus showed small, but significant effects on the vegetation after six years of fertilization. In addition it was possible to extract a major coenocline in pine forest vegetation, and relate it to environmental factors. This indicates that fertilization studies, in which only moderate effects have been demonstrated, may also have relevance for knowledge of the natural variation in the vegetation. Furthermore, it clearly demonstrates the potentials of gradient analysis techniques for detection of compositional trends in vegetation data.

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APPENDICES

Appendix 1. List of species, with abbreviations.

Abbreviations	Species names
Pinu syl	<i>Pinus sylvestris</i>
Sorb auc	<i>Sorbus aucuparia</i>
Call vul	<i>Calluna vulgaris</i>
Empe nig	<i>Empetrum nigrum</i>
Vacc myr	<i>Vaccinium myrtillus</i>
Vacc uli	<i>Vaccinium uliginosum</i>
Vacc vit	<i>Vaccinium vitis-idaea</i>
Desc fle	<i>Deschampsia flexuosa</i>
Cera pup	<i>Ceratodon pupureus</i>
Dicr fus	<i>Dicranum fuscescens</i>
Dicr mon	<i>Dicranum montanum</i>
Dicr pol	<i>Dicranum polysetum</i>
Dicr sco	<i>Dicranum scoparium</i>
Dicr spu	<i>Dicranum spurium</i>
Pohl nut	<i>Pohlia nutans</i>
Pleu sch	<i>Pleurozium schreberi</i>
Poly com	<i>Polytrichum commune</i>
Poly pil	<i>Polytrichum piliferum</i>
Raco het	<i>Racomitrium heterostichum</i>
Ceph sp	<i>Cephaloziella</i> sp
Ptil cil	<i>Ptilidium ciliare</i>
Ptil pul	<i>Ptilidium pulcherrimum</i>
Cetr isl	<i>Cetraria islandica</i>
Clad arb	<i>Cladonia arbuscula</i>
Clad bac	<i>Cladonia bacillaris</i>
Clad bel	<i>Cladonia bellidiflora</i>
Clad car	<i>Cladonia carneola</i>
Clad cen	<i>Cladonia cenotea</i>
Clad chl	<i>Cladonia chlorophaea</i> agg
Clad cor	<i>Cladonia cornuta</i>
Clad cri	<i>Cladonia crispata</i>
Clad def	<i>Cladonia deformis</i>
Clad gra	<i>Cladonia gracilis</i>
Clad mit	<i>Cladonia mitis</i>
Clad ran	<i>Cladonia rangiferina</i>
Clad squ	<i>Cladonia squamosa</i>
Clad ste	<i>Cladonia stellaris</i>
Clad sul	<i>Cladonia sulphurina</i>
Clad unc	<i>Cladonia uncialis</i>

Appendix 2. Untransformed abundance values for the ME 144pc (percentage cover on a scale from 0 to 100) and ME 144sf (subplot frequencies on a scale from 0 to 16) data sets. Abbreviations for the species names are in accordance with Appendix 1.

Species	MN 1		MN 2		MN 3		MN 4		MN 5		MN 6		MN 7		MN 8		MN 9		MN 10		MN 11		MN 12	
	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf
Pinu syl	1	3	-	-	-	-	1	2	1	2	1	2	1	3	-	-	-	-	1	2	-	-	-	-
Sorb auc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Call vul	-	-	-	-	1	1	4	3	-	-	-	-	-	-	-	-	-	5	7	-	-	5	2	
Empe nig	-	-	-	-	5	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vacc myr	2	2	-	-	-	-	-	-	-	-	-	1	3	-	-	1	2	-	-	-	-	-	-	-
Vacc uli	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vacc vit	1	6	2	9	50	16	30	16	10	16	20	16	60	16	5	16	40	16	15	16	20	12	15	16
Desc fle	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cera pup	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicr fus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicr mon	2	5	-	-	-	-	1	1	1	5	1	2	1	1	-	-	-	-	-	-	-	-	-	-
Dicr pol	-	-	-	-	-	-	1	1	-	-	-	-	1	6	-	-	2	3	-	-	1	1	5	8
Dicr sco	-	-	1	1	-	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicr spu	-	-	2	4	-	-	-	-	1	2	1	3	1	6	-	-	-	-	-	-	-	-	-	-
Poh nut	15	10	2	2	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pleu sch	-	-	2	4	-	-	2	3	2	8	-	-	5	8	5	11	20	15	-	-	1	1	5	15
Poly com	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Poly pil	1	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Raco het	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ceph sp	1	5	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	2	2	-	-
Ptil cil	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ptil pulc	-	-	1	4	-	-	-	-	-	-	1	3	1	2	1	1	-	-	-	-	1	2	-	-
Cetr isl	2	7	2	15	10	16	1	2	2	7	5	16	15	11	10	8	1	2	15	16	20	16	-	-
Clad arb	3	5	5	14	5	15	5	12	2	15	5	16	25	15	20	14	10	16	-	-	15	13	10	13
Clad bac	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clad bel	1	4	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-
Clad car	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clad cen	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clad chl	2	2	1	1	-	-	-	-	5	12	-	-	1	2	2	7	1	1	1	3	2	5	2	8
Clad cor	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clad cri	-	-	-	-	-	-	-	-	-	-	-	-	2	3	-	-	-	-	-	-	-	-	1	1
Clad def	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clad gra	1	1	1	6	1	5	1	2	1	1	1	2	-	-	-	-	1	3	-	-	1	2	1	1
Clad mit	-	-	-	-	1	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clad ran	2	8	-	-	-	-	-	-	1	5	1	5	10	8	15	14	-	-	5	11	2	5	10	14
Clad squ	-	-	-	-	-	-	-	-	-	-	-	-	1	5	-	-	-	-	-	-	-	-	-	-
Clad ste	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	5	-	-	-	-	-	-
Clad sul	1	4	2	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clad unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-

Appendix 2 (continued).

Species	M 1		M 2		M 3		M 4		M 5		M 6		M 7		M 8		M 9		M 10		M 11		M 12	
	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf	pc	sf
Pinu syl	-	-	1	3	-	-	1	2	-	-	-	-	-	-	1	3	-	-	-	-	-	-	-	-
Sorb auc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Call vul	-	-	2	3	2	4	-	-	-	-	-	-	-	1	3	-	-	-	-	-	-	-	-	-
Empe nig	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vacc myr	-	-	-	-	-	-	-	-	-	-	1	2	-	-	1	1	-	-	10	1	-	-	-	-
Vacc uli	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Vacc vit	50	16	30	16	20	16	10	16	15	16	40	16	30	16	60	16	10	16	5	11	50	16	50	16
Desc fle	-	-	1	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cera pup	-	-	1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicr fus	-	-	-	-	2	5	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicr mon	-	-	1	2	1	3	1	2	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
Dicr pol	30	14	2	5	1	2	1	3	5	4	1	4	1	3	5	3	5	4	2	2	15	8	2	2
Dicr sco	-	-	1	1	-	-	1	2	-	-	-	-	-	-	-	-	3	4	-	-	-	-	-	1
Dicr spu	1	3	-	-	5	9	-	-	1	4	1	5	2	5	-	-	-	-	-	-	1	1	-	-
Poh nut	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pleu sch	5	13	-	-	5	14	2	4	5	6	5	12	2	13	55	16	10	11	2	3	3	4	10	15
Poly com	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Poly pil	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Raco het	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-
Ceph sp	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ptil cil	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
Ptil pulc	-	-	-	-	1	6	1	2	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	10
Cetr isl	-	-	1	1	5	8	20	16	10	11	5	7	10	11	3	2	-	-	2	4	10	12	-	-
Clad arb	10	16	15	14	10	13	20	15	20	16	20	16	15	16	15	14	20	14	20	15	15	14	15	15
Clad bac	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
Clad bel	-	-	-	-	1	1	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clad car	-	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clad cen	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clad chl	-	-	1	2	2	13	1	7	1	1	-	-	30	15	-	-	-	-	1	4	1	5	-	-
Clad cor	-	-	-	-	1	1	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
Clad cri	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	1	2	-	-	-	-
Clad def	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clad gra	1	3	1	5	2	14	1	7	-	-	1	2	-	-	1	2	-	-	1	1	-	-	-	-
Clad mit	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clad ran	15	15	15	16	10	10	1	1	20	16	20	14	15	16	10	9	25	16	20	16	15	16	15	16
Clad squ	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clad ste	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clad sul	-	-	-	-	1	1	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
Clad unc	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-

Appendix 3. Untransformed values for the 28 explanatory variables in the 144 meso plots. Abbreviations for the explanatory variables are in accordance with Tab. 1.

Meso plot	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
MN1	1.9	-1	-0.1	6	80	2.5	5.5	4	7	3.9	33.79	34.27	0.73	1.60	5.70	17	6.76	9.08	0.30	1	4	1	3	11.4	11.4	2	1	0
MN2	2	1	2.1	10	44	3.5	5.5	2	7	3.7	47.82	30.25	0.87	1.44	0.00	28	19.5	3.48	0.00	1	1	0	4	0	11.9	2	1	0
MN3	1.4	0	-0.6	0	25	3	7.5	7	10	3.8	34.79	26.05	0.77	1.74	25.35	26	0.78	10.63	1.15	0	1	3	6	12.1	12.2	2	1	0
MN4	2.1	-2	-1.6	2	40	3	5.5	0	11	3.9	31.76	23.67	0.78	1.38	6.06	20	13.78	8.75	0.20	0	0	1	3	10.2	10.5	2	1	0
MN5	1	0	0.4	8	10	3.5	6	4	7	3.8	31.93	25.41	0.81	1.55	12.32	23	13	7.53	0.10	0	2	1	10	11.6	11.6	2	1	0
MN6	0.8	0	0.4	2	4	2	5.5	3	6	4.2	37.27	22.14	0.82	1.73	20.20	25	6.76	5.85	0.45	0	0	1	7	9.4	11.9	2	1	0
MN7	2.3	-1	-0.1	4	30	3	4	4	6	3.8	46.95	36.94	0.64	1.73	79.49	26	12.22	8.50	0.50	0	4	2	6	0	13.2	2	1	0
MN8	2	1	0.9	2	20	2	5.5	4	6	3.9	35.89	32.68	0.87	1.49	23.41	28	8.84	8.30	0.45	0	1	1	4	12	13.3	2	1	0
MN9	3.6	-1	-1.9	10	50	3	8	5	18	3.6	48.85	47.5	0.92	1.34	10.70	30	3.38	10.13	0.15	1	6	1	4	10.7	10.7	2	1	0
MN10	1	0	0	3	5	2.5	0.5	0	1	4.3	29.98	11.08	0.51	2.08	41.23	30	8.84	10.35	0.28	0	0	0	5	0	14.2	2	1	0
MN11	1.9	-1	0	0	12	2.5	3	0	5	4	41.46	19.14	0.74	1.62	75.53	34	4.68	13.98	0.20	0	0	0	7	0	13.3	2	1	0
MN12	1.6	-1	-0.1	2	16	2	8	5	10	3.7	37.77	33.81	0.81	1.46	0.59	21	11.96	6.28	0.05	0	3	1	2	13.1	13.1	2	1	0
M1	1.7	0	-0.6	4	28	0.5	4.5	1	7	3.7	37.11	17.83	0.42	1.67	25.02	28	5.46	7.95	1.25	0	0	2	4	12.3	12.3	0	1	0
M2	1.9	0	1	2	4	1	5	3	6	3.7	28.37	17.72	0.76	1.27	16.40	29	1.3	9.98	0.25	0	0	1	5	13.1	14.5	0	1	0
M3	1.2	0	1.2	1	10	2	6	5	10	3.5	27.52	22.05	0.88	1.44	43.25	22	5.46	10.75	0.75	0	1	0	3	0	14.4	0	1	0
M4	1.9	-1	-1.7	7	35	1	6	3	7	3.6	29.5	21.64	0.80	1.53	12.02	29	9.1	5.05	0.73	1	1	2	5	11.3	11.4	0	1	0
M5	1.1	0	-0.3	3	25	2	5.5	4	12	3.6	31.92	29.06	0.82	1.46	13.26	32	1.82	10.25	0.85	0	1	3	6	14.2	14.2	0	1	0
M6	0.9	0	-0.2	0	20	1	7	4	8	3.5	25.49	17.99	0.91	1.42	5.48	34	0.78	7.60	0.18	0	0	1	5	14.6	14.6	0	1	0
M7	1.5	-1	-1.9	3	18	1.5	5.5	1	11	3.9	44.95	27.89	0.65	1.64	30.00	30	3.64	9.63	0.55	1	3	1	7	13.2	13.2	0	1	0
M8	4.1	1	2.3	0	60	1	7.5	6	11	3.5	29.57	30.58	0.88	1.20	32.81	30	4.94	12.83	1.10	1	3	1	4	10.8	14.2	0	1	0
M9	2.5	1	2.6	8	20	1	5.5	4	12	3.8	45.58	18.91	0.71	1.41	3.23	30	1.3	8.30	0.28	0	0	7	12	13.2	13.6	0	1	0
M10	2.6	0	1.4	12	35	1	5.5	3	8	3.8	39.12	35.69	0.56	0.71	10.03	34	3.12	8.53	0.45	1	1	3	6	11	13	0	1	0
M11	2.4	-1	-1.8	3	25	0	9	6	11	3.6	37.32	34.61	0.90	1.14	9.99	26	2.08	9.20	1.30	0	1	2	5	7.9	7.9	0	1	0
M12	1.4	0	-0.9	0	5	1	7	8	6	3.5	41.66	27.22	0.89	1.29	10.60	34	3.12	10.20	0.80	0	0	2	8	10.4	12.5	0	1	0

Appendix 3 (continued).

Meso plot	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
PMn1	3.9	-1	0.2	20	45	2	4	1	7	3.7	35.2	37.46	0.52	2.36	42.79	19	1.04	17.20	1.40	1	3	2	2	12.2	12.2	1	1	1
PMn2	5.2	2	5.7	25	35	1.5	5	5	12	3.7	32.49	18.22	0.94	1.36	6.69	21	5.46	11.65	0.63	0	1	3	5	10.7	10.7	1	1	1
PMn3	2	1	1	5	10	1.5	7.5	7	14	3.8	26.89	19.63	0.91	1.45	17.34	20	3.64	12.25	1.00	0	0	4	8	0	11.6	1	1	1
PMn4	2.7	1	1.1	3	8	1	5	4	7	3.6	32.59	28.85	0.84	1.39	0.00	17	24.44	3.03	0.00	0	2	2	3	13.9	13.9	1	1	1
PMn5	3.1	-1	0.9	8	30	2	4.5	3	7	3.6	46.05	32.73	0.85	1.37	16.61	22	0.52	15.40	0.53	0	2	4	10	12.6	12.6	1	1	1
PMn6	3	1	4.2	0	20	3	8.5	5	12	3.7	36.44	25.33	0.94	1.30	11.50	22	2.34	12.75	1.00	0	2	1	4	11.5	11.5	1	1	1
PMn7	4.2	2	5.7	0	40	1	4	2	7	3.8	25.76	22.78	0.84	1.66	31.59	19	16.9	7.95	0.68	1	3	0	1	0	11.7	1	1	1
PMn8	2.5	0	-0.1	2	20	0.5	4.5	1	11	3.5	31.72	16.34	0.83	1.54	60.65	13	5.46	14.83	0.70	1	2	1	3	10.8	12.9	1	1	1
PMn9	1.9	0	-1.2	5	30	1.5	8	7	10	3.6	23.3	19.55	0.56	1.68	11.12	25	2.08	11.00	0.63	0	1	4	9	12.3	12.3	1	1	1
PMn10	4	1	-0.2	28	40	1.5	4.5	4	6	3.6	40.6	28.23	0.86	1.38	17.79	20	4.94	17.85	0.25	1	1	0	7	11.8	11.9	1	1	1
PMn11	2.4	-1	-1.1	0	20	1	3	2	4	3.4	31.74	16.47	0.81	1.66	14.24	17	11.96	9.45	0.18	0	0	0	3	0	12.9	1	1	1
PMn12	2.4	-1	-2.4	8	28	1.5	7	6	10	3.3	28.67	19.22	0.86	1.32	26.61	22	6.5	21.85	0.40	1	3	0	7	0	12.2	1	1	1
PMN1	2.4	1	2.1	0	8	3	7	5	7	4.1	37.34	19.81	0.94	1.53	24.98	14	9.62	20.38	1.13	0	0	4	8	12.5	13.8	2	1	1
PMN2	3	-1	0.1	12	26	2.5	6.5	4	9	3.7	37.04	26.6	0.90	1.34	5.56	21	2.34	15.05	1.00	0	2	5	8	11.1	11.1	2	1	1
PMN3	4.6	2	6.7	18	28	4	7.5	6	9	3.7	38.86	29.55	0.93	1.27	12.10	16	0	14.85	1.00	0	0	1	2	12.1	12.1	2	1	1
PMN4	2.2	-1	-0.8	0	10	2	7.5	5	8	4	38.72	29.27	0.82	1.38	27.95	16	2.86	18.28	0.88	0	0	4	5	12.4	12.4	2	1	1
PMN5	3.1	1	0.7	4	40	4.5	8.5	3	10	3.6	39.05	16.92	0.93	1.35	12.30	16	3.64	11.13	1.00	0	3	1	2	12.3	12.3	2	1	1
PMN6	2.2	1	-0.3	0	50	1.5	3.5	2	5	3.8	28.17	20.6	0.82	1.16	10.40	13	15.08	12.18	0.10	1	2	1	4	4.9	11	2	1	1
PMN7	2.7	-1	-1.7	8	35	2.5	5	2	8	3.9	38.22	32.41	0.87	1.50	11.74	15	2.08	17.08	1.00	0	0	2	3	12.5	12.5	2	1	1
PMN8	2.1	-1	-1	0	20	1.5	7	4	8	3.6	32.92	23.67	0.88	1.39	0.00	21	10.14	12.40	0.00	0	1	0	3	0	12.8	2	1	1
PMN9	4.4	-1	-1	0	40	3	7	3	12	3.9	40.8	20.74	0.86	1.45	24.00	16	9.36	10.15	0.90	1	4	1	1	12.7	12.7	2	1	1
PMN10	2.1	1	1.3	7	20	2	4	3	5	3.9	33.92	19.32	0.84	1.35	28.25	22	14.04	13.30	0.23	0	0	0	2	0	12.5	2	1	1
PMN11	2.7	-1	0.5	11	30	5	7	4	11	3.8	41.19	22.91	0.87	1.33	13.33	17	1.04	10.63	0.85	0	1	3	6	12.5	12.6	2	1	1
PMN12	3.3	1	3.7	0	30	1.5	5.5	1	8	4.2	40.08	23.76	0.70	1.51	35.23	15	8.58	13.90	0.35	0	2	0	5	0	12.2	2	1	1

Appendix 3 (continued).

Meso plot	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
n1	1.1	0	0.2	2	20	2.5	3.5	2	4	3.7	41.41	21	0.77	1.40	19.47	21	10.66	16.58	0.10	0	1	0	5	0	11.8	1	0	0
n2	3.4	2	3.4	10	70	0.5	5.5	5	7	3.7	30.4	24.76	0.91	1.32	19.45	21	15.08	7.83	0.53	1	2	1	3	12.7	15.2	1	0	0
n3	1.2	0	-0.2	1	25	2	4.5	4	5	3.5	43.56	31.44	0.77	1.55	20.21	16	16.9	8.03	0.18	0	1	0	0	0	0	1	0	0
n4	1.1	0	1.5	1	20	2	5	3	7	3.6	36.62	18.23	0.53	1.73	8.50	29	0.26	13.08	0.80	0	2	5	8	10.4	11.6	1	0	0
n5	1.7	1	0.1	6	10	2.5	4.5	3	5	3.5	33.77	16.75	0.67	1.65	21.06	22	9.62	13.45	0.45	0	1	0	2	0	11.7	1	0	0
n6	2.1	1	2.2	6	13	1.5	6.5	5	13	3.7	37.68	35.17	0.82	1.49	21.22	22	1.04	13.70	1.15	0	0	2	4	13.5	13.5	1	0	0
n7	1.8	0	-0.5	6	25	1.5	4.5	4	5	3.6	33.23	22.34	0.88	1.54	135.78	16	17.68	10.45	0.75	0	1	0	2	0	12.4	1	0	0
n8	2.1	-1	-2.2	4	20	3	3	2	5	3.4	29.33	18.56	0.93	1.26	20.37	20	2.08	12.23	0.60	1	3	2	4	11.3	11.3	1	0	0
n9	1.2	1	0.7	0	38	1	5	3	9	3.5	43.34	35.64	0.85	1.39	3.90	19	5.72	15.38	0.13	1	2	2	5	0	13	1	0	0
n10	1.3	0	0.3	0	10	1.5	6	6	10	3.6	39.66	19.33	0.81	1.47	13.35	17	3.38	10.55	0.23	0	0	1	5	11.3	11.3	1	0	0
n11	2	-1	-2.3	0	20	2	10	6	11	3.4	28.69	17.63	0.91	1.26	10.97	15	0.78	14.58	0.73	0	0	5	8	14	14	1	0	0
n12	2.6	1	0.8	0	10	5	4.5	4	7	3.6	27.02	18.78	0.92	1.34	16.06	24	2.6	11.98	1.48	0	1	8	11	12.3	12.3	1	0	0
P1	2.3	-1	-1.8	4	30	2.5	7	3	12	3.7	31.48	21.39	0.55	1.30	11.41	17	3.38	12.90	0.80	0	0	1	4	8.1	12.5	0	0	1
P2	2.4	1	0.4	12	20	1.5	6.5	5	7	3.4	36.19	31.38	0.78	1.37	27.16	15	8.84	13.13	0.23	0	1	1	4	12.3	12.3	0	0	1
P3	3.1	-1	1.4	4	44	1	5.5	3	9	3.4	31.16	16.93	0.81	1.38	10.70	11	10.92	10.15	1.00	0	1	1	2	10.7	10.7	0	0	1
P4	4.7	2	4.9	10	70	1.5	7.5	6	9	3.3	30.14	19.91	0.72	1.26	11.66	20	6.76	10.83	1.05	0	4	4	6	11.3	12.6	0	0	1
P5	2.3	1	2.9	10	30	2	6.5	6	10	3.5	28.01	31.52	0.70	1.70	32.32	12	0.52	16.33	0.63	1	3	2	7	12.6	13.8	0	0	1
P6	3.1	2	4.8	20	30	2	5	1	9	3.6	26.34	20.38	0.92	0.90	13.80	20	0.78	17.53	1.00	1	1	3	14	13.8	13.8	0	0	1
P7	1.1	0	0.6	0	20	1	3	2	5	3.6	35.43	20.16	0.78	1.46	0.00	18	28.34	2.78	0.00	0	1	0	3	0	12.5	0	0	1
P8	1.3	0	-0.6	0	20	0	5.5	5	9	3.4	27.4	24.75	0.87	1.27	9.47	22	15.6	6.88	0.20	0	4	2	6	9.7	13.8	0	0	1
P9	1.2	0	-0.1	0	10	1.5	5	4	6	3.6	40.46	33	0.54	0.80	10.67	13	22.1	6.48	0.00	0	2	0	3	0	11.4	0	0	1
P10	4.8	2	6.1	0	40	1	4.5	3	7	3.5	46.56	25.21	0.68	0.85	10.19	14	5.98	15.05	0.55	1	1	2	5	11.1	11.1	0	0	1
P11	4.7	-1	-1.2	14	40	2.5	6	4	7	3.5	31.1	26.17	0.69	1.46	13.30	22	0.26	18.40	1.18	0	1	5	12	12.6	15.1	0	0	1
P12	1.4	1	0.4	4	20	1	4.5	1	7	3.3	36.93	23	0.76	1.63	9.03	19	6.5	15.83	0.73	0	1	1	3	10.9	11.7	0	0	1

Appendix 3 (continued).

Meso plot	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
PN1	0	-1	-0.7	0	20	3	3	1	6	4.1	41.4	31.5	0.73	1.68	10.75	14	4.42	12.40	0.25	0	0	0	2	0	9.5	2	0	1
PN2	1.6	1	0.5	12	40	3.5	6.5	4	7	3.6	31.01	18.9	0.89	1.41	14.10	18	1.04	12.55	1.00	0	1	3	4	14.1	14.9	2	0	1
PN3	1.2	0	0.5	0	10	2.5	4.5	4	6	3.8	41.26	31.81	0.79	1.61	10.72	25	0	10.88	1.03	0	0	2	4	12.6	12.6	2	0	1
PN4	1.2	0	0.4	0	15	3.5	5	3	5	3.9	37.58	36.73	0.93	1.88	55.49	25	5.2	19.18	0.65	0	0	1	5	13.6	15.4	2	0	1
PN5	1.2	-1	-1.1	0	20	3	5	4	9	3.8	39.83	28.94	0.83	1.47	56.42	16	0.52	16.77	1.08	0	0	1	1	13.5	13.5	2	0	1
PN6	1.6	0	-0.7	5	20	5.5	5.5	4	8	3.9	29.48	28.38	0.90	1.43	24.55	15	3.12	13.88	1.10	0	1	2	2	13.9	13.9	2	0	1
PN7	1.4	0	0.6	4	20	3	5.5	1	8	3.7	40.13	29.82	0.77	1.30	21.28	25	2.6	13.40	0.48	0	1	0	2	0	14.2	2	0	1
PN8	2.9	1	3.6	0	40	3.5	4	3	5	3.9	46.51	38.08	0.65	1.51	10.80	21	3.38	15.53	1.00	0	0	1	2	10.8	13	2	0	1
PN9	3.3	1	-2.6	15	40	3	3	1	3	3.9	43.53	23.6	0.72	1.58	12.54	22	4.96	11.20	0.45	1	3	2	2	14.5	14.5	2	0	1
PN10	1	0	-0.4	4	10	4	5.5	3	5	3.7	36.62	31.76	0.72	1.56	18.53	26	1.82	14.93	1.00	0	0	1	6	13.9	13.9	2	0	1
PN11	0.8	0	0.7	0	2	2.5	2.5	2	3	3.6	26.27	19.18	0.64	1.54	8.16	26	12.74	13.00	0.48	0	0	0	1	0	9	2	0	1
PN12	1	0	0	0	4	3	4.5	4	6	3.9	44.67	29.28	0.84	1.46	23.50	18	5.72	15.98	1.00	0	1	1	4	15.5	15.5	2	0	1
MP1	2.5	-1	-2.2	2	30	2.5	5	4	10	3.5	31.38	18.74	0.94	1.39	10.76	24	1.3	8.45	0.95	0	0	4	6	14.7	14.7	0	1	1
PM2	1.3	0	-0.4	4	20	0	6	6	8	3.5	39.13	24.07	0.63	1.43	38.92	19	2.08	14.20	0.50	0	0	1	5	12.7	14.2	0	1	1
PM3	1.4	0	0.4	10	10	2.5	4	3	4	3.5	31.42	22.7	0.52	1.78	18.70	23	10.66	8.35	0.55	0	0	4	8	10	12.3	0	1	1
PM4	1.4	0	0.1	0	5	2	4	2	5	3.5	40.93	20.06	0.83	1.04	20.00	14	2.6	13.05	0.53	0	0	0	3	0	12.7	0	1	1
PM5	3	0	-1.9	0	25	1.5	7.5	7	9	3.4	35.6	25.33	0.79	1.41	0.00	16	15.08	10.25	0.00	0	1	0	2	0	11	0	1	1
PM6	1.9	-1	-0.9	4	20	2	7.5	3	13	3.5	34.48	23.23	0.74	1.31	6.67	18	11.18	6.38	0.63	0	1	1	2	9.7	12.9	0	1	1
PM7	1.8	0	-0.1	0	5	3.5	4	2	5	3.7	45.49	32.73	0.79	1.46	51.69	16	4.16	14.65	1.03	0	0	1	3	13.2	13.8	0	1	1
PM8	1.8	0	0.5	4	30	2.5	4	3	4	3.5	34.84	17.07	0.87	1.17	21.05	19	4.16	12.08	0.33	0	0	2	5	10.3	16.7	0	1	1
PM9	1	-1	-0.3	0	20	1.5	5	4	5	3.4	37.12	21.54	1.17	0.68	0.00	18	30.42	3.75	0.00	0	2	0	1	0	0	0	1	1
PM10	1.8	0	0.4	0	40	3	9	7	9	3.4	38.09	33.17	0.79	1.26	13.58	18	6.24	7.45	0.38	0	3	1	2	12.6	12.6	0	1	1
PM11	1.3	0	-0.4	0	8	1.5	2.5	1	3	4	26.05	25.28	0.70	1.51	10.80	22	5.46	8.40	0.40	0	1	1	4	12.1	13.8	0	1	1
PM12	1	0	-0.5	5	8	1.5	4	1	7	3.6	35.66	29.45	0.67	1.54	10.72	15	7.28	6.53	0.45	0	1	2	3	13.1	13.1	0	1	1

Appendix 3 (continued).

Meso plot	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Mn1	1.1	0	0.6	1	25	3	6.5	3	8	3.5	28.49	25.34	0.86	1.71	12.13	20	0	9.98	0.48	1	3	4	6	11.6	11.6	1	1	0
Mn2	2.9	0	-0.2	0	40	2	3.5	3	5	3.5	41.5	26.49	0.85	1.51	12.24	18	5.2	9.28	1.00	0	3	3	5	11.5	11.5	1	1	0
Mn3	1.7	0	1	5	25	1.5	3.5	3	7	3.5	35.6	22.1	0.69	1.43	24.35	15	0	22.58	1.83	0	0	2	7	11.4	12.5	1	1	0
Mn4	1.2	0	0.5	0	8	2.5	3.5	2	4	3.9	33.15	29.72	0.54	1.64	24.93	16	2.86	10.38	0.43	0	1	3	6	11.8	11.9	1	1	0
Mn5	1.3	0	0.3	2	30	1	3.5	3	6	3.5	36.13	21.64	0.84	1.65	24.24	19	4.94	16.13	0.63	0	0	1	4	10.9	12.6	1	1	0
Mn6	4.4	2	7.3	0	60	3	4	3	5	3.4	23.61	21.17	0.89	1.57	23.79	18	1.04	12.45	0.88	1	1	1	3	10.3	12.6	1	1	0
Mn7	1.1	0	-0.1	0	4	2	3	3	6	3.7	32.03	18.88	0.79	1.46	15.59	29	0	15.00	0.65	0	1	4	8	11.4	11.4	1	1	0
Mn8	0.9	0	0.3	10	20	2	2.5	2	6	3.8	34.37	26.53	0.78	1.51	55.62	23	0	15.75	0.70	0	2	2	8	10.7	12.9	1	1	0
Mn9	1.8	-1	-3.2	0	30	1	4	3	5	3.7	32.04	27.56	0.82	1.38	17.06	15	4.94	11.40	0.98	0	1	3	4	11.1	11.1	1	1	0
Mn10	1.3	-1	-0.5	3	20	1.5	7	4	9	3.6	27.36	20.21	0.71	1.51	39.01	24	3.12	12.14	0.88	0	6	4	9	12.6	13.2	1	1	0
Mn11	1.7	1	2.8	0	10	2	3.5	3	5	3.8	33.16	23.34	0.73	1.46	15.50	22	0.52	10.55	1.15	0	1	2	3	10	12.5	1	1	0
Mn12	1.3	0	0.7	0	17	2	5.5	1	6	3.5	46.6	30.25	0.07	0.65	12.60	18	1.04	12.38	0.15	0	3	0	7	0	14.8	1	1	0
Pn1	2.7	1	2.8	5	20	2	5	5	7	3.6	28.5	14.72	0.07	1.41	15.76	20	0	15.23	1.38	0	1	4	9	13.2	13.2	1	0	1
Pn2	1.6	0	1.1	0	8	1	1.5	1	6	3.6	37.97	15.06	0.74	1.63	5.70	17	7.28	10.23	0.25	0	2	2	5	9.5	9.5	1	0	1
Pn3	1.4	0	0.6	0	5	2	6.5	3	10	3.4	36.67	17.55	0.87	1.39	16.07	22	3.64	10.75	0.23	0	2	2	8	11.9	11.9	1	0	1
Pn4	0.9	0	1.2	0	4	1	2	1	4	3.4	33.31	15.38	0.81	1.52	2.09	14	24.96	9.03	0.03	0	0	0	4	0	11.9	1	0	1
Pn5	2.2	-1	2.4	0	10	2	5.5	5	7	3.5	31.16	15.44	0.73	1.29	8.43	21	0.52	12.23	0.55	0	0	2	8	10.4	11.7	1	0	1
Pn6	1.3	0	-0.8	5	20	1	6	2	8	3.6	46.69	33.42	0.65	1.66	15.43	15	21.58	8.45	0.40	0	0	2	3	12.4	12.3	1	0	1
Pn7	1.3	-1	-0.8	0	15	2	6	6	11	3.6	30.95	17.34	0.81	1.43	18.93	16	1.04	12.19	1.03	0	0	1	4	12	12	1	0	1
Pn8	0.9	0	-0.5	2	18	1	4	1	5	3.6	31.52	18.82	0.85	1.56	21.43	16	15.6	14.63	0.13	0	1	0	4	0	12.7	1	0	1
Pn9	2.3	1	-0.4	0	40	2	6.5	4	9	3.4	35.26	29.04	0.80	1.29	20.15	25	3.12	10.45	1.05	1	2	3	10	11.5	11.7	1	0	1
Pn10	1.4	-1	-0.6	3	18	1	3	1	4	3.6	31.25	15.13	0.64	1.71	15.85	16	4.16	10.18	1.00	0	2	2	3	11.7	11.7	1	0	1
Pn11	4	2	4.6	0	40	1	5.5	3	6	3.9	31.75	18.49	0.80	1.20	7.13	19	5.98	13.50	0.30	1	2	3	5	10.8	11.4	1	0	1
Pn12	1.6	0	0.8	0	4	2.5	6	5	8	3.2	26.26	19.02	0.94	1.24	15.36	17	0.78	13.05	0.45	2	8	4	9	9.1	12.3	1	0	1

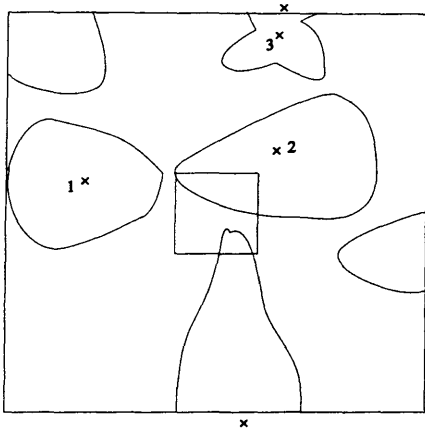
Appendix 3 (continued).

Meso plot	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
C1	1.7	0	0.2	0	20	1.5	4	2	5	3.7	24.34	13.59	0.83	1.68	1.93	20	10.92	6.28	0.13	0	3	1	1	9	9	0	0	0
C2	0.9	0	0.2	0	7	3.5	2	1	6	3.5	23.2	17.95	0.88	1.57	27.84	21	1.82	9.53	0.80	0	1	2	5	9.7	12.5	0	0	0
C3	1.4	0	-0.7	8	40	4.5	4.5	1	8	3.6	33.76	30.18	0.66	1.39	17.56	23	1.56	10.33	0.25	0	2	6	7	14.3	14.3	0	0	0
C4	1	0	0.2	0	5	1	4	3	6	3.6	29.2	27.37	0.65	1.64	11.85	24	7.28	7.35	0.65	0	0	1	2	10.8	14.1	0	0	0
C5	1.8	0	-1.6	2	20	0.5	2	1	3	3.6	27.53	16.88	0.67	1.86	0.00	21	20.8	8.98	0.00	0	2	0	5	0	11.5	0	0	0
C6	1.1	0	-0.2	10	25	2.5	2.5	0	10	3.8	24.55	21.41	0.82	1.16	4.91	24	4.42	13.18	0.20	0	3	2	8	9.2	13	0	0	0
C7	1	0	0	0	10	0	7	4	8	3.4	20.68	18.05	0.74	1.10	27.66	30	0.78	13.10	0.78	0	1	2	6	13.2	13.2	0	0	0
C8	2.7	2	4.1	0	45	1.5	3	1	6	3.8	21.73	15.56	0.84	1.52	15.63	22	4.94	12.23	0.30	1	2	0	7	12.5	13.8	0	0	0
C9	2	1	0.6	12	40	1	5	2	5	3.6	20.46	15.91	0.78	1.49	7.22	21	3.12	11.88	0.65	0	2	2	5	9.9	12.6	0	0	0
C10	1	1	0.9	0	12	3	5	1	7	3.8	30.34	32.27	0.72	1.48	4.64	19	5.46	10.65	0.15	0	1	1	4	11.6	12.7	0	0	0
C11	1.3	0	-1.1	3	10	1	4	1	5	3.5	26.89	21.27	1.03	1.13	8.42	28	7.28	6.62	0.30	0	1	2	5	9.9	11.9	0	0	0
C12	3.5	1	1.6	12	22	1.5	7.5	7	10	3.8	22.49	22.03	0.92	1.33	0.00	12	9.88	6.88	0.00	2	5	1	3	9.9	9.9	0	0	0
N1	2.9	-1	-2.3	8	50	5	5.5	3	13	3.9	33.92	26.16	0.76	1.36	21.86	33	0.52	17.10	1.08	0	1	3	7	16.1	16.2	2	0	0
N2	1.3	0	-1.2	8	30	5.5	6	2	7	4.2	37.08	30.91	0.87	1.58	23.13	20	4.68	8.73	1.00	0	0	2	3	13.3	13.3	2	0	0
N3	2.9	0	3.1	4	16	4	3.5	3	5	4	39.74	25.77	0.56	1.52	18.90	26	4.94	9.45	0.90	1	1	2	3	11.5	13.6	2	0	0
N4	1.2	0	0.2	0	22	3.5	2.5	2	6	4.2	40.34	23.45	0.63	1.34	25.38	32	0.78	11.58	0.50	0	0	1	4	15.5	15.5	2	0	0
N5	0.9	0	0.8	0	10	2	1.5	1	3	4.2	38.49	22.49	0.42	1.95	50.34	33	2.86	14.75	0.53	0	0	0	7	0	14.1	2	0	0
N6	1	0	-1	0	10	3.5	3.5	3	4	3.8	35.39	18.42	0.58	1.61	9.45	28	9.36	5.43	0.08	0	2	2	4	12	13.3	2	0	0
N7	2.7	2	-0.8	0	25	6	8	4	11	4.1	41.22	35.43	0.94	1.35	37.77	18	0.26	14.35	1.05	1	4	4	10	14	15.1	2	0	0
N8	3.8	1	3	20	50	3.5	4	1	15	3.8	38.31	30.9	0.71	1.66	31.76	26	2.08	11.60	0.60	1	2	1	4	14.6	16.3	2	0	0
N9	1.2	-1	0.5	2	20	2.5	5.5	4	7	4.2	38.43	33.21	0.66	1.59	15.81	23	0.52	11.75	0.58	0	3	3	6	14.4	14.4	2	0	0
N10	1.2	0	1.3	2	16	4	6	5	9	3.7	36.47	29.88	0.82	1.28	26.75	24	0.52	13.48	0.65	0	1	3	9	14.5	14.5	2	0	0
N11	2	1	-1.5	0	40	6.5	3	3	5	4	34	24.23	0.76	1.58	22.43	22	10.92	5.95	0.38	1	4	0	1	0	13.8	2	0	0
N12	1.1	0	-0.4	3	8	3	5.5	5	6	4.1	32.7	28.2	0.42	1.56	39.36	25	0.78	10.80	0.80	0	1	1	2	16.4	16.4	2	0	0

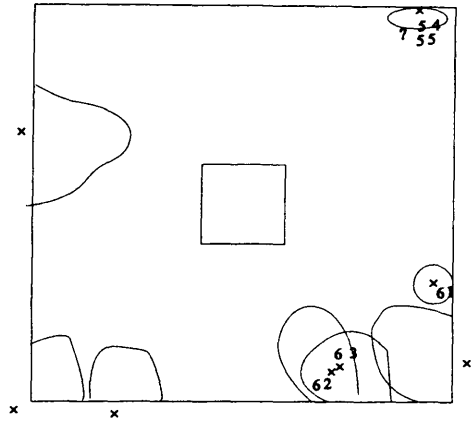
Appendix 4. Sketch maps of 25 m² (5x5 m) plots, each with one of the 144 meso plots in the centre. Centre of tree stems indicated by x; crown perimeters indicated by continuous lines. Trees are numbered in accordance with Nilsen & Abrahamsen (1995).

x

MN1

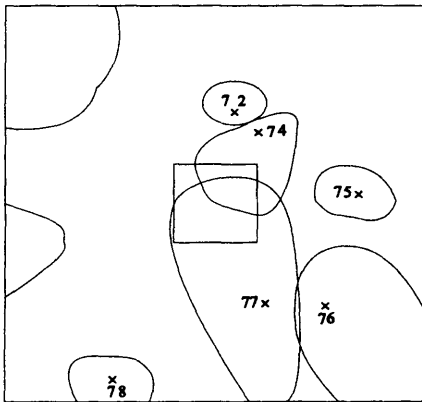


MN2

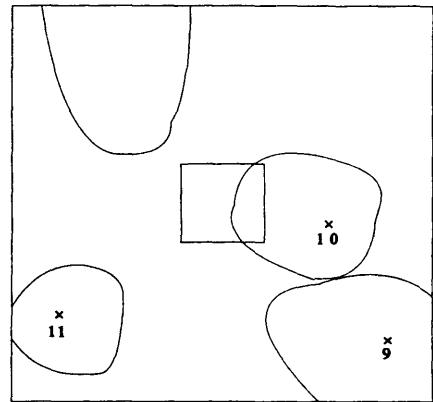


x

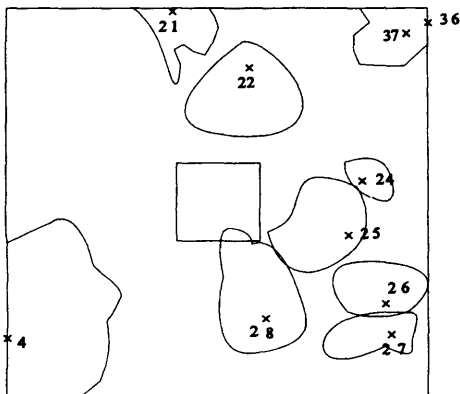
MN3



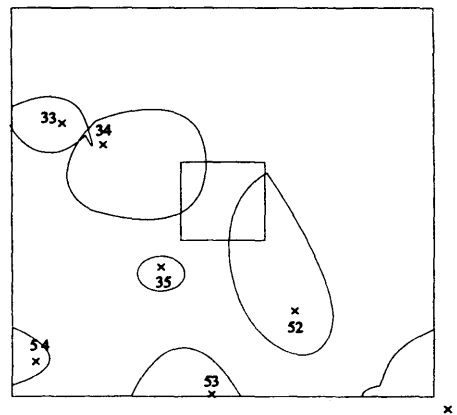
MN4*



MN5

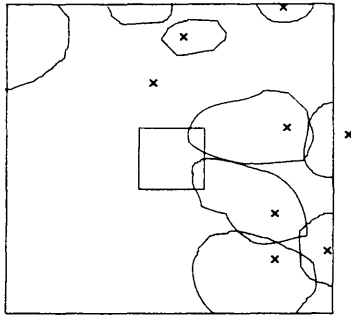


MN6

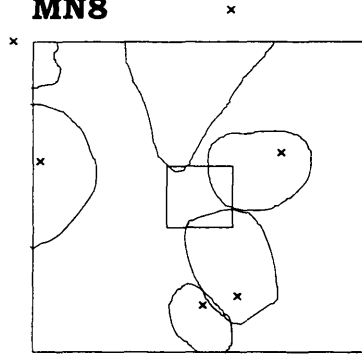


Appendix 4 (continued).

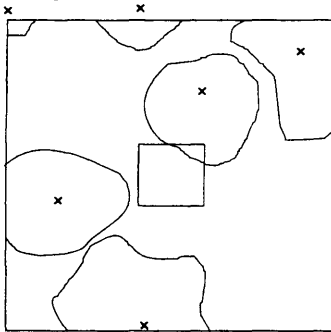
MN7



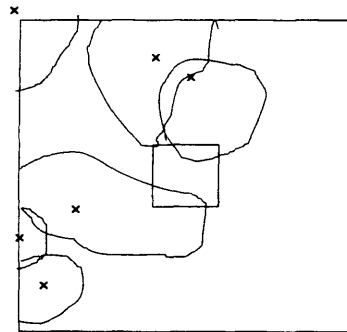
MN8



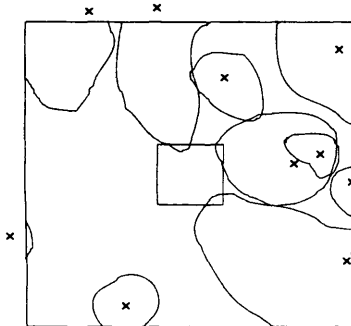
MN9



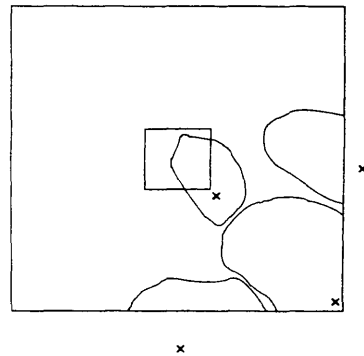
MN10



MN11

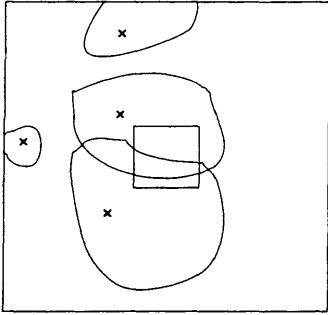


MN12

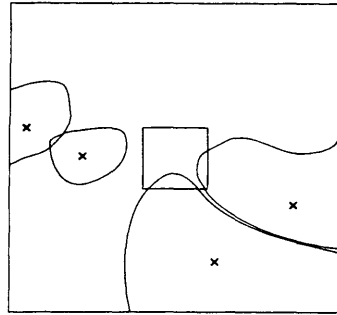


Appendix 4 (continued).

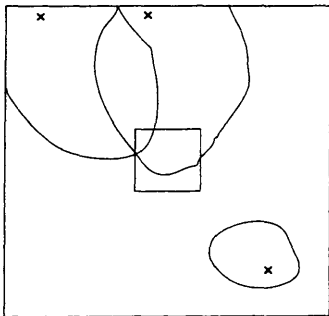
M1



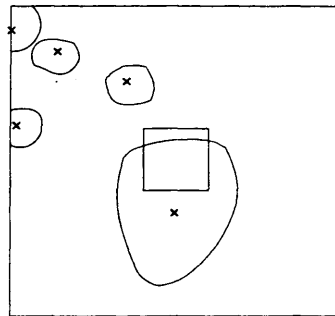
M2



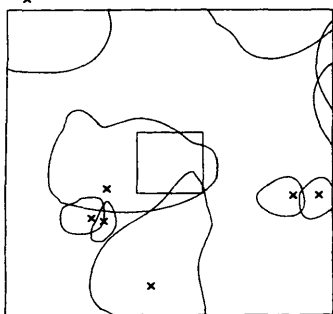
M3



M4



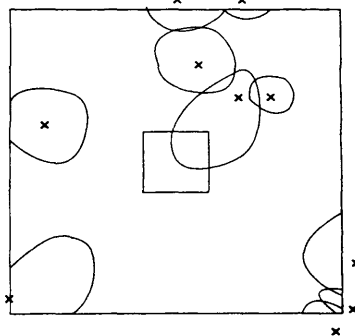
M5



x
↓

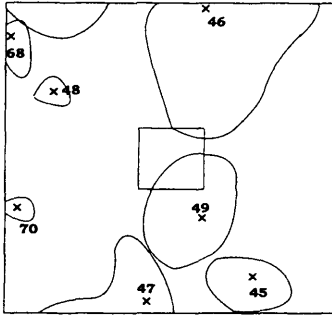
← x
← x

M6

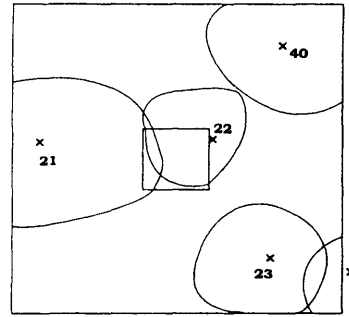


Appendix 4 (continued).

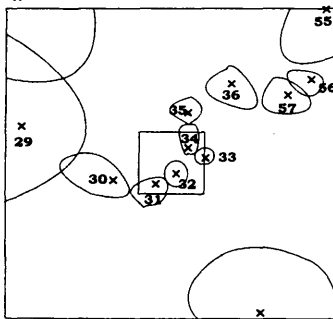
M7



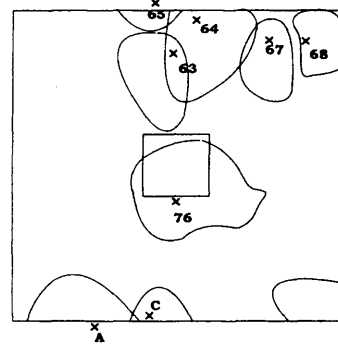
M8



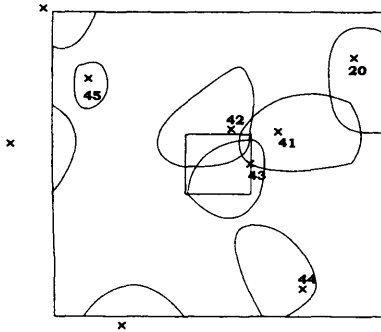
M9



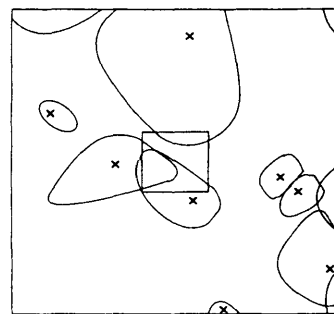
M10



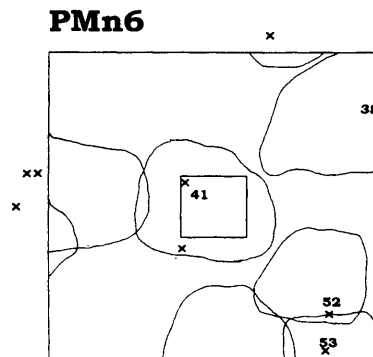
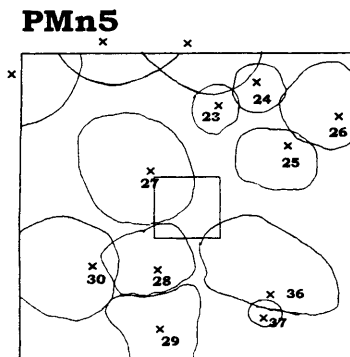
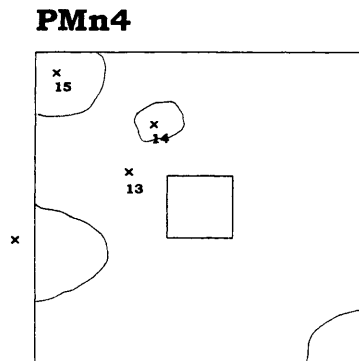
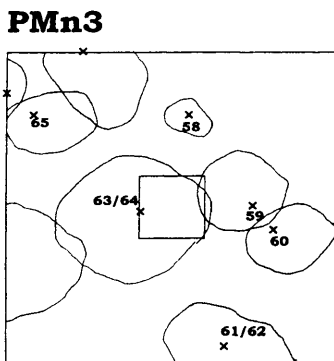
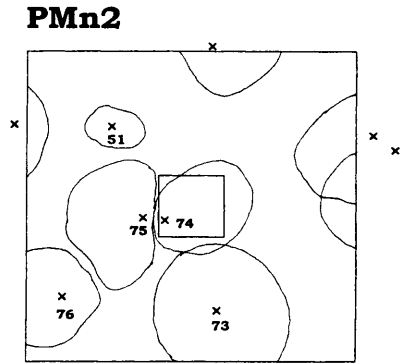
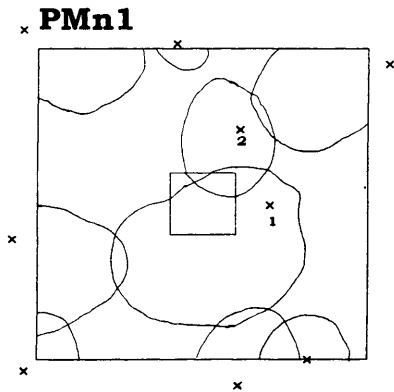
M11



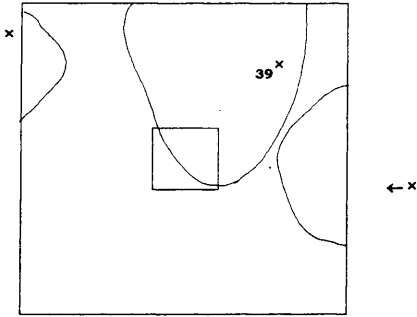
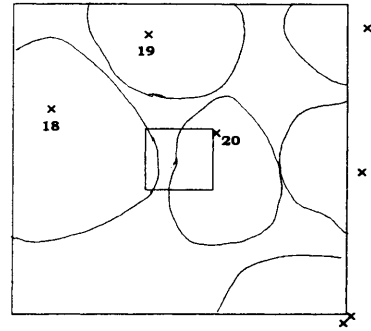
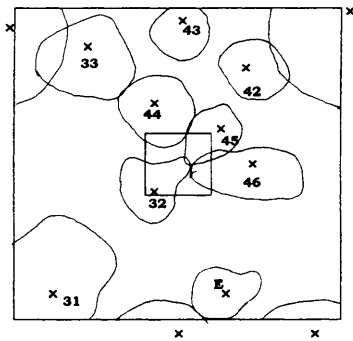
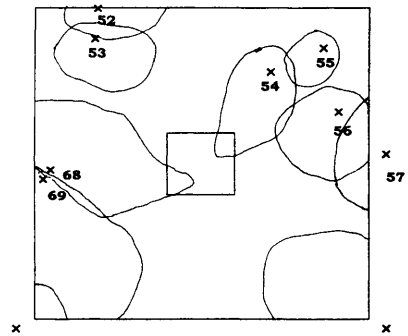
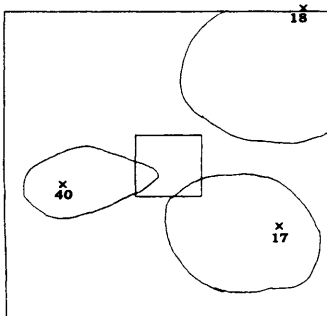
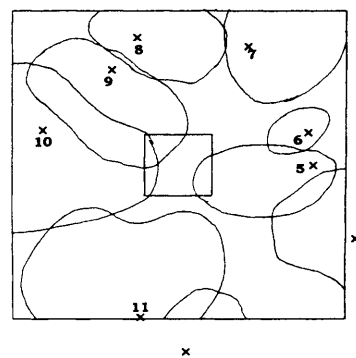
M12



Appendix 4 (continued).

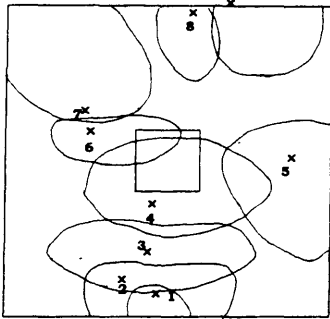


Appendix 4 (continued).

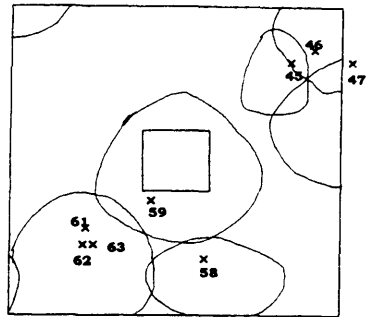
PMn7**PMn8****PMn9****PMn10****PMn11****PMn12**

Appendix 4 (continued).

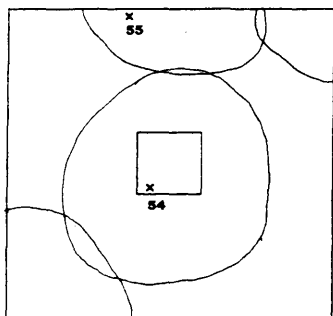
PMN1



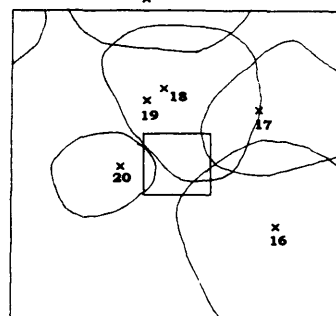
x
PMN2



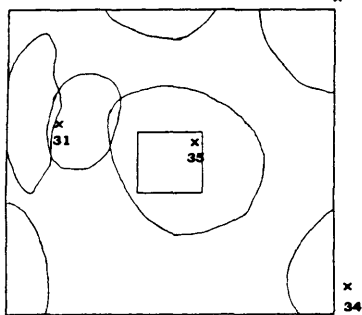
PMN3



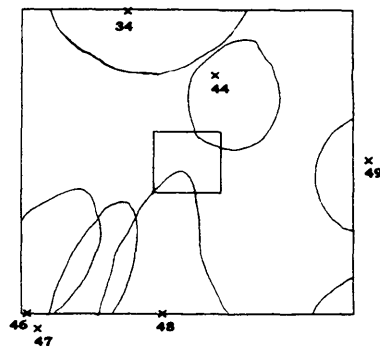
x
PMN4



PMN5

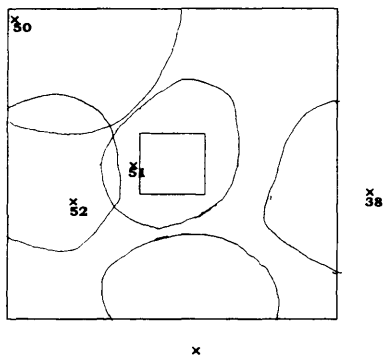
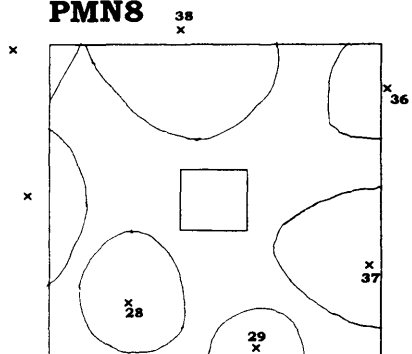
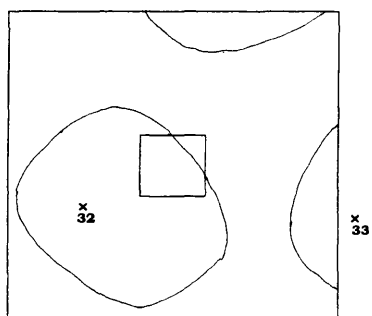
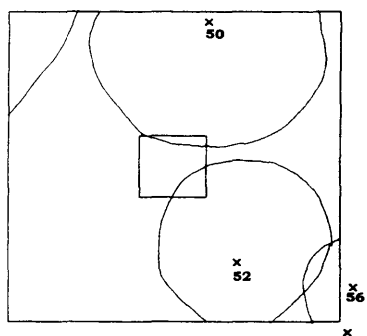
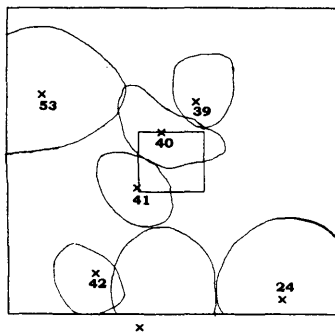
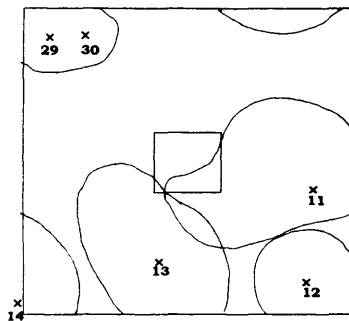


PMN6



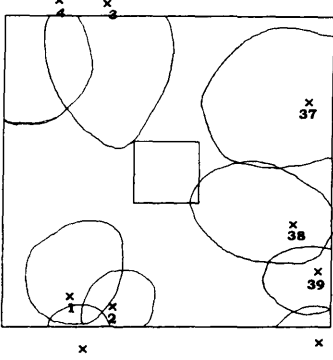
x
9

Appendix 4 (continued).

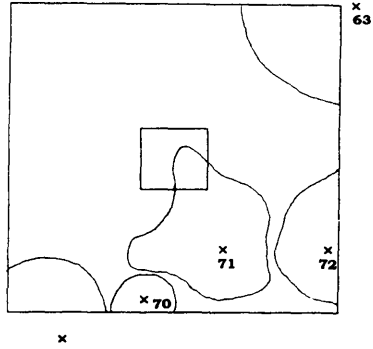
PMN7**PMN8****PMN9****PMN10****PMN11****PMN12**

Appendix 4 (continued).

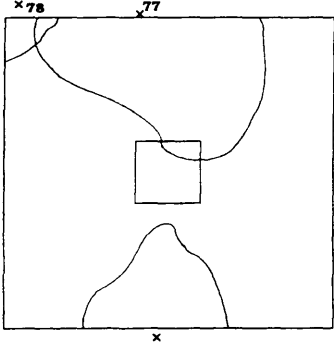
n1



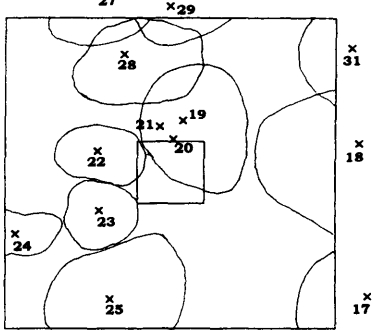
n2



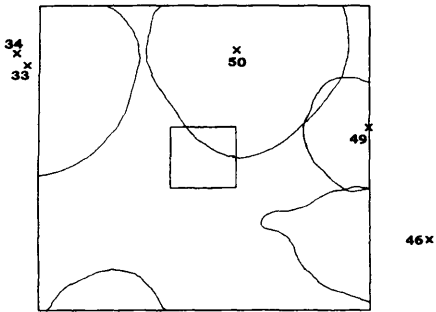
n3



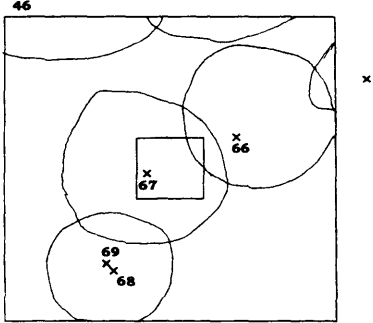
n4



n5

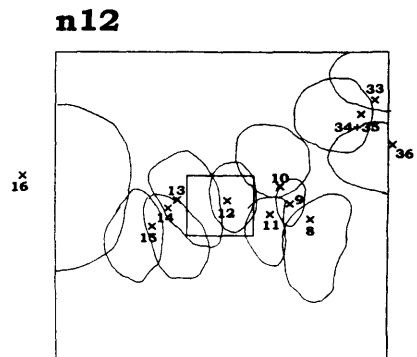
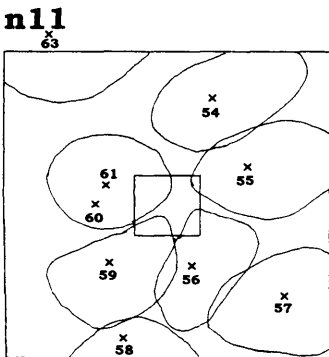
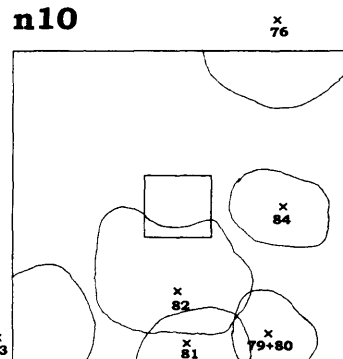
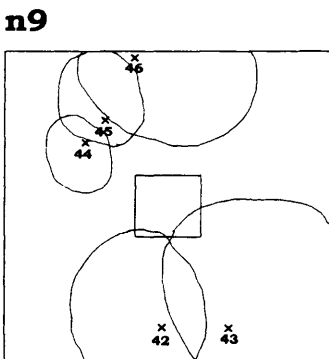
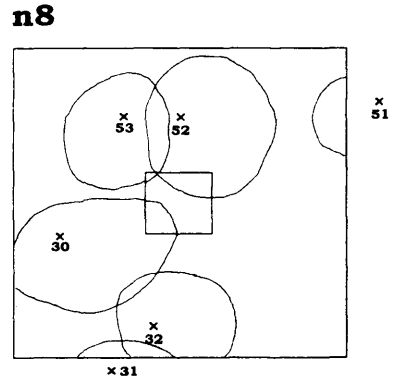
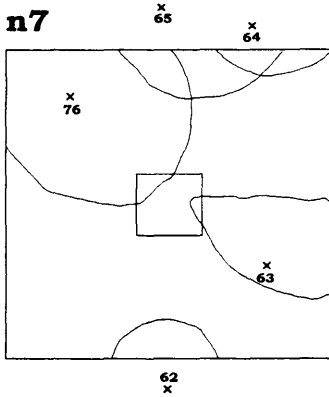


n6



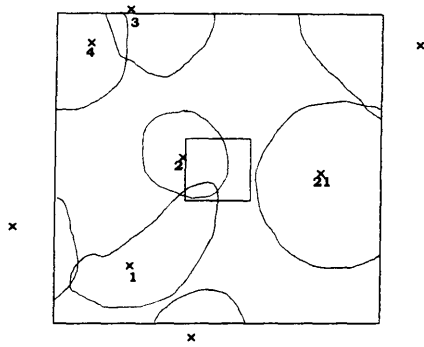
37
x

Appendix 4 (continued).

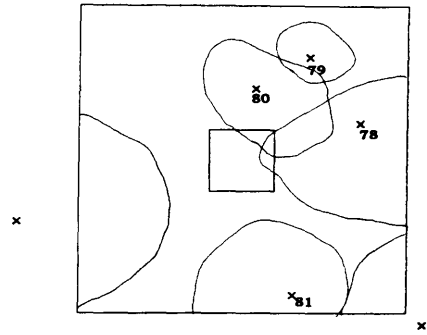


Appendix 4 (continued).

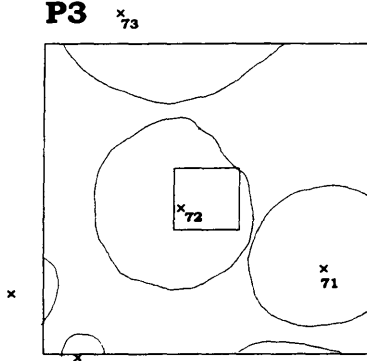
P1



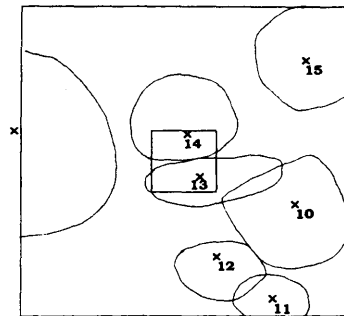
P2



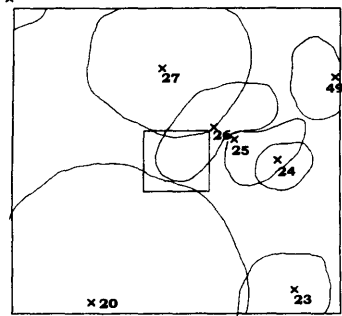
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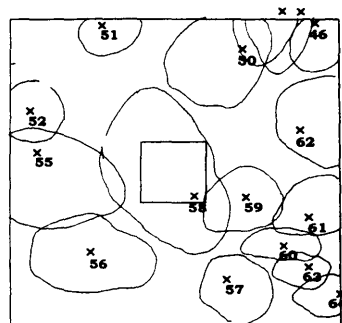
P4



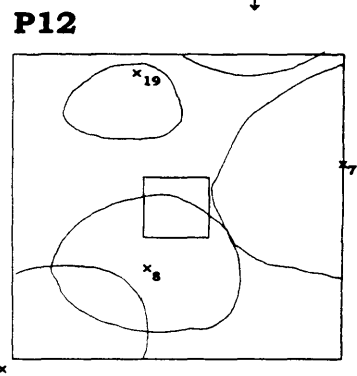
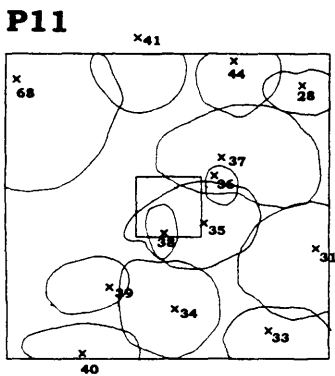
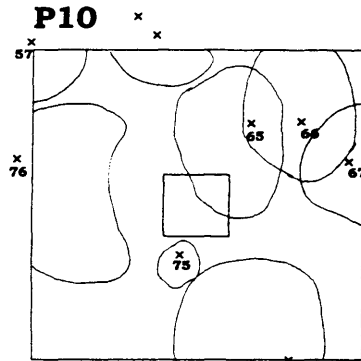
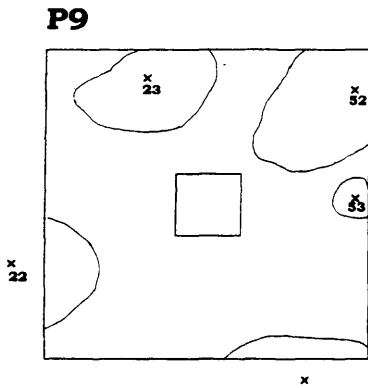
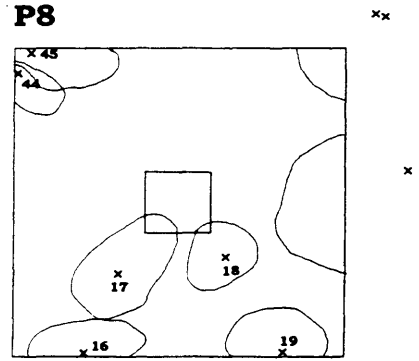
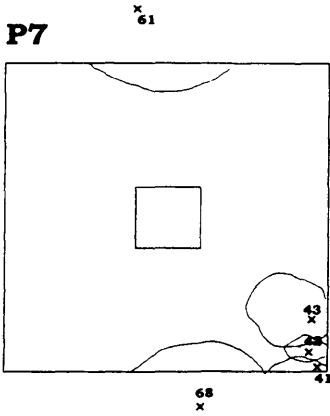
P5



P6

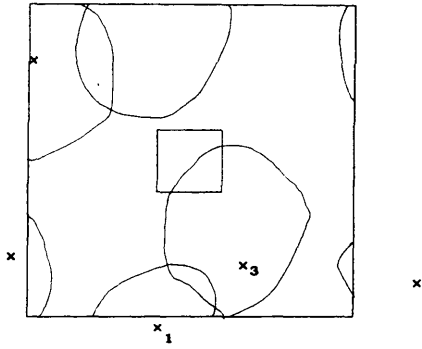


Appendix 4 (continued).

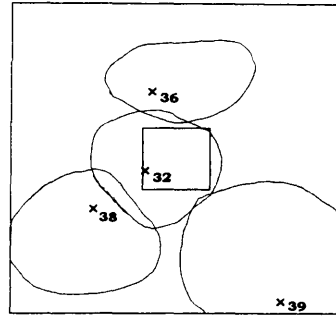


Appendix 4 (continued).

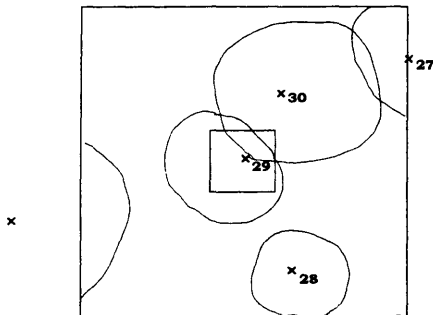
PN1^{x₅}



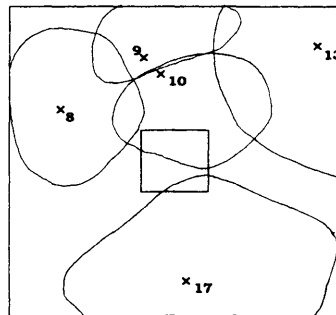
PN2



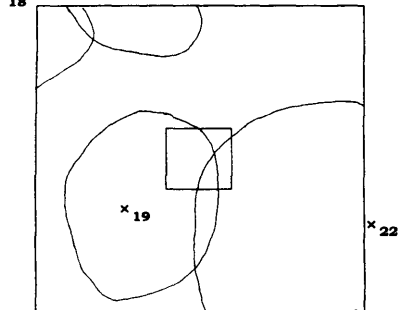
PN3



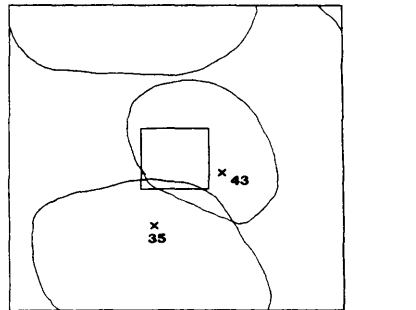
PN4



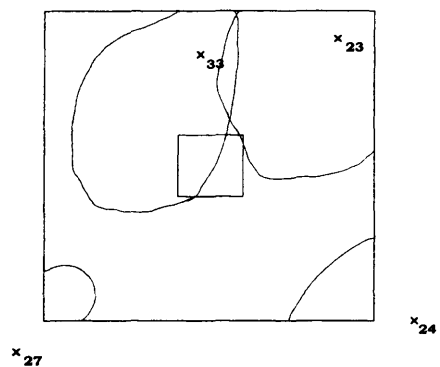
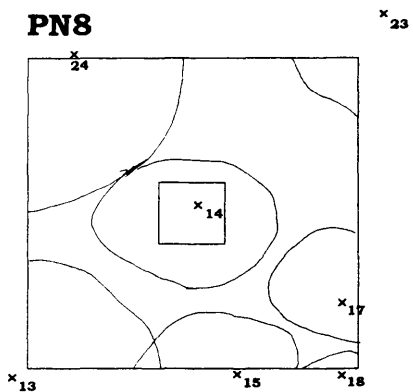
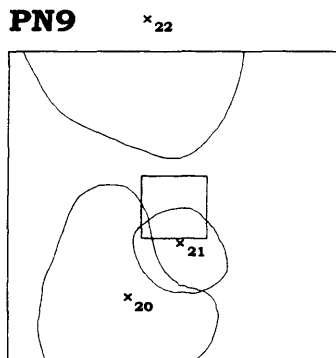
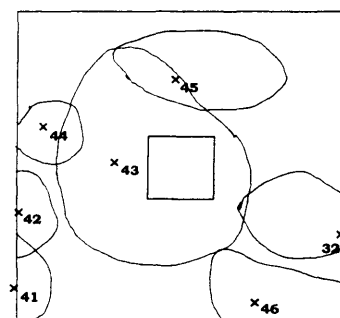
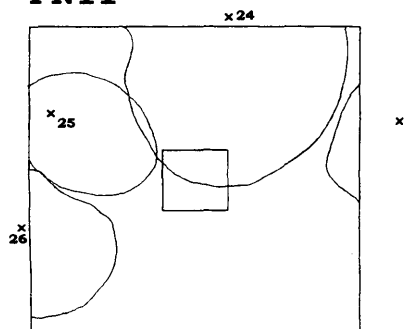
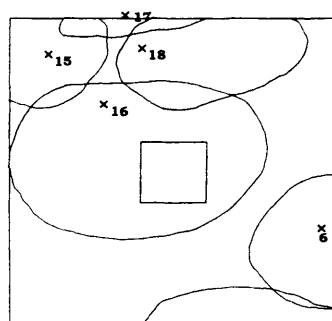
PN5^{x₁₇}



PN6



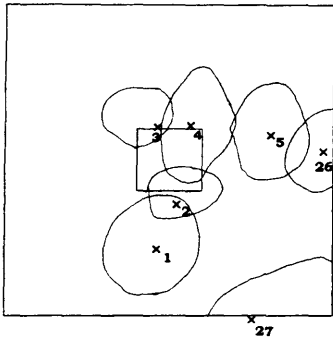
Appendix 4 (continued).

PN7**PN8****PN9****PN10****PN11****PN12**

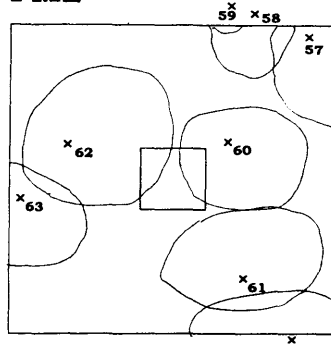
x

Appendix 4 (continued).

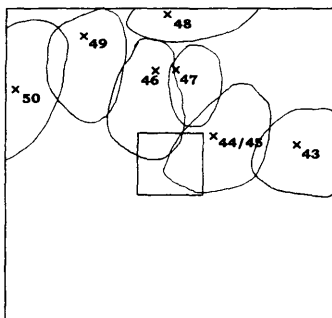
PM1



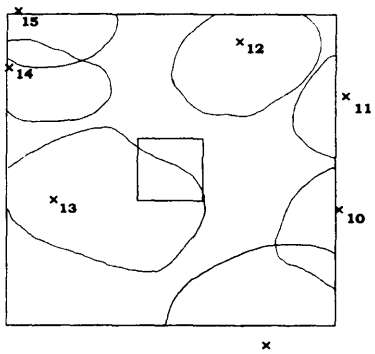
PM2



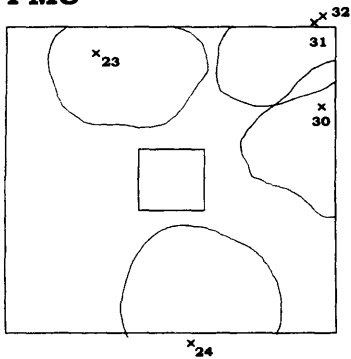
PM3



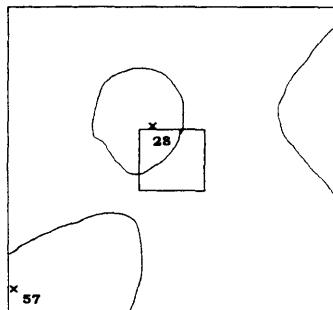
PM4



PM5

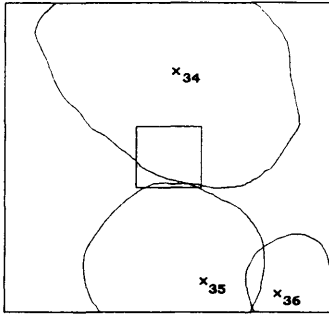
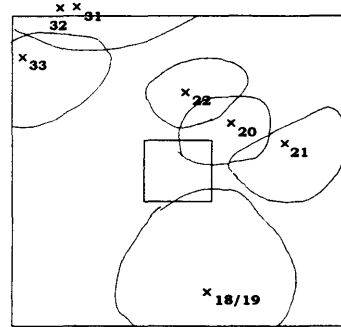
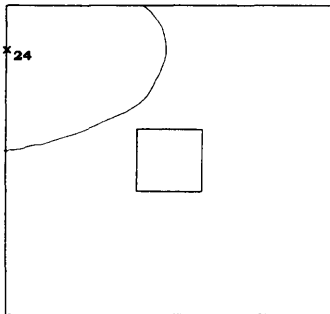
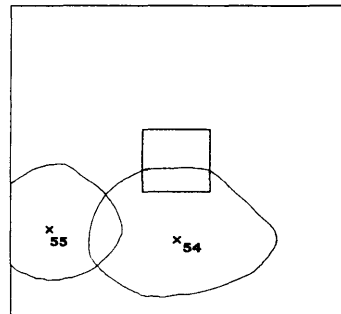
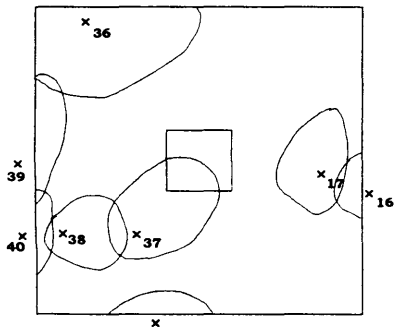
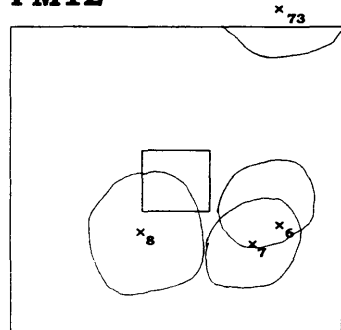


PM6

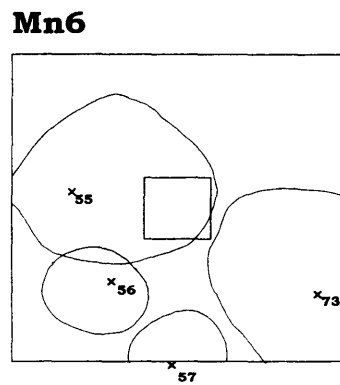
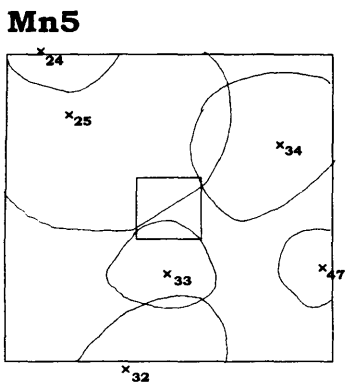
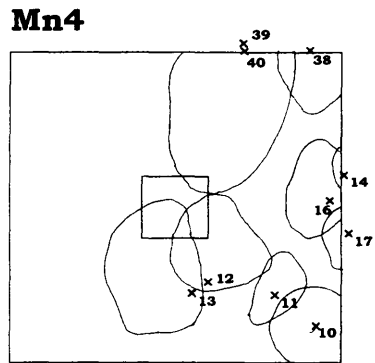
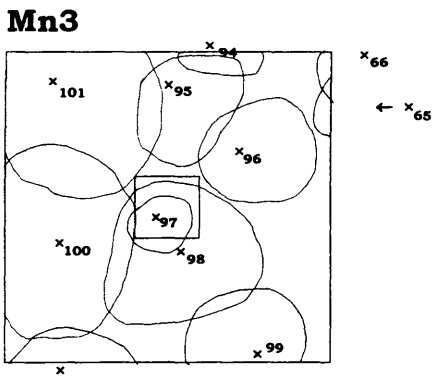
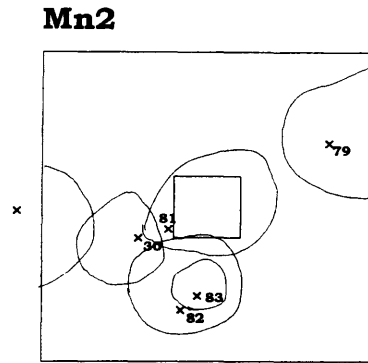
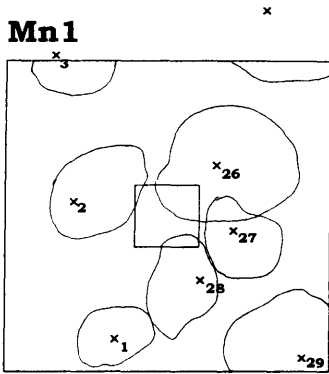


x 31

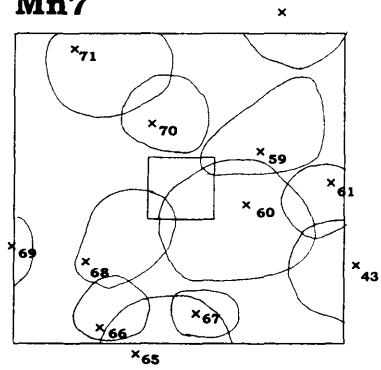
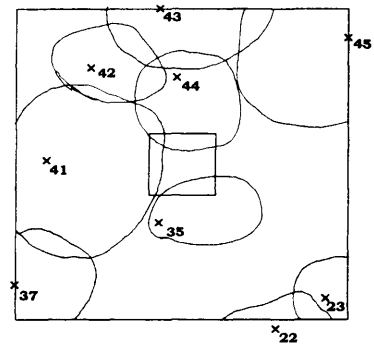
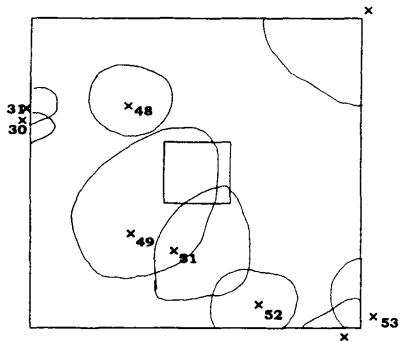
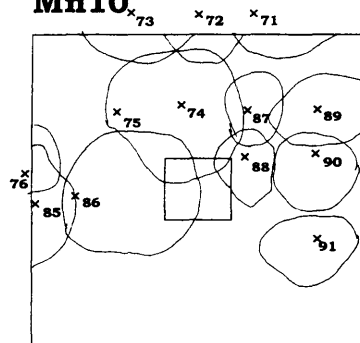
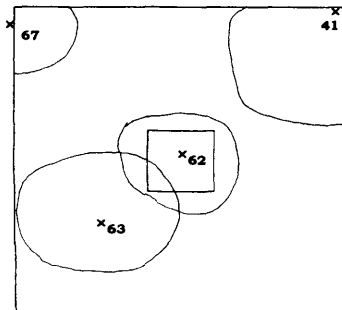
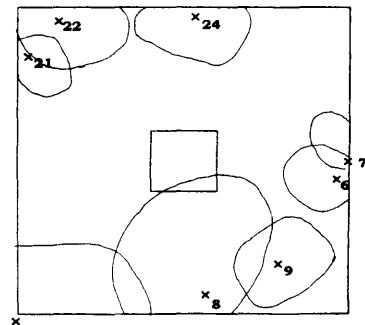
Appendix 4 (continued).

PM7**PM8****PM9****PM10****PM11****PM12**

Appendix 4 (continued).

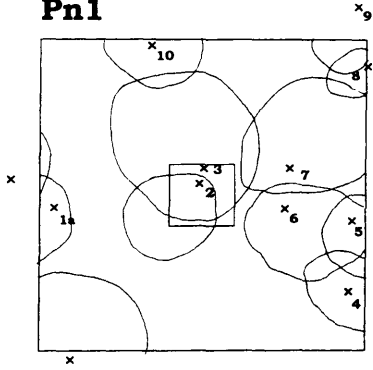


Appendix 4 (continued).

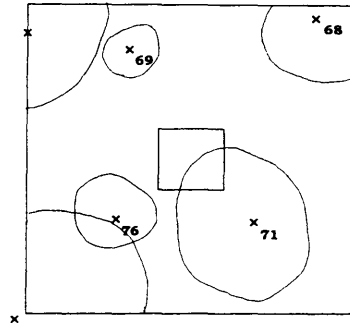
Mn7**Mn8****Mn9****Mn10****Mn11****Mn12**

Appendix 4 (continued).

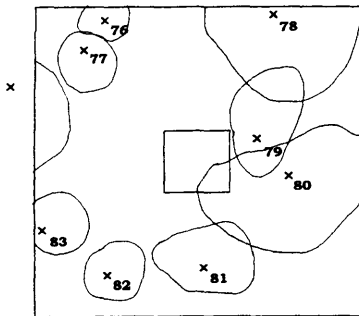
Pn1



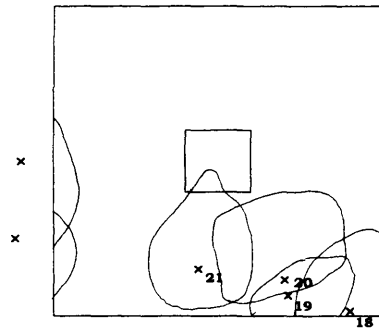
Pn2



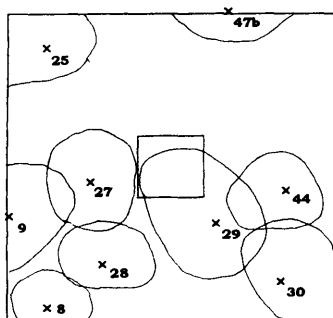
Pn3



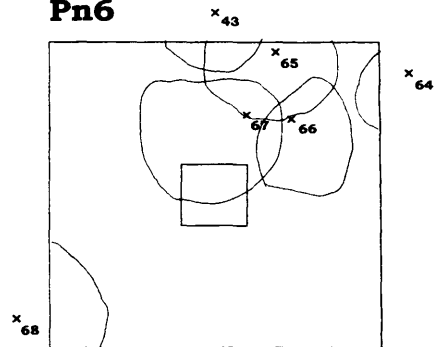
Pn4



Pn5

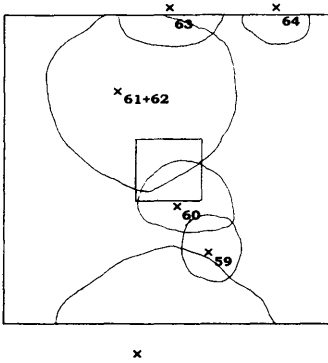


Pn6

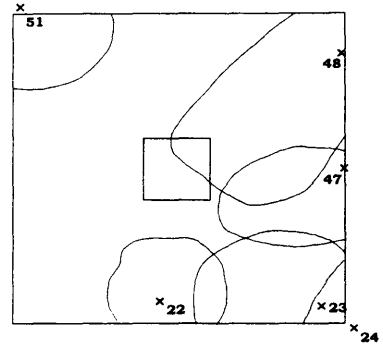


Appendix 4 (continued).

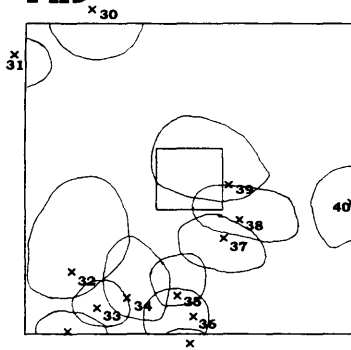
Pn7



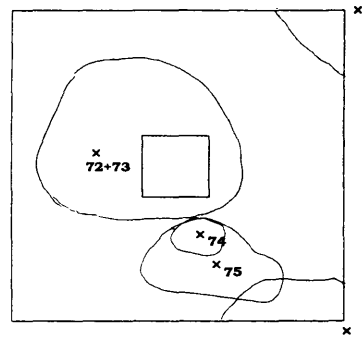
Pn8



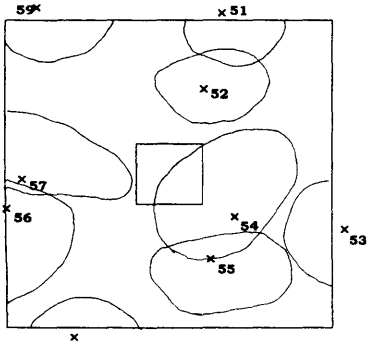
Pn9



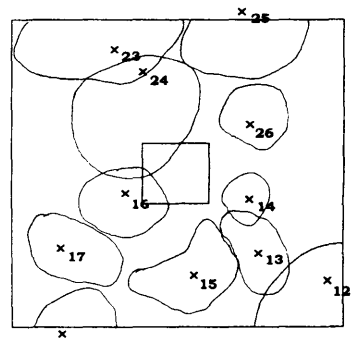
Pn10



Pn11

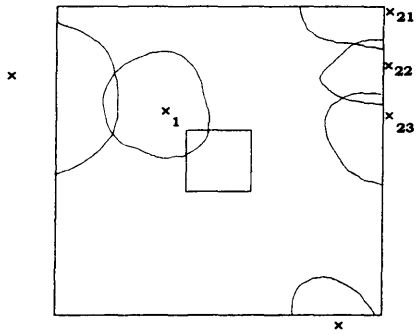


Pn12

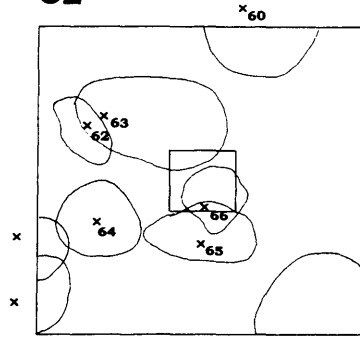


Appendix 4 (continued).

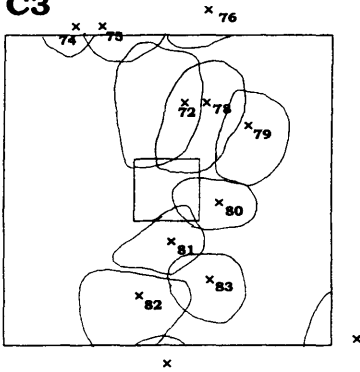
C1



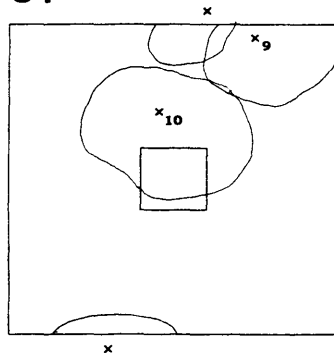
C2



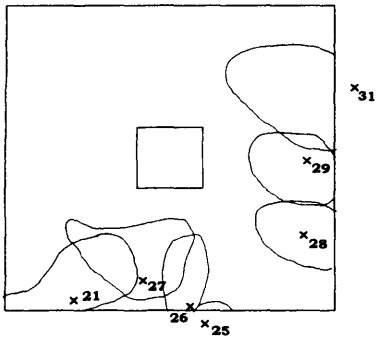
C3



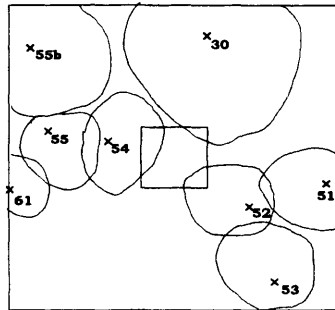
C4



C5

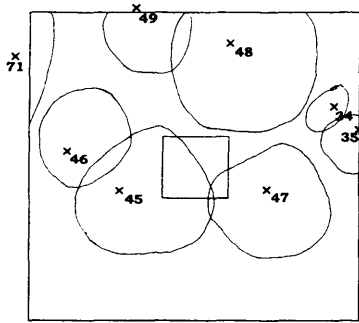


C6

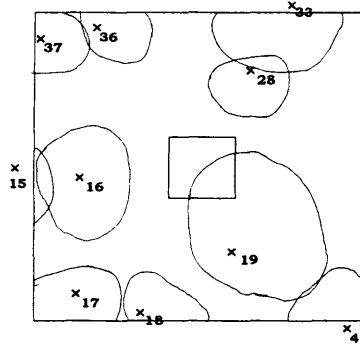


Appendix 4 (continued).

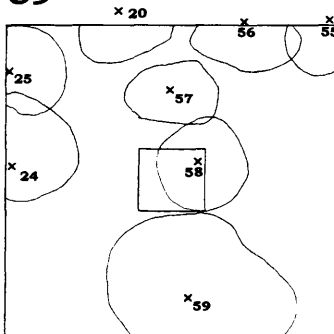
C7



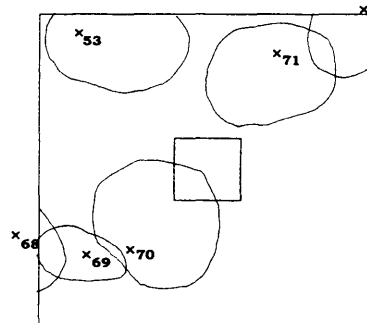
C8



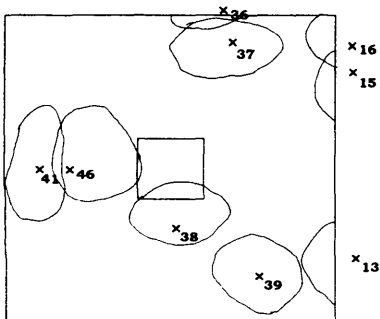
C9



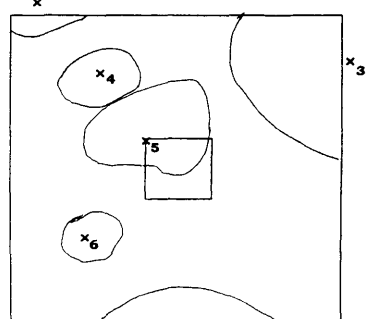
C10



C11

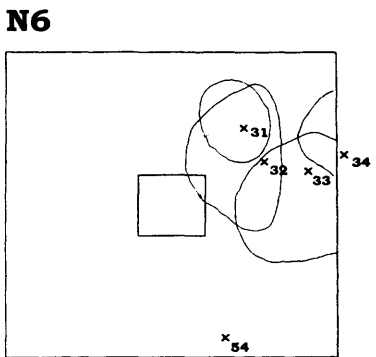
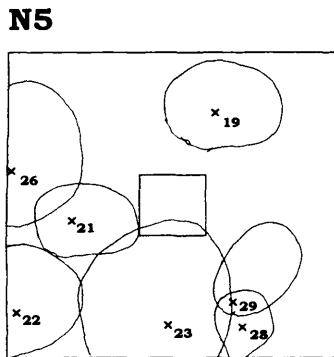
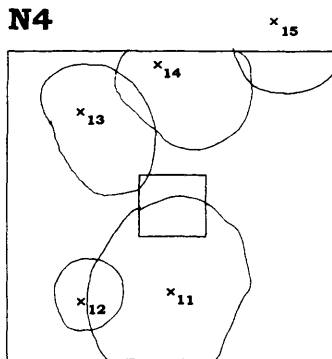
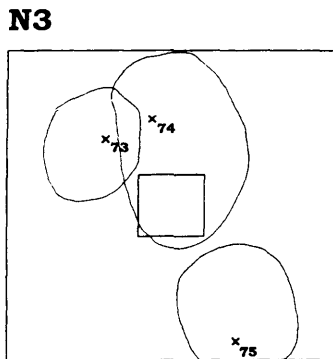
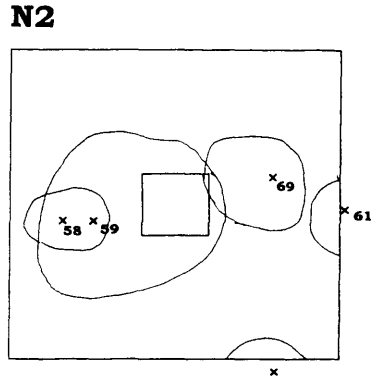
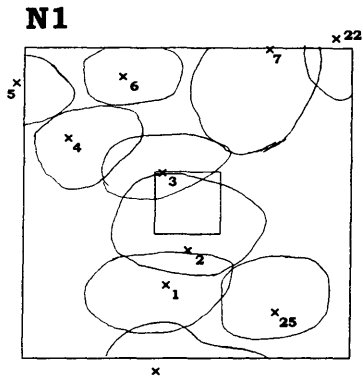


C12



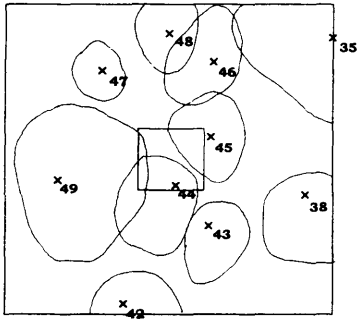
x

Appendix 4 (continued).

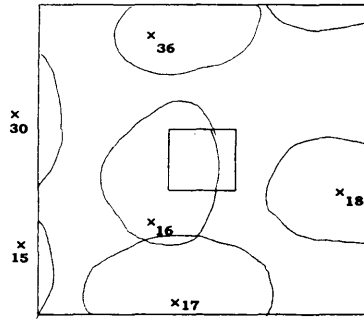


Appendix 4 (continued).

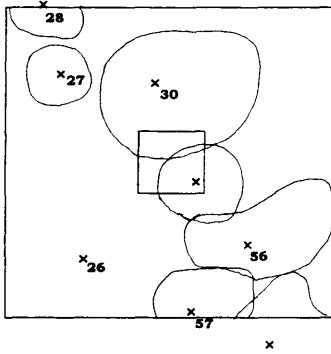
N7



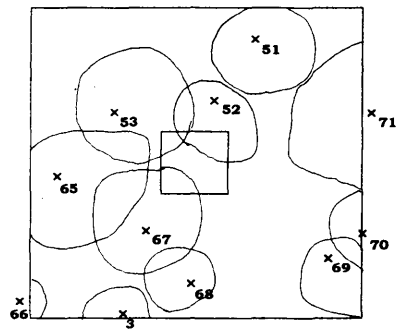
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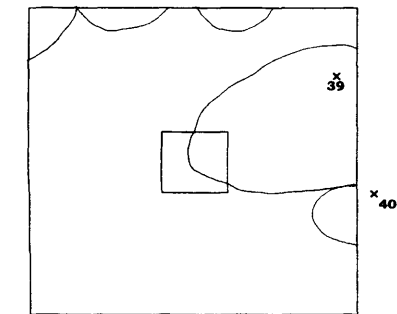
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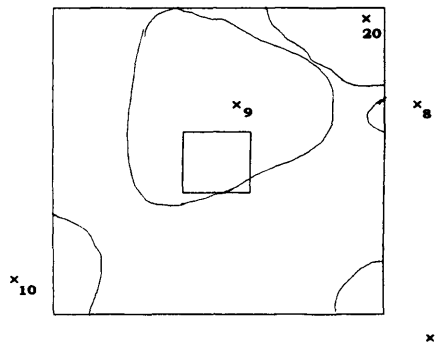
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N11



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