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HETEROGENEITY OF SPECIES COMPOSITION OF FOREST FLOOR VEGETATION ALONG ENVIRONMENTAL GRADIENT

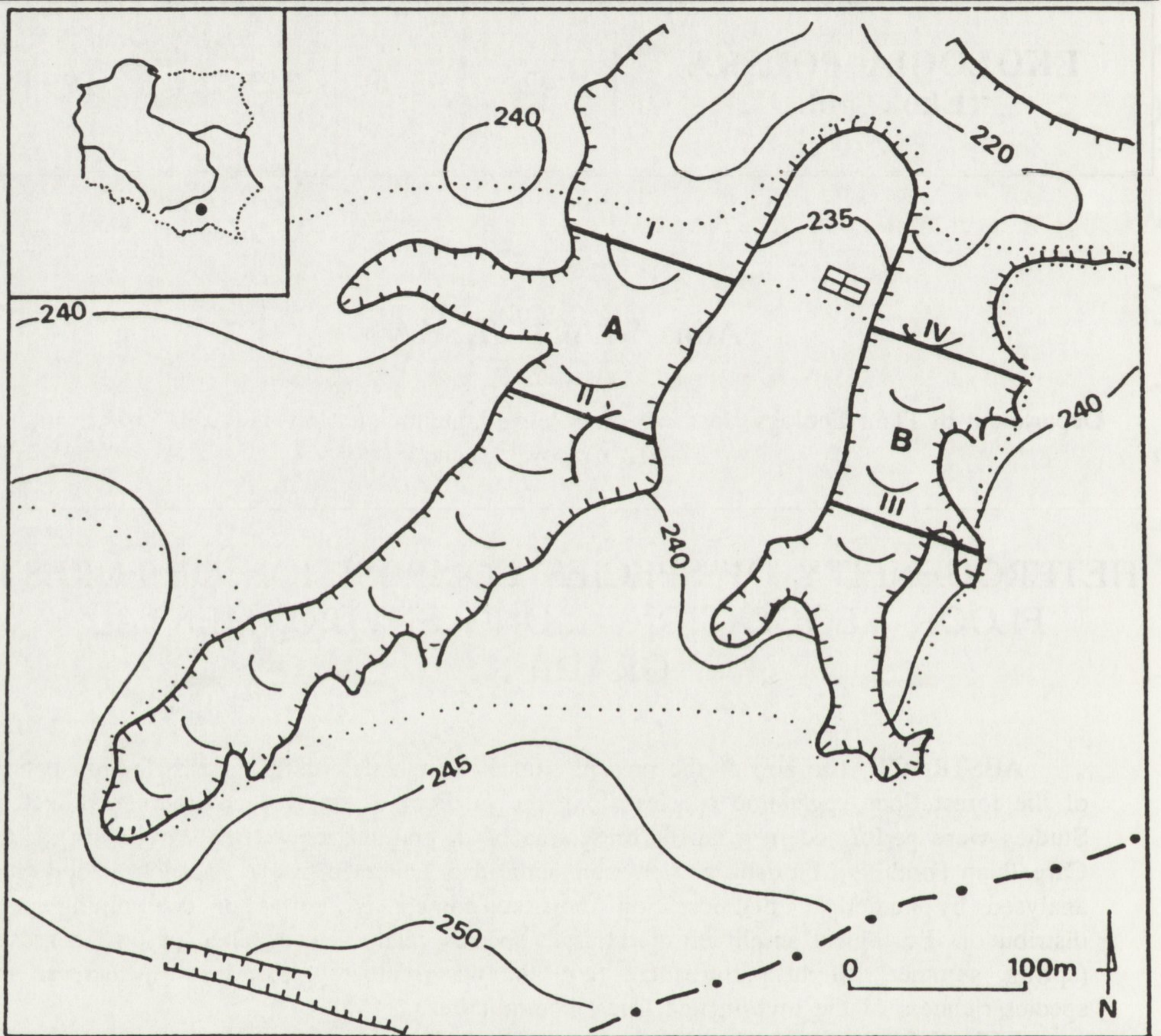
ABSTRACT: The aim of the present studies was to determine the distribution pattern of the forest floor vegetation species along the gradient of selected environmental factors. Studies were performed in a small forest area of diversified relief (Brzesko Headland, the Carpathian Foothills). Floristic and environmental data collected by the transect method were analysed by numerical methods. Soil moisture content is the factor determining plant distribution. Ecological amplitude of different species changes in dependence on the season (spring, summer). Slight perturbances (e.g. the occurrence of fox burrows) increase the species richness of the investigated forest communities.

KEY WORDS: ecological amplitude, ecological optimum, key factor, environmental gradient, forest floor vegetation, transect method, DCA, CCA, Wieliczka Foothills.

1. INTRODUCTION

Random distribution of individuals in communities is extremely infrequent in nature. It is assumed that this phenomenon occurs when there is no factor ordering the spatial structure of the population of a given species (MacArthur and Connell 1971, MacArthur and Kershaw 1978, Greig-Smith 1979). In the plant kingdom the mosaic structure of species distribution may be due to many ecological factors that include abiotic factors (e.g. terrain relief, edaphic factors, light intensity) and biotic ones resulting from inter- or intraspecific interactions (Rabotnov 1985). Frequently it is very difficult to reveal the causes of spatial distribution of species. With reduction of the scale of the investigated problem, the number of difficulties in identification of the environmental differences increases.

Ecological studies of plants, aimed at elucidation of the spatial pattern of heterogeneity of species distribution, follow two directions. Namely, there are autecological studies initiated in Poland by K. Zarzycki (1976). They afford



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Fig. 1. Distribution of transects, as confronted with the morphology of the "Ligeżianka" forest (Tarnów voivodeship, near the town of Bochnia)

1 - NW boundary of the Stara Rzeka drainage basin, 2 - forest edge, 3 - ravines, 4 - transects, 5 - indentations of the terrain

ecodiagrams that illustrate the habitat requirements of different species (Borysiak 1984, Czarnicka 1986, Szwed 1986, Węglarski 1991). Moreover, there are studies dealing with correlations between species distribution and environmental variables, with the aim of revealing the parameter ordering plant distribution (review of papers in: Mueller-Dombois and Ellenberg 1974, Kershaw 1978, Greig-Smith 1979, Olsvig-Whittaker 1988; papers by Franklin and Merlin 1992, Leduc et al. 1992).

The objective of the present studies was to detect the heterogeneity of the species composition of forest floor vegetation along the gradient of selected environmental factors. Attention was given to the optima and amplitudes of plant occur-

rence. Furthermore, it was attempted to establish the key factor influencing species distribution. In the first place attention was directed to edaphic factors decisive (particularly on a micro scale) of spatial distribution of vegetation (Daubenmire 1973, Czarnicka 1986, Tilman 1986). The effect of climatic factors, that on the microscale is relatively slight, was left out of account.

2. PHYSIOGRAPHIC CHARACTERIZATION OF THE TERRAIN OF STUDIES

Studies were performed in the "Ligęzianka" forest in the Tarnów voivodeship, in the Łazy village situated ca. 5 km eastward of the town of Bochnia (South Poland) (Fig. 1). The terrain of studies is located south-eastward of the Stara Rzeka drainage basin that is the object of complex investigations performed by the Institute of Geography, Jagiellonian University in Cracow. The terrain of studies is characterized by extremely diversified relief related to the geological structure of the substrate. This terrain is situated on the lower level at the Carpathian Foothills edge which superposes the overlap range of the Subsilesian unit covered with Miocene formations and a thick layer of loess-like formations (Święchowicz 1991). Processes of erosion have greatly influenced the present form of the "Ligęzianka" forest which, despite its small area (ca. 10 ha), is intersected by ravines at the mature stage, that pass into gullies with a S-NE, S-NW course. The difference in elevation between the lowest and highest situated point of the investigated terrain is 25 m (220–245 m a.s.l.). The slope of the hill-sides fluctuates between 10–40° (Fig. 1). The geomorphological conditions promote periodic flow of water to the bottom of ravines and its stagnation in the lower parts.

Soil cover consists of two units: 1) lesivated soils (Haplic Luvisols) and 2) pseudogley soils (Stagnic Luvisols). Profile differentiation is typical of soils subjected to lessivage processes (Skiba 1992).

The area of the Carpathian Foothills is classed into the moderately warm climatic floor, with mean annual temperature of 6–8° (Obrebska-Starkłowa and Leśniak 1988). Because of the presence of the Carpathian Foothills edge, the isolines of many climatic factors run across the Brzesko Headland. Detailed data are available in the Atlas of the Tarnów voivodeship (1988) and Archives of the Research Station in Łazy, Institute of Geography, Jagiellonian University.

In the geobotanical division of Poland, the Brzesko Headland makes part of the Loess Foothills subregion (district: Beskidy Mts., division: West Carpathians) (Szafer and Zarzycki 1972).

In the "Ligęzianka" forest the following phytosociological units were singled out: Circaeo-Alnetum, Tilio-Carpinetum stachyetosum, T-C. typicum form with *Galeobdolon luteum*, T-C. form with *Rubus hirtus*, T-C. form with *Poa nemoralis*, T-C. caricetosum pilosae (Stachurska 1995).

3. METHODS OF STUDIES

The applied method involved nonrandom systematic collection of data at constant intervals along transects (Zarzycki 1976, Kershaw 1978, Silander and Antonovics 1982, Borysiak 1984, Olsvig-Whittaker 1988, Begon and Mortimer 1989, Węglarski 1991).

Transects running perpendicularly through the ravines A and B (2 transects per ravine) were demarcated. Along the transects 42 plots (1 m² each) were delimited either every 10 m or 5 m (at the bottom of ravines) (Fig. 1).

In May, July and September 1991, at each plot determination was made of:

- elevation a.s.l., slope and exposure;
- frequency of each species per 100 meshes of measurement grid;
- current moisture content and pH of soil;
- relative light intensity (10 16 type luxometer).

In July 1991, soil samples derived from the fermentative sublevel A₀F were taken for laboratory analysis. They were tested for active and exchangeable acidity. Additional analyses were performed for the 3rd transect (plots 21–29) and for selected plots located in the other transects. Hydrolytic acidity, sum of exchangeable bases, current sorption capacity, degree of saturation with basic cations, percentage of total nitrogen, C/N ratio, and contents of assimilable phosphorus and potassium compounds were determined.

Chemical analysis of soils was performed using routine methods (Lityński 1971, Komornicki 1987).

The results were treated by multivariate analysis making part of the computational, package PC-ORD (McCune 1987) and CANOCO (ter Braak 1987). Detrended Correspondence Analysis (DCA, DECORANA program, Hill and Gauch 1980) was used for the quantitative floristic data obtained for plots, in order to determine their heterogeneity on the plane defined by the first two DCA axes. DCA is a modification of CA analysis (Brzeziecki 1984, Kershaw and Looney 1985). Canonical Correspondence Analysis (CCA, CANOCO program, ter Braak 1987) was applied to determine the relationships between the environmental variables and different plant species. In this case, the co-ordinates of the plots in n-dimensional space are linear combinations of the environmental variables. Canonical ordination is intended for revealing the differentiation pattern in the species – involving data, that is best explained by the observed environmental variables. In CCA the linear combinations of the environmental variables are selected in such a manner that the dispersion of species scores is maximal. Sites scores are limited to linear combinations of the environmental variables (Jongman et al. 1987).

Dynamics of seasonal and plot heterogeneity were analysed with the use of the following indices (Odum 1982):

1. species richness (S) – number of species occurring at a plot (1 m²)

2. evenness index (e):

$$e = H/\log S$$

H – Shannon index, S – number of species.

3. Shannon index of total diversity (H):

$$H = -\left(\frac{n_i}{N}\right) \log \left(\frac{n_i}{N}\right)$$

n_i – importance coefficient for each species, N – sum of importance coefficients.

Analysis of variance of these indices in single classification was performed. The significance of the differences between means was tested by Tukey's method (Okta b a 1976).

4. RESULTS

4.1. ANALYSIS OF FLORISTIC DATA – DCA

Application of DCA analysis allowed for an overall approach to the differentiation of the plots in the investigated area, that was reflected by plant species composition. Moreover, significant seasonal fluctuations were observed.

Ordination of the data for the plots, obtained in spring, resulted in singling out five groups: the first group (I) included three plots situated in the upper parts of the ravines, where *Majanthemum bifolium*, *Luzula pilosa* and *Polygonatum multiflorum* occurred. The second group (II) comprised three plots characterized by the presence of *Rubus hirtus*. The third group (III) was composed of hill-side and ravine upper-part plots, with the occurrence of *Anemone nemorosa*, *Asarum europaeum*, *Galeobdolon luteum*, *Viola riviniana*, as well as of *Melandrium rubrum* and *Ajuga reptans*. The fourth group (IV) consisted of plots located at ravine bottoms and of several plots situated in the lower parts of the hill-side, with the presence of *Adoxa moschatellina*, *Aegopodium podagraria*, *Chrysosplenium alternifolium*, *Ficaria verna*, *Filipendula ulmaria* and *Primula elatior*. The fifth group (V) comprised one plot at the bottom of the 4th transect, characterized by the occurrence of *Cardamine amara*. The eigenvalues were for the first and second axis 0.864 and 0.343, respectively (Fig. 2).

In summer the species composition of the plots greatly differed from that found in spring. The individual character of the different plots was accentuated, and the similarities within the groups singled out decreased; nevertheless, evident differences between groups were manifested in the two-dimensional DCA plane. The eigenvalues amounted for the first and second axis to 0.796 and 0.629, respectively (Fig. 3).

In September, vegetation of the major part of species came to an end, this resulting in a decrease in the number and frequency of species. Whereas the earlier distinguished groups could still be singled out, there was a tendency for their unifor-

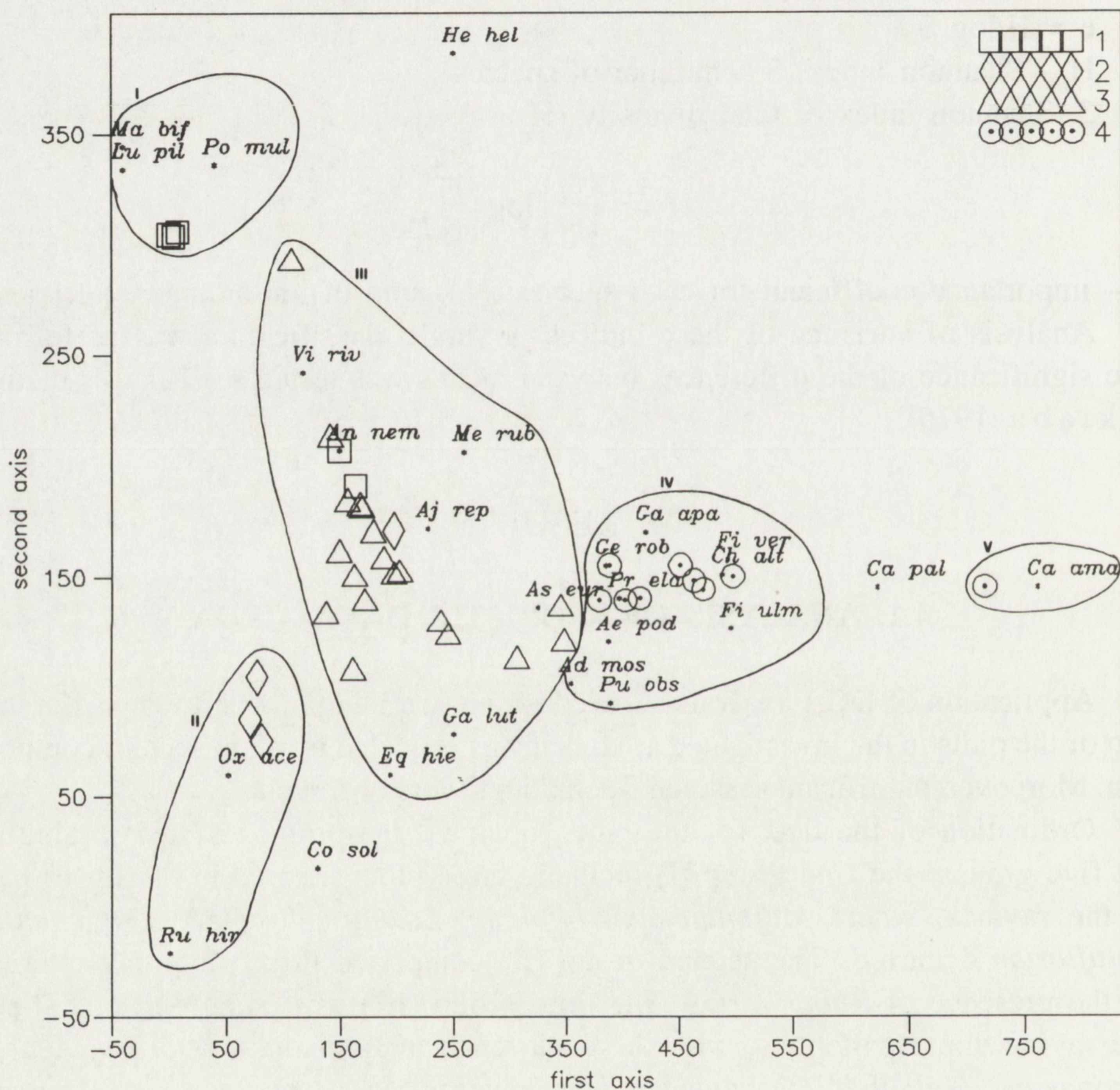


Fig. 2. Distribution of plots and forest floor vegetation species on a plane defined by the first two axes in DCA – spring 1991

1 – plots in ravine upper parts; 2 – plots with *Rubus hirtus*; 3 – plots on hill sides; 4 – plots at ravine bottoms. Explanations of the abbreviations of species names are given in the Annex.

Groups of plots singled out (I, II, III, IV, V) – explanations in the text

mization. However, the plots located at ravine bottoms, that were widely extended along the first axis (eigenvalue 0.931), continued to display high variation. The ravine upper part plots stood out along the second axis (eigenvalue 0.722) (Fig. 4).

4.2. SPECIES DISTRIBUTION VERSUS MICROSITE CONDITIONS – CCA

CCA analysis allowed for singling out the floor vegetation groups correlated with different environmental parameters. In spring, the species associated with very humid habitats included *Chrysosplenium alternifolium*, *Caltha palustris*, *Cardamine amara*, *Galium aparine*, *Urtica dioica*, *Ficaria verna*, *Filipendula*

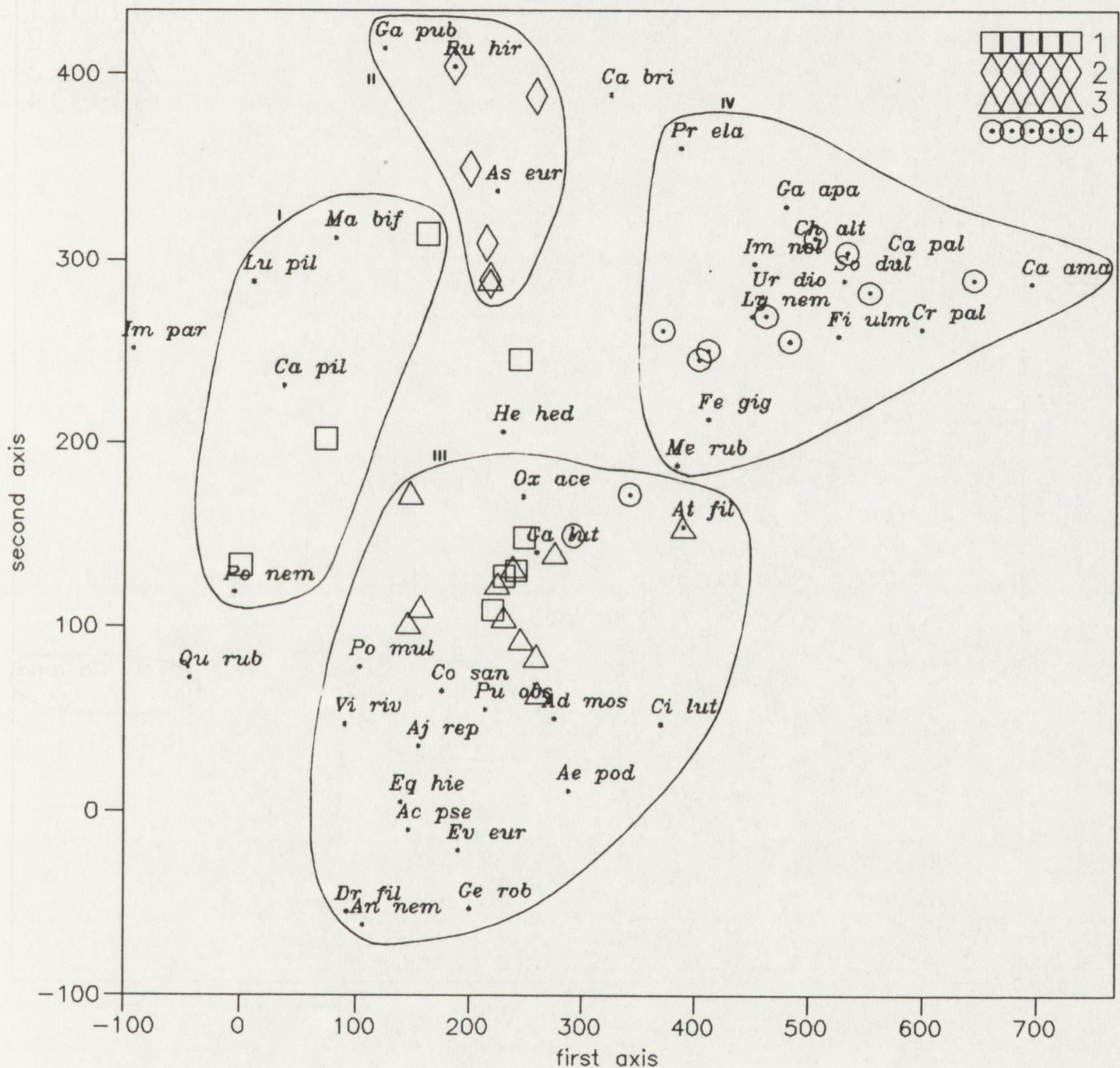


Fig. 3. Distribution of plots and forest floor vegetation species on a plane defined by the first two axes in DCA – summer 1991

1 – plots in ravine upper parts; 2 – plots with *Rubus hirtus*; 3 – plots on hill sides; 4 – plots at ravine bottoms. Explanations of the abbreviations of species names are given in the Annex.

Groups of plots singled out (I, II, III, IV, V) – explanations in the text

ulmaria and *Primula elatior*, while the species preferring low – moisture soils consisted of *Majanthemum bifolium*, *Luzula pilosa*, *Carex pilosa*, *Viola riviniana*, *Geranium robertianum*, *Poa nemoralis* and *Equisetum hiemale*. Soils of pH slightly acid and close to neutral were preferred by *Cardamine amara*, *Primula elatior*, and also by *Chrysosplenium alternifolium*, *Caltha palustris*, *Ficaria verna*, *Urtica dioica*, *Aegopodium podagraria*, *Pulmonaria obscura* and *Galium aparine*, whereas strongly acid soils were preferred by *Rubus hirtus*, *Hedera helix*, *Majanthemum bifolium*, *Poa nemoralis*, *Luzula pilosa*, *Polygonatum multiflorum* and *Carex pilosa*. The occurrence of *Rubus hirtus* was very strongly correlated

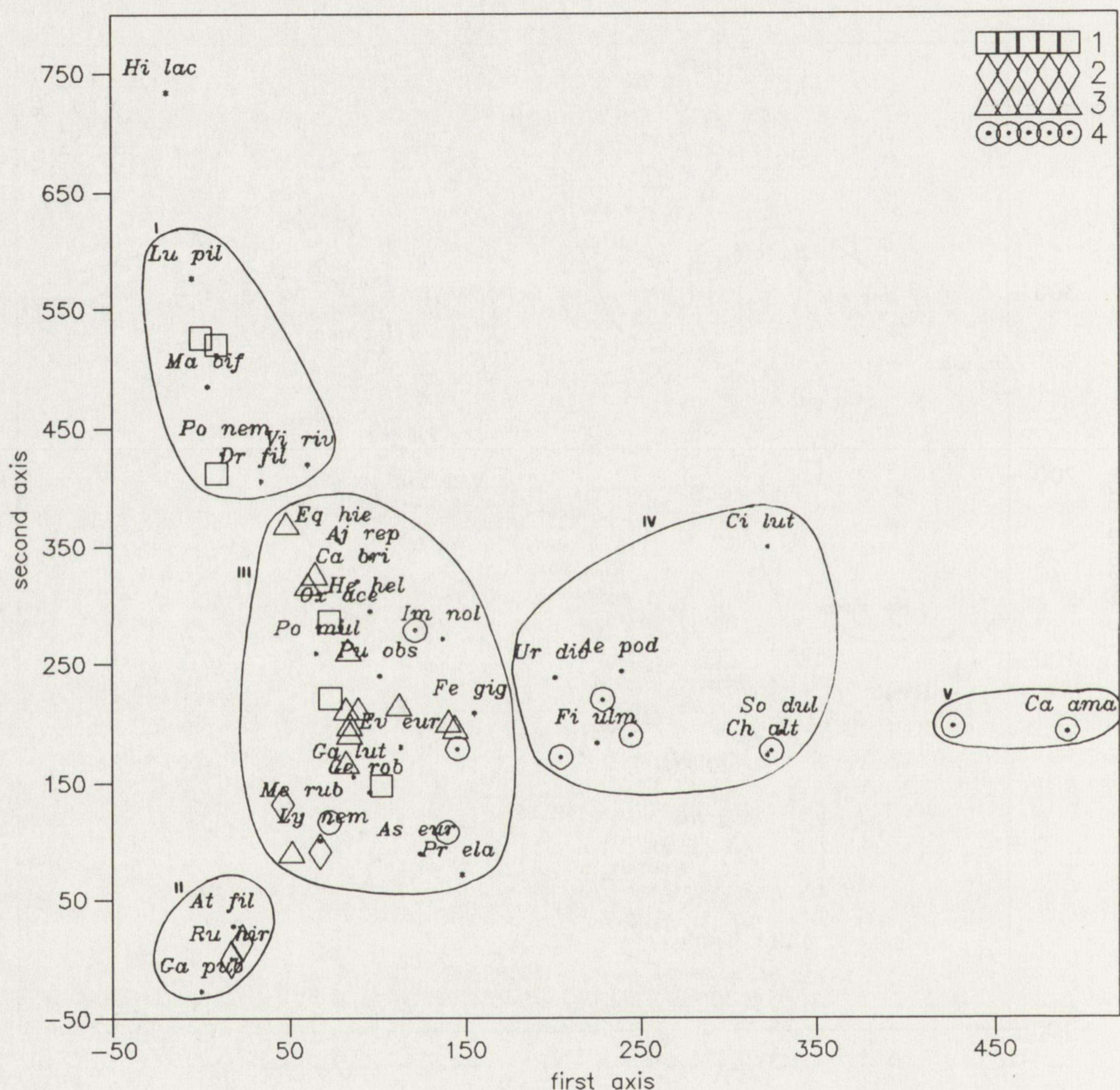


Fig. 4. Distribution of plots and forest floor vegetation species on a plane defined by the first two axes in DCA – autumn 1991

1 – plots in ravine upper parts; 2 – plots with *Rubus hirtus*; 3 – plots on hill sides; 4 – plots at ravine bottoms. Explanations of the abbreviations of species names are given in the Annex.

Groups of plots singled out (I, II, III, IV, V) – explanations in the text

with substantial light access. Shading was well tolerated by *Geranium robertianum*, *Equisetum hiemale*, *Pulmonaria obscura*.

Eigenvalues of the first and second axis were 0.628 and 0.284, respectively. The percentage variance, explained by the axes for the relationships between species and environmental variables was: first axis (I) 54.5%, first and second axis (I+II) 79.2% (Fig. 5a).

In summer, the aspect of forest vegetation differed from that observed in spring, owing to species development dynamics and seasonal variation of some environmental parameters. The group of species preferring humid habitats included, in addition to the above-mentioned species, *Solanum dulcamara*, *Impatiens noli-tangere*

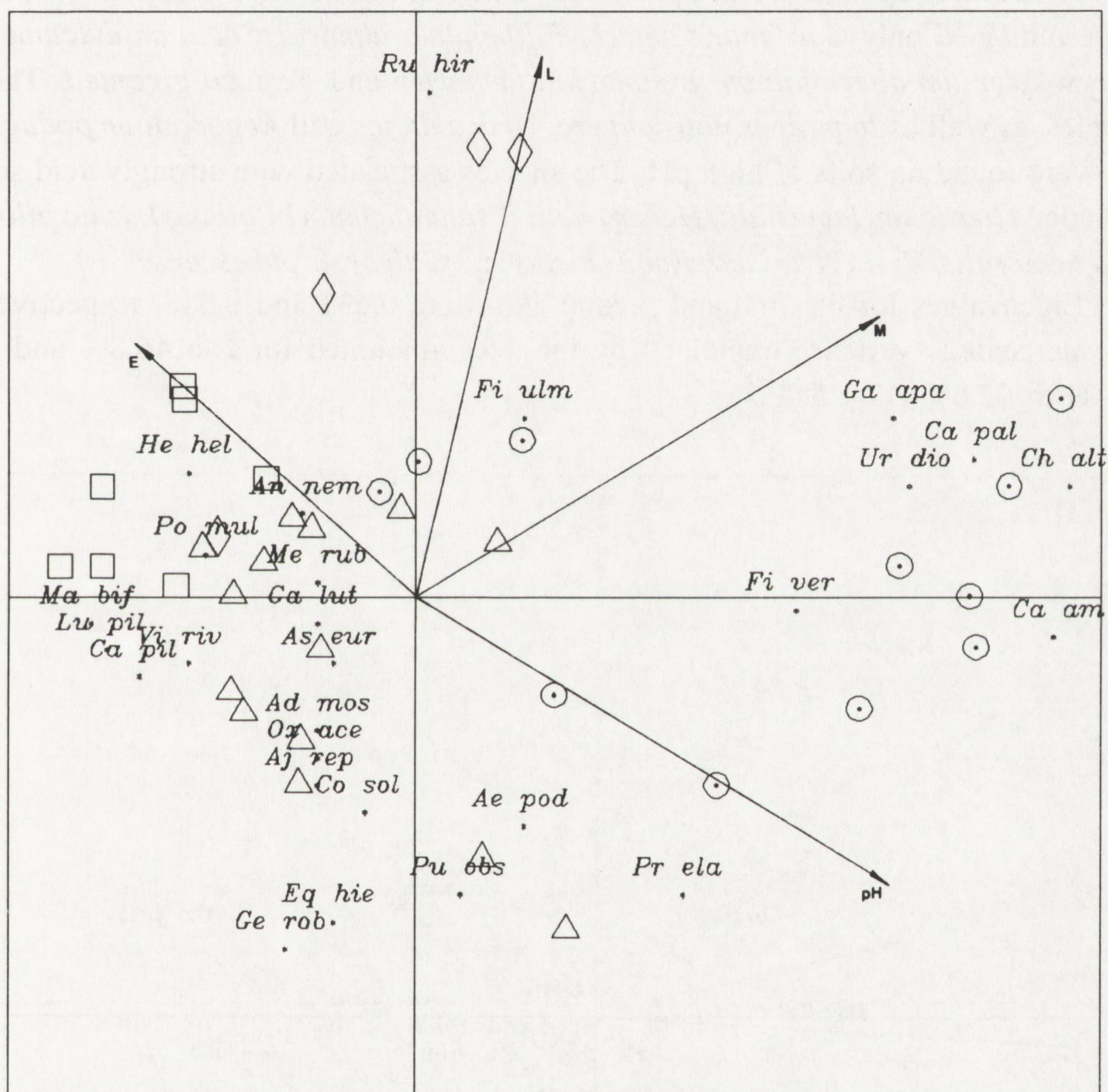


Fig. 5a. Distribution of plots and forest floor vegetation species as related to environmental variables – CCA analysis – spring 1991

L – light intensity; M – soil moisture content, pH – soil pH, E – elevation of plot a.s.l.

Explanations of the abbreviations of species names and symbols as in Fig. 2

and *Lysimachia nemorum*. At the same time, these species preferred high soil pH values.

Humus content was correlated with the occurrence of *Rubus hirtus*, and – in a lesser measure – with the presence of *Carex brizoides*, *Hedera helix*, *Ajuga reptans*, *Athyrium filix-femina* and *Oxalis acetosella*. Low humus content was tolerated by *Poa nemoralis*, *Luzula pilosa*, *Dryopteris filix-mas*, *Geranium robertianum*, *Equisetum hiemale*, *Majanthemum bifolium* and *Viola riviniana*.

Eigenvalues for the first and second axis were 0.449 and 0.376, respectively. The percentage variance explained by the axes were for I 30.1% and for I + II 55.9% (Fig. 5b).

In autumn, the number of species occurring at humid sited was reduced, and there remained only *Cardamine amara*, *Filipendula ulmaria*, *Solanum dulcamara*, *Chrysosplenium alternifolium*, *Lysimachia nemorum* and *Festuca gigantea*. These species, as well as *Impatiens noli-tangere*, *Urtica dioica* and *Aegopodium podagraria* were found on soils of high pH. The species associated with strongly acid soils included *Hieracium lachenalii*, *Hedera helix*, *Majanthemum bifolium*, *Luzula pilosa*, *Poa nemoralis*, *Viola riviniana*, *Rubus hirtus* and *Galeopsis pubescens*.

Eigenvalues for the first and second axis were 0.631 and 0.348, respectively. The percentage variance explained by the axes amounted for I to 46.8% and for I + II to 72.6% (Fig. 5c).

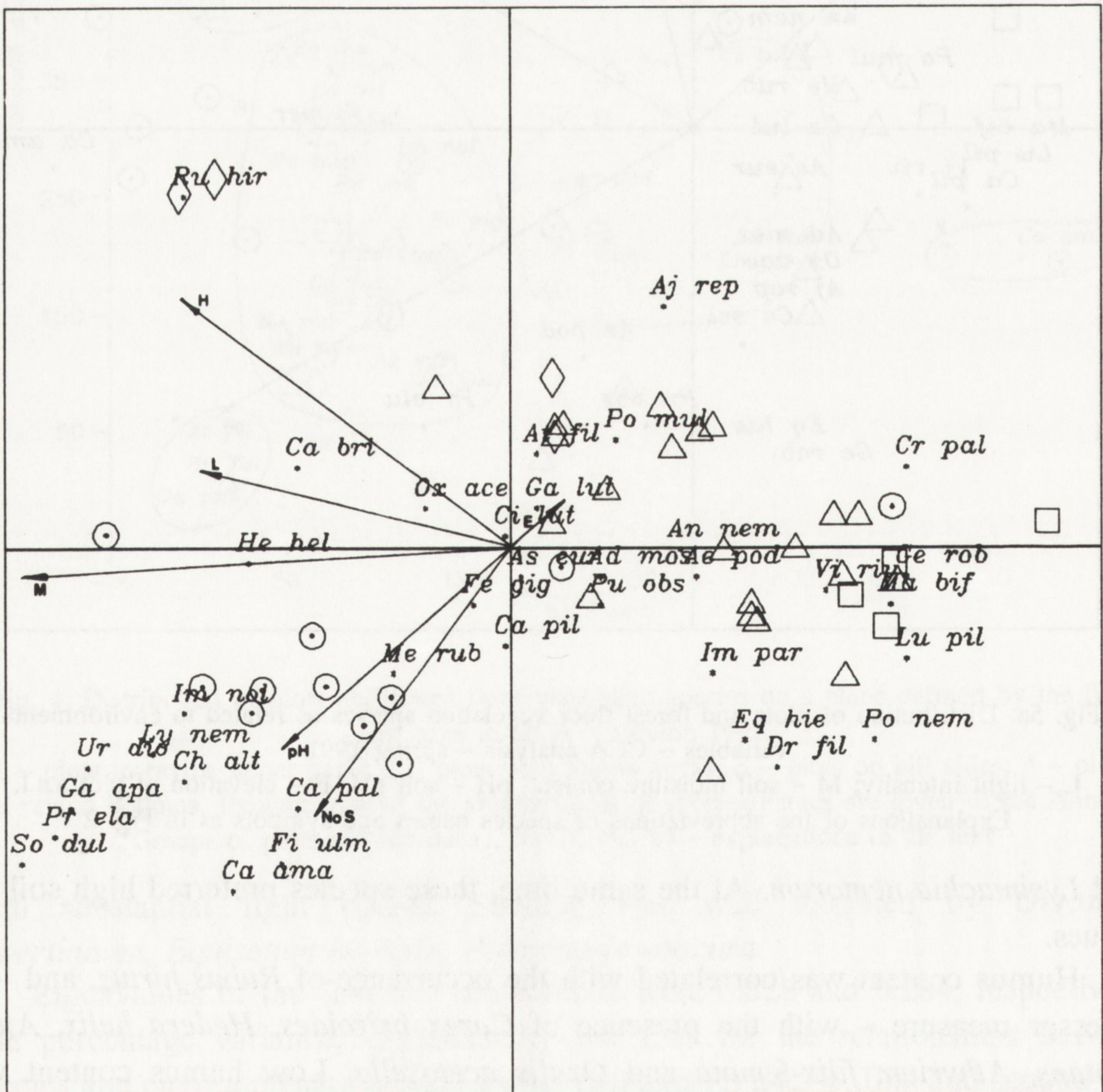


Fig. 5b. Distribution of plots and forest floor vegetation species as related to environmental variables – CCA analysis – summer 1991

L – light intensity; M – soil moisture content, pH – soil pH, E – elevation of plot a.s.l., H – soil humus content (%), NoS – number of species per plot

Explanations of the abbreviations of species names and symbols as in Fig. 2

The strongest effect on the distribution of species, and thus of the plots, was exerted by soil moisture content (the longest axis, as compared with all other variables studied). Moreover, soil pH was of considerable importance. There was a clear-cut relationship between high values of soil pH and increased species richness. At the same time, soil pH was correlated negatively with elevation, i.e. the highest situated plots exhibited a strongly acid pH.

The variable taking into account humus content was markedly correlated with relative light intensity. Both these parameters were decisive of the distinctness of the group of plots with very high frequency of *Rubus hirtus*.

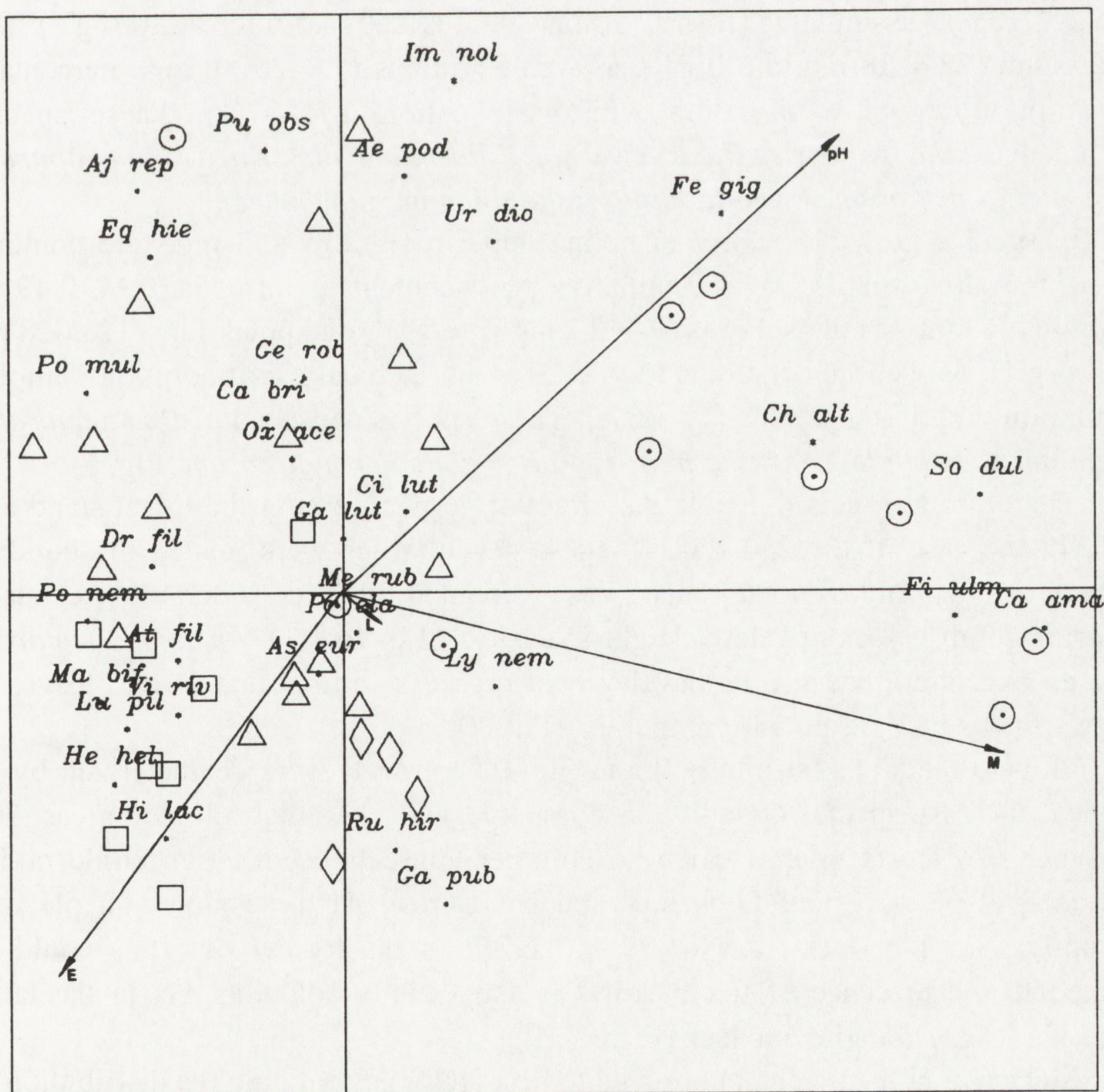


Fig. 5c. Distribution of plots and forest floor vegetation species as related to environmental variables – CCA analysis – autumn 1991

L – light intensity; M – soil moisture content, pH – soil pH, E – elevation of plot a.s.l.,
Explanation of the abbreviations of species names and symbols as in Fig. 2

Configuration of the environmental variables changed in the course of the vegetation season owing to seasonal fluctuations in soil moisture content.

Spatial distribution of species, with consideration of their frequency, as confronted with environmental factors, is illustrated for the consecutive transects in Figs. 6, 7, 8, 9. Particularly in the case of the third transect (Fig. 8), there was an evident division into species with either a wide or a narrow ecological amplitude. The former group included *Anemone nemorosa*, *Galeobdolon luteum* and *Oxalis acetosella*.

The latter group comprised:

a. the species growing at ravine bottoms: high soil moisture contents (22.5–45%); soil pH (3.8, 4.4) 6.5–7.6; relatively high contents of nitrogen (0.22–1.19%); assimilable forms of phosphorus $2.2\text{--}4.2\text{ mg} \times 100\text{ g}^{-1}$ and potassium ($22.8\text{--}28\text{ mg} \times 100\text{ g}^{-1}$), as well as humus (4.0–20%); high percentage of sorption complex saturation with basic cations (75–97%). These species included *Caltha palustris*, *Ficaria verna*, *Filipendula ulmaria*, *Galium aparine*, *Lysimachia nemorum*, *Primula elatior* and *Solanum dulcamara*;

b. species growing mainly in ravine upper parts: low soil moisture contents (5.5–15%); low soil pH (3.4–4.7); relatively low contents of nitrogen (0.11–0.49%); assimilable forms of phosphorus ($0.4\text{--}2.2\text{ mg} \times 100\text{ g}^{-1}$) and potassium ($12.4\text{--}28\text{ mg} \times 100\text{ g}^{-1}$), as well as of humus (3.4–7.2%); low percentage of sorption complex saturation with basic cations (11–46%). These species consisted of *Poa nemoralis*, *Majanthemum bifolium*, *Luzula pilosa* and *Polygonatum multiflorum* (Fig. 6).

The other transects illustrate the effect of perturbances in the forest stand and soil. In the case of the 2nd transect these perturbances were related to abundant occurrence of *Rubus hirtus*, that was correlated with considerable tree-stand clearing (high values of relative light intensity: 11.6–16.4%). *Anemone nemorosa* was an exception, because its development precedes in time that of the leaves of *Rubus hirtus* being a potent competitor (Fig. 7).

Plots 10 and 11 (1st transect) and 36 (4th transect) were characterized by an evident increase species diversity, as compared with the other hill-side areas. The presence of *Ficaria verna* (which in the other transects occurred at humid ravine bottoms) at plots 10 and 11 was of special interest. At these plots soil pH rose abruptly: No. 11 – pH 5.0, No. 36 – pH 7.7. In the former case this could be related to the presence of fox burrows in the vicinity of plots 11; in the latter case, the cause remains unclear (Figs. 8, 9).

Since soil moisture content proved to be a factor determining the distribution of the forest vegetation species, diagrams presenting the frequencies of selected species at plots along the moisture gradient, with the period of data collection taken into account, were prepared (Fig. 10). This approach allowed for revealing of several phenomena. Variation of the ecological amplitude and ecological optimum of different species was most evident. In spite of the diversity of the occupied plots, in the

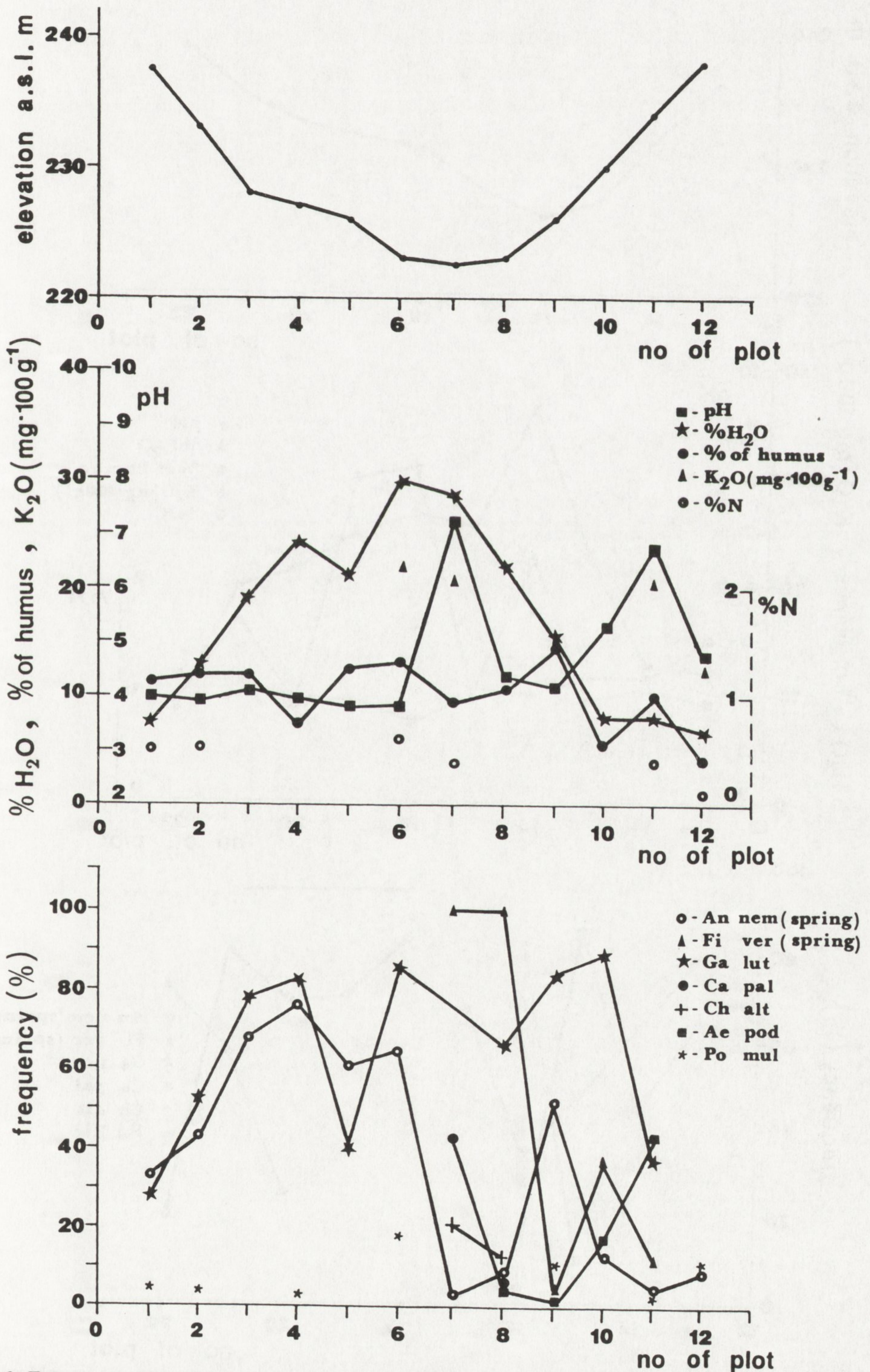


Fig. 6. Frequency of selected plant species as confronted with environmental variables – transect I
 Explanations of the abbreviations of species names are given in the Annex

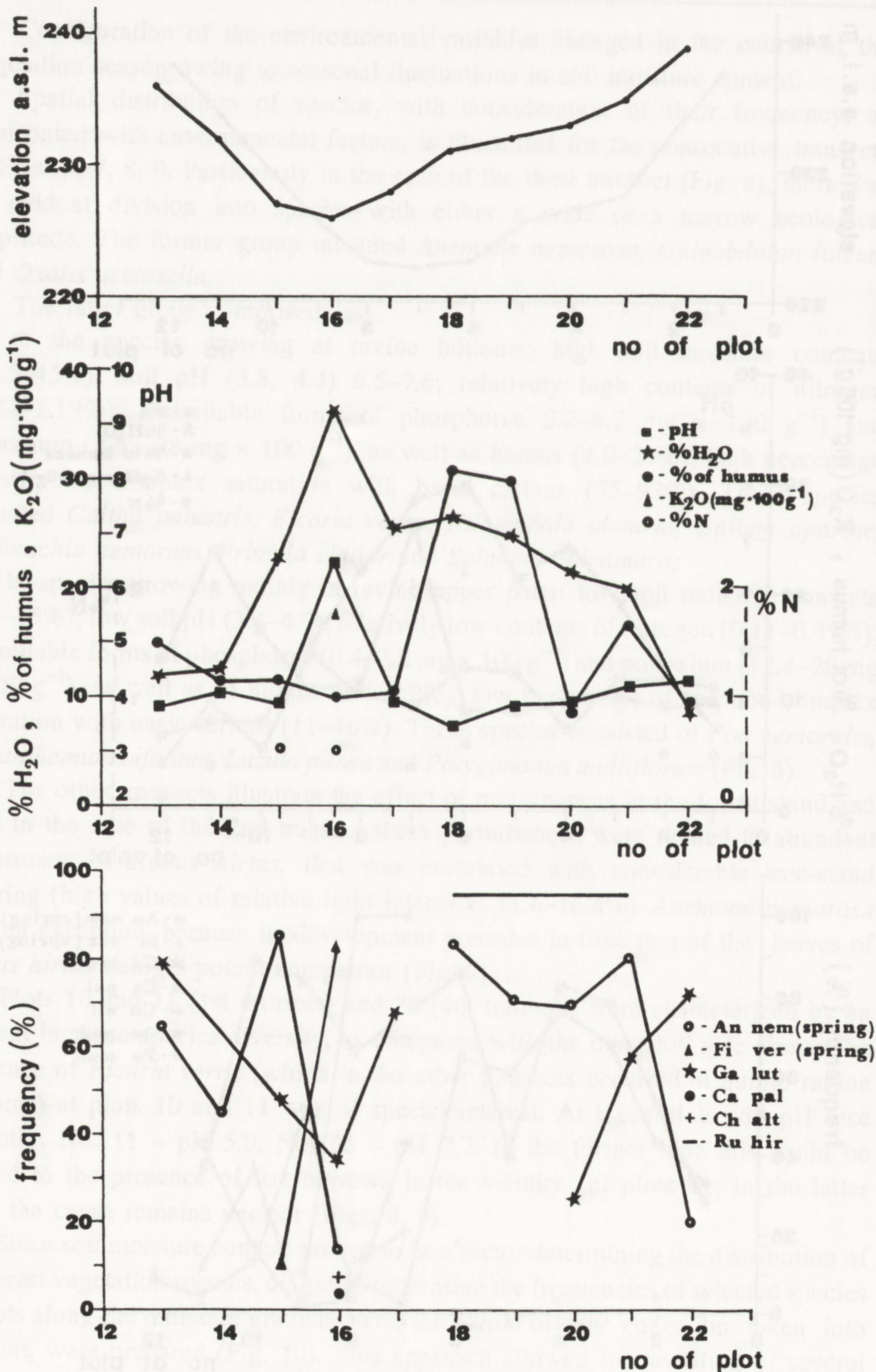


Fig. 7. Frequency of selected plant species as confronted with environmental variables
- transect II

Explanations of the abbreviations of species names are given in the Annex

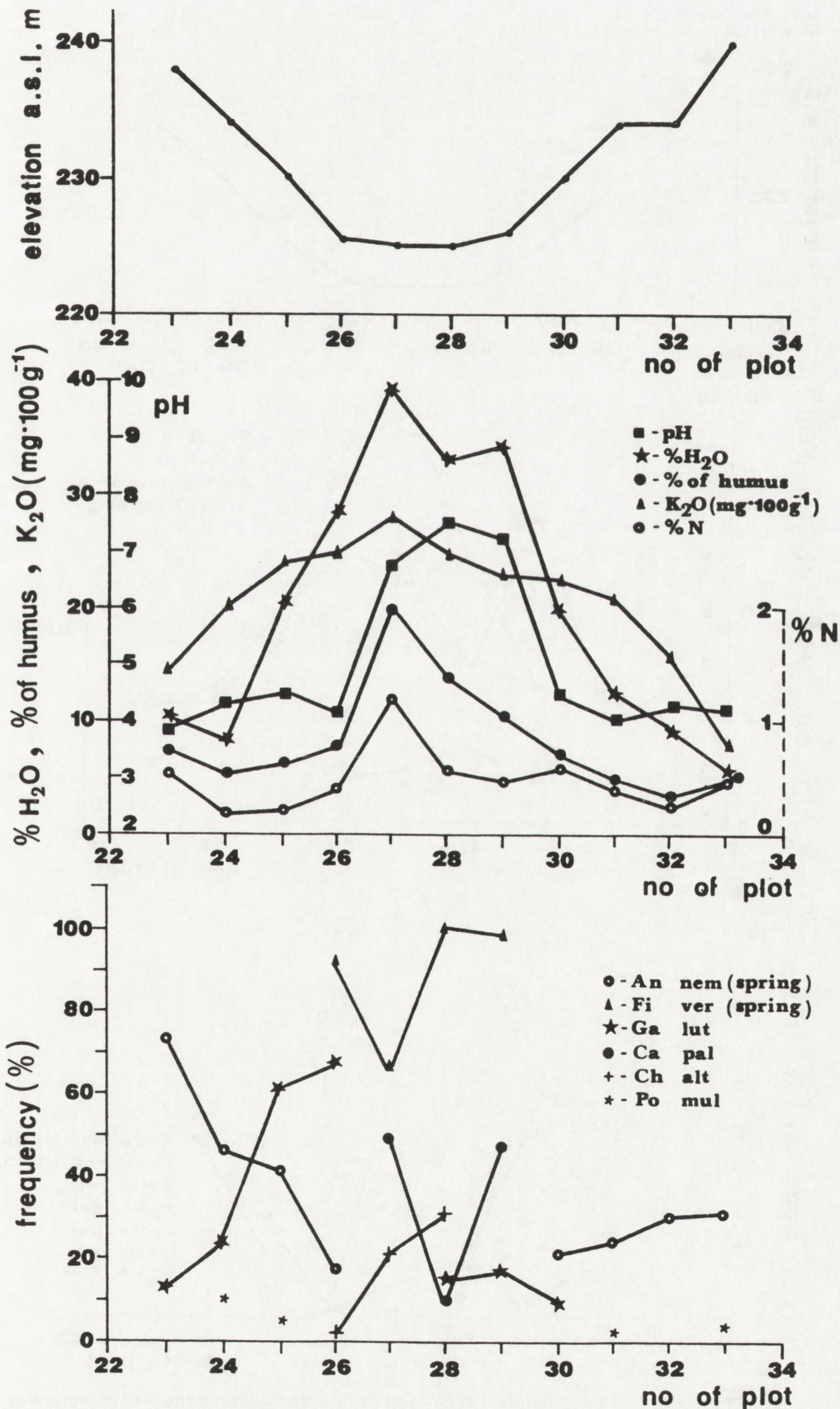


Fig. 8. Frequency of selected plant species as confronted with environmental variables
- transect III

Explanations of the abbreviations of species names are given in the Annex

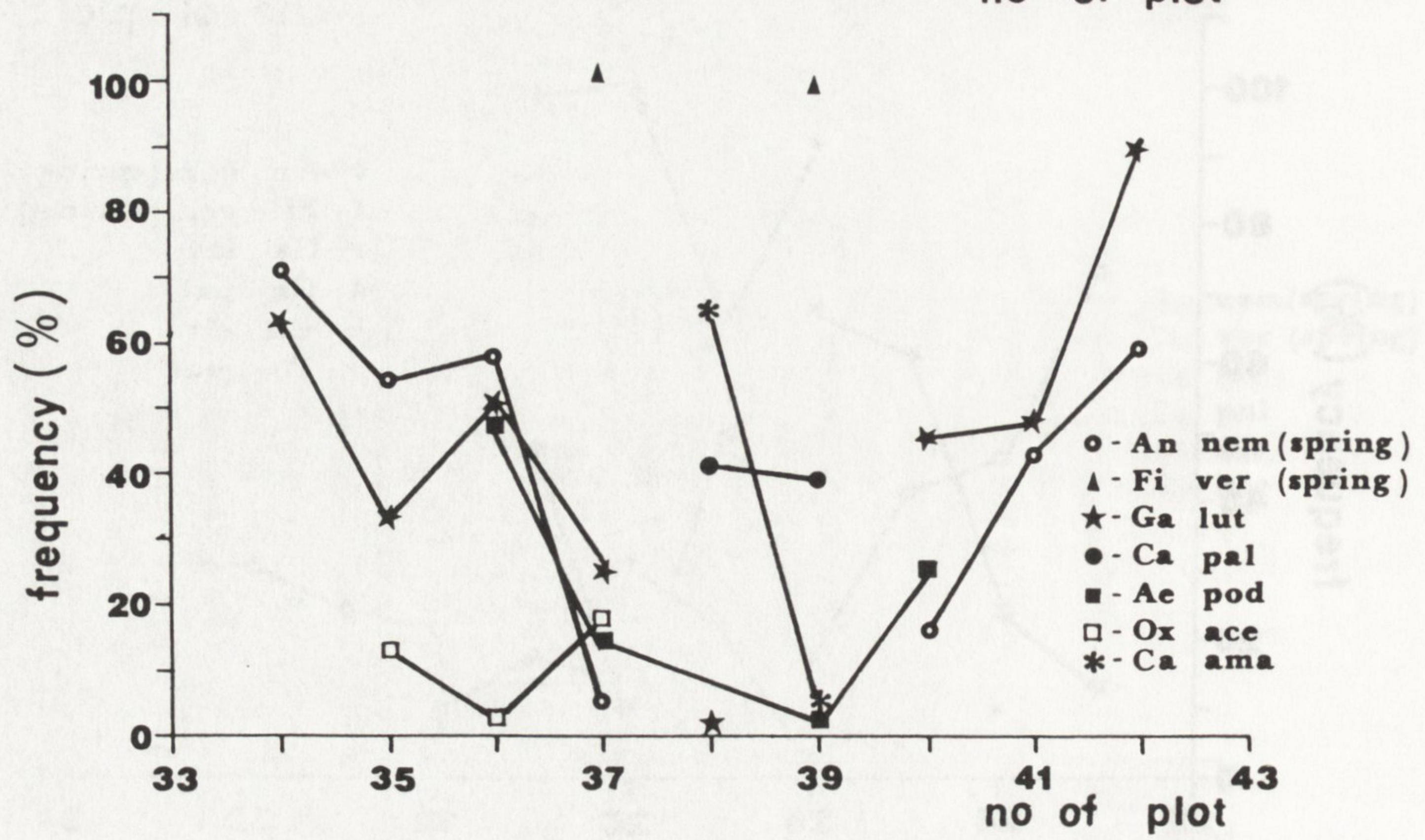
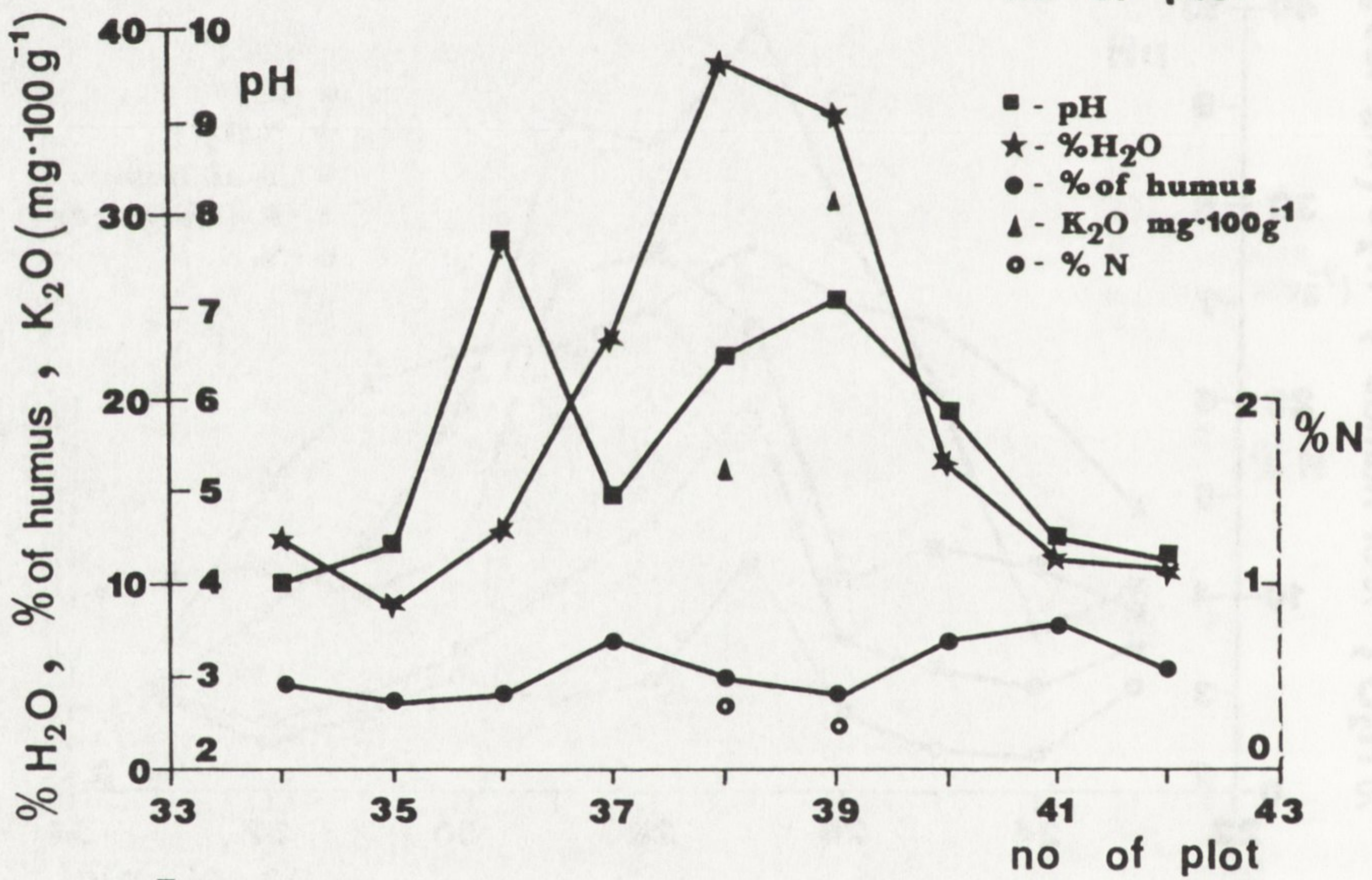
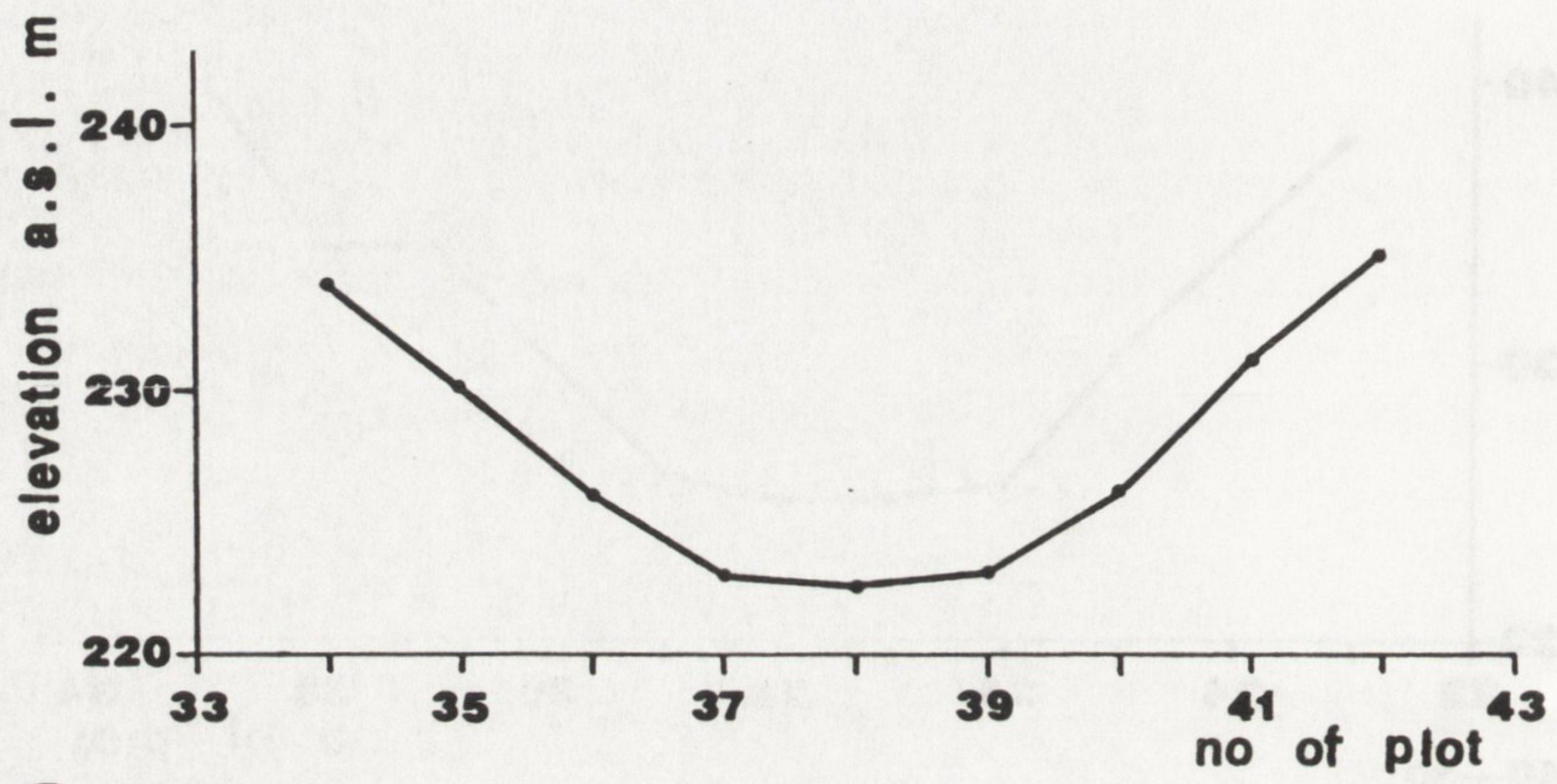


Fig. 9. Frequency of selected plant species as confronted with environmental variables - transect IV

Explanations of the abbreviations of species names are given in the Annex

case of *Anemone nemorosa* and *Galeobdolon luteum* the frequency in the class of moist soils evidently increased.

Adoxa moschatellina and *Aegopodium podagraria*, for which humid soils were optimal, had to be added to the species with a narrow occurrence range.

Polygonatum multiflorum that in spring displayed two optima: on low-moisture and moist soils, was of interest.

In general, the plot optimum was shifted over time. For species that in spring preferred dry and moist soils, in summer the optimum was shifted towards moist and humid ones, whereas in the case of species preferring in spring wet and very

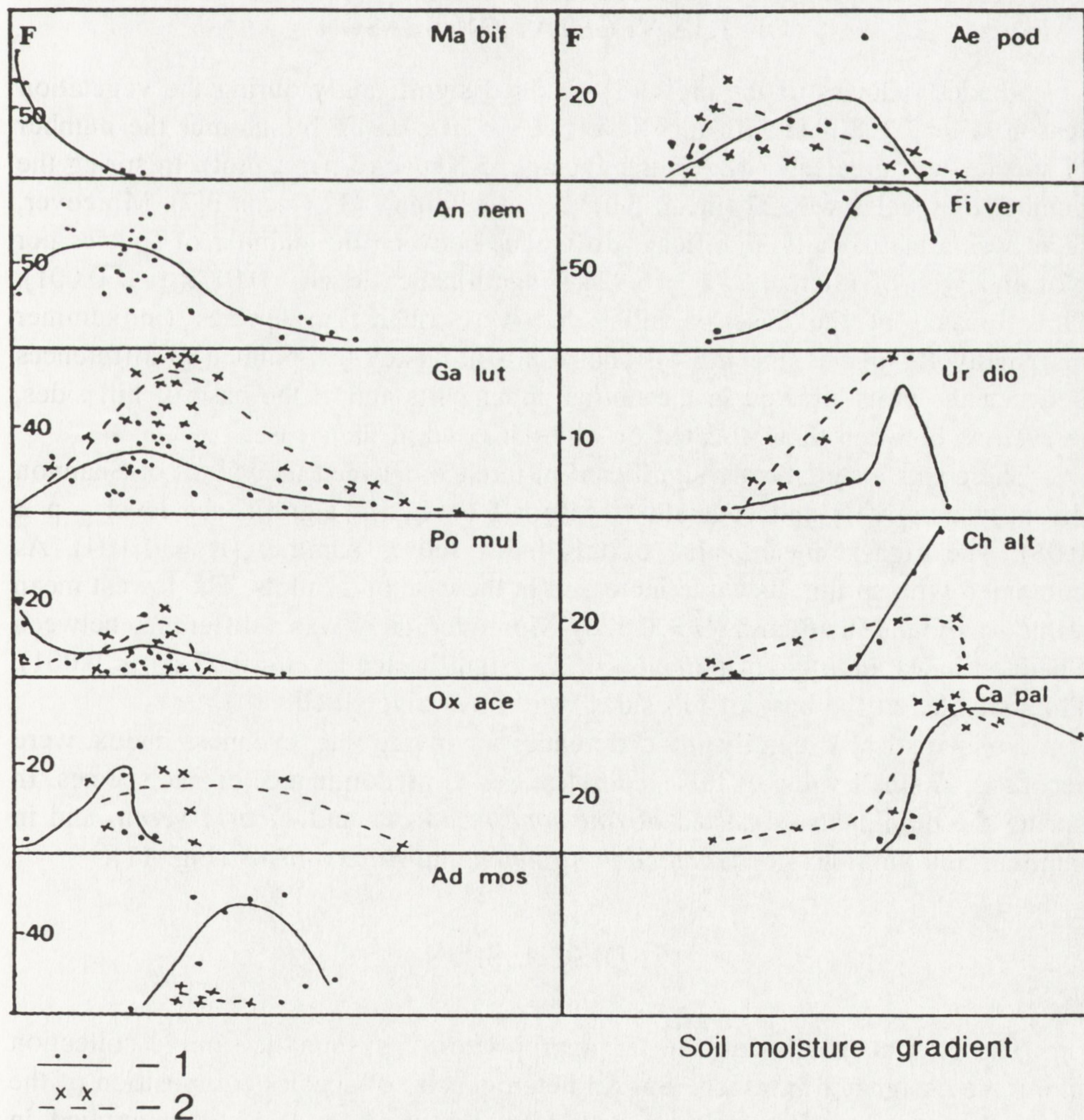


Fig. 10. Frequency (F) of selected forest floor vegetation species in soil moisture gradient (axis I in DCA ordination). The course of the curves was fitted manually
1 – spring 1991, 2 – summer 1991

Explanations of the abbreviations of species names are given in the Annex

humid soils, in summer this optimum was shifted towards humid ones. This was closely related to seasonal fluctuations in soil moisture content.

The observed change in the occurrence range of *Oxalis acetosella* in summer, as compared with spring, was a very interesting result. In spring this species was present in the first place in the class of moist soils. In July its plot preference range extended to the class of moist and humid soils. This species occurred at sites where in spring *Ficaria verna* had been dominant.

4.3. DYNAMICS OF MICROSITE DIVERSITY IN THE COURSE OF THE VEGETATION SEASON

Species richness of the plots (S) changed significantly during the vegetation season ($F = 7.318$ – significance level $0.05 \leq p \leq 0.01$). In summer the number of species was greatest – 42 (on the average, 5.3 species per 1 plot). In spring the number of species was 27 (mean 5.0) and in autumn – 37 (mean 3.7). Moreover, there was a statistically significant difference between the number of species per plot and type of microsite ($F = 6.924$ – significance level – $0.01 \leq p \leq 0.001$). Plots located at the base of hill sides were richest in species (in summer maximally 12 species, mean 6.4). The results of Tukey test pointed to differences between the plots situated in the ravine upper parts and at the base of hill sides, as well as between those located on hill sides and at their base.

There was a statistically significant difference between the values of Shannon diversity index (H) and vegetation season ($F = 4.75$ – significance level – $p \leq 0.05$). The highest mean value of this index fell to summer ($\bar{H} = 1.104$). As compared with spring, its value increased in the case of 27 plots. The lowest mean value was found in autumn ($\bar{H} = 0.826$). Moreover, there was a difference between Shannon index and type of plot ($F = 4.22$ – significance level – $0.05 \leq p \leq 0.001$). Plots situated at the base of hill sides were most diversified.

No statistically significant differences involving the evenness index were recorded. A small value of this index testifies to predominance of one species. In spring the dominants consisted of *Anemone nemorosa* and *Ficaria verna*, and in summer and autumn – of *Galeobdolon luteum* and *Rubus hirtus* (Fig. 11).

5. DISCUSSION

The present results confirm the appropriateness of systematic sample collection along the designated transects. Spatial heterogeneity of species composition of the vegetation can be effectively expressed by this method. It is often applied in ecological studies (e.g. Zarzycki 1976, Collier et al. 1977, Kershaw 1978, Silander 1982, Olsvig-Whittaker et al. 1983, Borysiak 1984, Czarnecka 1986, Szwed 1986, Olsvig-Whittaker 1988, Begon and Mortimer 1989, Węglarski 1991). This method is, however, charged with

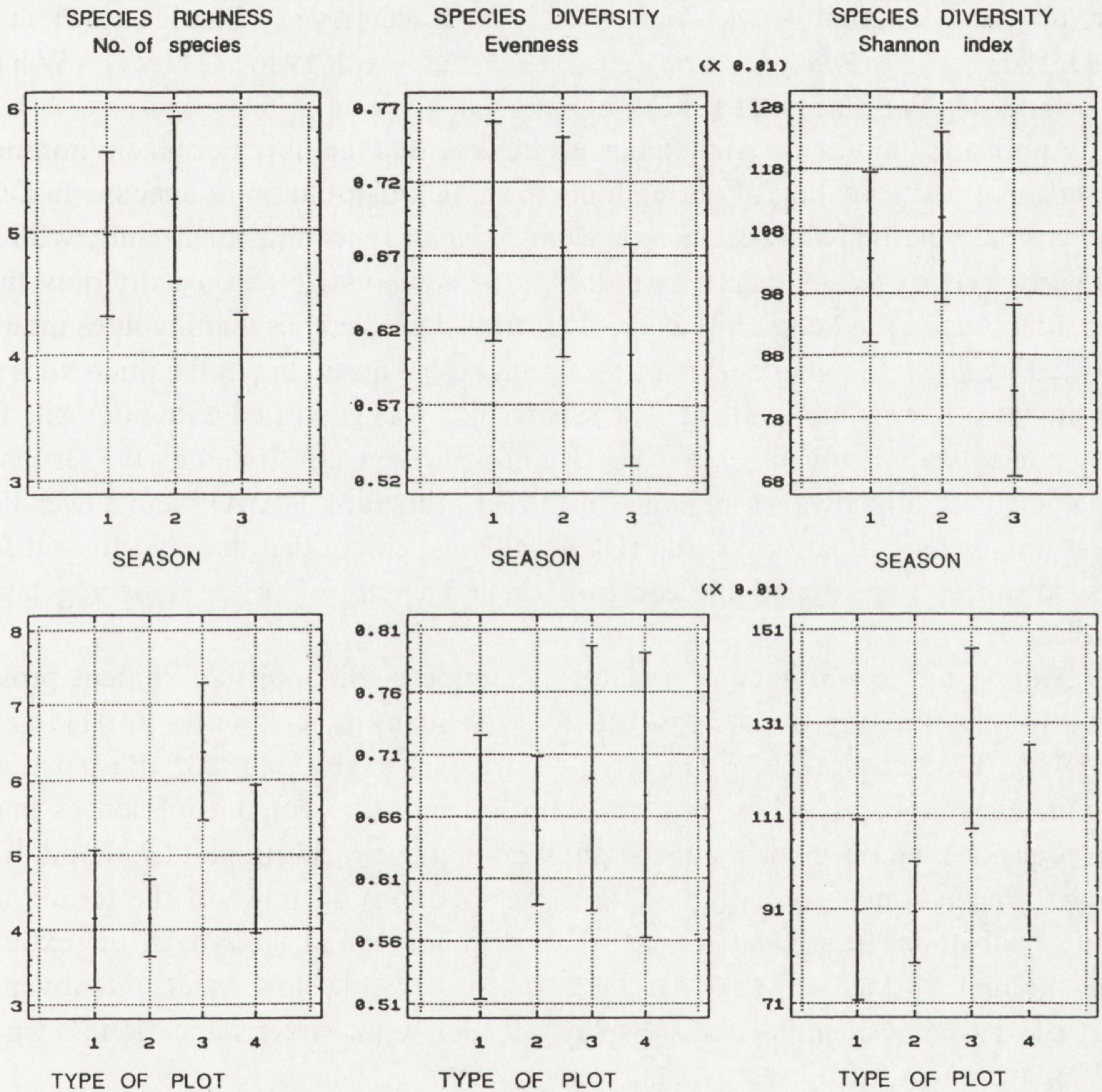


Fig. 11. Seasonal variation and plot heterogeneity – analysis of variance in single classification, and significance of the differences between means

Season: 1 – spring, 2 – summer, 3 – autumn; type of plot: 1 – plots on ravine upper parts, 2 – those on hill sides, 3 – those at the base of hill sides, 4 – those at ravine bottoms

a risk inherent in the selection of the distance between plots. When this distance is too large, the results may be erroneous and inconsistent with the real state (Kershaw 1978). For correct selection of this distance it is necessary to take into account the heterogeneity of the terrain and heterogeneity scale of plant communities. The 10-m distance accepted in the present studies permits proper illustration of plot heterogeneity.

Moreover, in studies involving transect utilization the area of the plot is of essential importance. According to Kershaw (1978), the most appropriate plot ought to be as small as it is possible for a given type of community. Most often a

square (1 m^2) is adopted. It seems that this surface area is appropriate for the major part of plant communities (Zarzycki 1976, Olsvig-Whittaker et al. 1983, Borysiak 1984, Czarnecka 1986, Szwed 1986, Olsvig-Whittaker 1988, Węglarski 1991).

Application of numerical methods for treatment of the floristic and environmental data enabled revealing of correlations in spatial distribution of species. In DCA analysis only the first and second axis were taken into account, consistently with the opinion of Olsvig-Whittaker et al. (1983) who state that usually only the I and II DCA axis can be interpreted ecologically. This analysis that involves indirect concluding about the microsite parameters suggested arranging of the microsites according to soil moisture gradient. The second axis was identified with microsite fertility conceived in a broad sense. The assumptions were confirmed by the results of CCA analysis. Eigenvalues obtained in direct ordination (CCA) were lower than those found in indirect ordination (DCA), this indicating that the investigated factors do not account for all the causes of heterogeneity of forest floor vegetation species.

Among the environmental variables examined, soil moisture content proved to be the determining factor, consistently with many other reports (Collier et al. 1977, Kershaw 1978, Olsvig-Whittaker et al. 1983, Begon and Mortimer 1989, Leduc et al. 1992). Soil moisture content influences many soil processes, and is decisive of the physical and chemical properties of soil. This content depends most often (apart from precipitation) on relief of the terrain and kind of substrate. In lessivated soils, their granulation and the size of the external and internal surface of soil particles are responsible for water retentiveness (Firek 1977). Pseudogley soils display a tendency for water stagnation (Uggla 1979), as confirmed by the present observations.

Seasonal variation of soil moisture content is a well known phenomenon that depends mainly on the distribution of precipitation during the months of studies (Wachowska-Serwatka 1966, Karkanis 1974, Uggla 1979). Soil moisture content is highest in May or June. In the "Ligęzianka" forest it was highest in May.

The ecological requirements of species with regard to soil moisture content, found in the present studies are as a rule in good agreement with the literature data (Ellenberg 1974, Borysiak 1984, Zarzycki 1984, Czarnecka 1986). Only *Galeobdolon luteum* is an exception to the rule; namely according to Borysiak (1984) this species is an indicator of moderately humid and humid soils containing 41–60% of water, whereas in the "Ligęzianka" forest it proved to prefer moist soils (though the amplitude of its occurrence was wide). Classification of *Geranium robertianum* into the group associated with low-moisture soils (in Zarzycki 1984 – moist soils was due to its low frequency in the total number of plots.

Plot fertility conceived in a broad sense was found to be the second factor influencing species distribution. This fertility depends on soil pH and content of mineral components. In studies of the Wielkopolski National Park, Węglarski (1991) has demonstrated that soil pH evidently differentiated the occurrence of the examined species. His results are confirmed by the present findings; namely, optimal pH reported for different species by this author and these found in the present studies are virtually the same. There are, however, some differences. Whereas Węglarski (1991) has stated that *Poa nemoralis* is widely tolerant to pH (according to Zarzycki 1984, pH > 5.5), in the "Ligęzianka" forest this species occurred only on strongly acid soils. Likewise, *Majanthemum bifolium*, reported by Węglarski (1991) to be associated with acid and slightly acid soils (according to Zarzycki 1984, pH 4.5–5.5), grew in the "Ligęzianka" forest on strongly acid soils. A similar result has been obtained by Borysiak (1984) in studies of the Babia Góra massif. Probably the fact that in the "Ligęzianka" forest optimal pH for *M. bifolium* was lower was due to the generally high acidity of lessivated soils. According to literature data (Zasoński 1983, Drożdż-Hara and Niemyska-Łukaszuk 1989), soils of the Wielickie Foothills undergo adverse processes of soil acidification. This phenomenon exerts an effect on many soil processes. In the first place low pH leads to excessive solubilization of aluminium and iron, that reduce the assimilability of phosphorus (Prończuk and Pawłat 1971, Daubenmire 1973, Uggla 1979). The low soil content of phosphorus compounds, found in the present studies, is confirmed by literature data dealing with the Wielickie Foothills (Drożdż-Hara and Niemyska-Łukaszuk 1989).

Altogether, an increase in soil pH was associated with a rise in the number of species per 1 m². Apart from ravine bottoms characterized in general by an increased substrate fertility that promotes species richness (Aulak 1976), the plots 11 and 36, situated on ravine hill sides, are of special interest. High soil pH enhances exchange sorption, facilitates coagulation of colloids, promotes humification and improves the access of nutrients to plant roots (Prończuk and Pawłat 1971, Daubenmire 1973). Very likely, the increased accessibility of macro- and microelements contributed to the presence of *Ficaria verna* in plots where was the low moisture content in the substrate. The phenomenon of ecological compensation has been confirmed in experimental studies, in which better accessibility of nitrogen compounds enhanced the resistance of plants to reduced soil moisture content (Mitka 1988, Goldberg 1990).

Wachowska-Serwatka (1966) has reported seasonal variation of soil pH. Later studies have shown, however, that these fluctuations are too slight to deserve being related to vegetation dynamics and to be attributed any greater importance (Karkanis 1974, Udziak et al. 1983). Consequently, soil pH fluctuations ought to be regarded as an error of the method.

It is not fully elucidated whether humic substances exert a direct stimulatory effect on plant growth. However, the uptake of high-molecular organic compounds by plants has been revealed in some cases (K r e e b 1979). Humic substances improve the chemical properties of soil, in the first place the sorption complex capacity that is a sink of plant nutrients. Moreover, they provide an appropriate soil structure which is important for soil aeration. In the case of the present results it is difficult to relate the occurrence of species to soil humus content, because of the scanty numbers of samples. A clear-cut elevation of soil humus level was observed in only two cases: plots situated at ravine bottoms and those of the 2nd transect. This elevation was in the former case related to the relief of the terrain (accumulation of organic substances at ravine bottom), and in the latter case – to the substantial number of leaves produced by *Rubus hirtus*. Therefore, it is difficult to discuss the requirements of different species, concerning soil humus content.

In general, the requirements of species with respect to the nitrogen, phosphorus and potassium contents in soil, as determined in the present studies, confirm the literature data (B o r y s i a k 1984, C z a r n e c k a 1986, W ę g l a r s k i 1991), when the generally lower phosphorus and potassium levels in lessivated soils of the Wielkie Foothills are taken into account. According to experimental studies, a uneven distribution of nitrogen and phosphorus influences, the patchiness of plants (T i l m a n 1986). In the "Ligęzianka" forest this was confirmed by the high proportion of *Urtica dioica* at the base of hill sides, where the soil nitrogen and phosphorus levels were elevated. Even the form of nitrogen may be a factor determining the presence of species. Such a result has been obtained by C z a r n e c k a (1986) in studies of the distribution of *Majanthemum bifolium* in forests of the Roztocze, where the ammonium compounds of nitrogen proved to be key form.

Usually forest communities are characterized by considerable shadiness, particularly in the period of maximal leaf production by trees (M o t y k a 1962, T r o j a n 1985). *Anemone nemorosa* and *Ficaria verna*, that in spring occur in masses, take advantage of the period of the greatest supply of solar energy to the floor of dry-site forests; this is related to phenology of the forests of this type (K a ź m i e r c z a k o w a 1971, F a l i ń s k a 1972, 1990, A u l a k 1976). *Rubus hirtus* proved to react very pronouncedly to tree stand clearing; a similar correlation between its occurrence and tree stand clearing has been reported by B o r y s i a k (1984).

Extension of the occurrence amplitude of *Oxalis acetosella* in the soil moisture gradient during the vegetation season is of special interest. With respect to soil pH, this species displays a wide spectrum of occurrence (Z a r z y c k i 1984, C z a r n e c k a 1986, own observations). However, with respect to the soil moisture level, its optimum corresponds to moist and humid soils (W ę g l a r s k i 1991). According to K u s s i p a l o (1987), *Oxalis acetosella* is a very poor competitor, and therefore it occurs at shaded sites where light insufficiency prevents other species from achieving a developmental success. Probably this is the cause of the seasonal shift of *Oxalis acetosella* distribution.

Microsites potentially suitable for this species are in spring occupied by expansive *Ficaria verna*. After dying out of the latter, geophytic *Oxalis acetosella* is able to develop. Thus, it may be assumed that in the case of these two species opportunistic specialization related to temporal variation takes place (MacArthur and Connell 1971). The observed perturbances that influence species diversity are of interest. Slight changes lead to an increase in species richness (Odum 1982, Begon and Mortimer 1989). This was observed in the "Ligęzianka" forest for the area that included plot 11 neighbouring with fox burrows. As a rule, the presence and impact of animals contribute to an increase in the diversity of the habitat and to its enrichment on a micro scale (Rabotnov 1985). On the other hand, severe environmental perturbances result in dominance of one species (Tilman 1986). In the "Ligęzianka" forest this relationship was confirmed by the reaction of *Rubus hirtus* to marked tree stand clearing due to human impact.

Shannon diversity index changes in space (along the transect) and in time. According to Collier et al. (1977) and Odum (1982), this index is one of the best measures that allow for making comparisons, the more so as it is relatively independent of sample size. In our studies Shannon index was highest for the plots situated at ravine bottoms, consistently with the finding that species diversity increases with a rise in habitat fertility (Aulak 1976).

6. CONCLUSIONS

1. Soil moisture content and microsite fertility, both negatively correlated with elevation of plot position were the factors determining species distribution.

2. Species with either a wide or narrow ecological range with respect to soil moisture content were distinguished.

The former group included *Anemone nemorosa* and *Galeobdolon luteum*.

The latter group comprised:

a. the species growing at humid sites: *Caltha palustris*, *Cardamine amara*, *Chrysosplenium alternifolium*, *Galium aparine*, *Ficaria verna*, *Filipendula ulmaria*, *Impatiens noli-tangere*, *Lysimachia nemorum*, *Primula elatior*, *Solanum dulcamara*, *Urtica dioica*;

b. species from relatively dry sites: *Carex pilosa*, *Luzula pilosa*, *Majanthemum bifolium*, *Poa nemoralis*, *Viola riviniana*.

3. Soil pH was an important factor influencing the number of species, that increased with a rise in pH.

4. Species preferring slightly acid and neutral soils were *Cardamine amara*, *Primula elatior*, as well as *Chrysosplenium alternifolium*, *Caltha palustris*, *Ficaria verna*, *Aegopodium podagraria*, *Galium aparine*.

Species growing on greatly acid soils consisted of *Rubus hirtus*, *Majanthemum bifolium*, *Poa nemoralis*, *Luzula pilosa*, *Polygonatum multiflorum*, *Carex pilosa*.

5. Species growing at ravine bottoms had a better supply of nutrients (N, P₂O₅, K₂O), because of this increased contents at these sites.
6. The species dominant at microsites were *Anemone nemorosa*, *Ficaria verna*, *Galeobdolon luteum*, *Rubus hirtus*.
7. In summer (July), species diversity of the associations studied was highest.
8. Results of soil analysis confirm that lessivated soils of the Wielickie Foothills are, in general, acidified and impoverished.
9. Seasonal fluctuations in soil pH are too small to be regarded as significant.
10. The investigated environmental factors fail to account for all causes of variation in species distribution; namely, the eigenvalues in CCA were lower than those in DCA.
11. The method of systematic collection of samples along transects reflects very well the spatial heterogeneity of species distribution.
12. It was demonstrated that the DCA and CCA numerical analysis is useful for interpretation of the causes of spatial heterogeneity of species distribution.

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7. SUMMARY

The aim of the present studies performed in 1991 (preliminarily, in 1990) was to reveal the factors decisive of the spatial pattern of the forest floor vegetation species on a small scale ("Ligeżianka" forest, Wielickie Foothills, Fig. 1). Edaphic parameters: soil moisture content, soil pH, content of the assimilable forms of N, P, K and of humus, elevation a.s.l. and insolation were examined. Floristic data (species frequency) collected by the transect method and environmental data were subjected to DCA (Figs. 2, 3 and 4) and CCA (Figs. 5a, 5b and 5c) ordination. The factor searched for proved to be the soil moisture content that was related to the relief of the terrain. Moreover, a considerable effect was exerted by microsite fertility conceived in a broad sense (soil pH, soil contents of humus and assimilable forms of N, P, K). Groups of species associated with the different parameters were singled out. Eigenvalues in indirect ordination (CCA) were lower than those in direct ordination (DCA); this indicates that the examined factors do not explain all causes of heterogeneity of forest floor vegetation.

The present results pointed to a clear-cut relationship between the occurrence of *Rubus hirtus* and tree stand clearing, an increase in species richness in the areas situated at ravine bottoms, and correlation between the species richness and elevated levels of the investigated mineral components, as well as to an effect of perturbances in the habitat (small changes caused an increase in the number of species and substantial ones led to dominance of one species) – (Figs. 6–9). Moreover, the ecological optima of selected species in soil moisture gradient and the ecological amplitudes were considered (Fig. 10). The observed opportunistic specialization between *Oxalis acetosella* and *Ficaria verna*, related to temporal variation, was of interest. Species richness and Shannon index changed significantly in the course of the vegetation season, and depended on the type of microsite. According to the Shannon index, species diversity was greatest in early summer, whereas in spring there was dominance of *Ficaria verna* (Circaeo-Alnetum) and *Anemone nemorosa* (Tilio-Carpinetum), and in

autumn – that of *Galeobdolon luteum*. The evenness index exhibited no significant changes both during the vegetation season and in relation to the type of plot (Fig. 11).

Results of soil analysis confirmed general acidification and impoverishment of the lessivated soils of the Wielickie Foothills.

8. POLISH SUMMARY

Celem badań przeprowadzonych w 1991 r. (wstępnie w 1990r.) było znalezienie czynnika decydującego o przestrzennym modelu gatunków runa leśnego w niewielkiej skali (las "Ligęzianka", Pogórze Wielickie, rys. 1). Rozpatrywano parametry edaficzne: wilgotność gleby, pH, zawartość przyswajalnych form N, P, K, próchnicy oraz wysokość n.p.m. i naświetlenie. Zebrane metodą transektu dane florystyczne (frekwencja) i środowiskowe poddano porządkowaniu DCA (rys. 2–4) oraz CCA (rys. 5 a–c). Poszukiwanym czynnikiem okazała się wilgotność gleby, która była związana z rzeźbą terenu. Duży wpływ miała również szeroko pojęta żyzność siedliska (odczyn gleby, zawartość próchnicy i przyswajalnych form N, P, K). Wyróżniono grupy gatunków związane z poszczególnymi parametrami. Wartości własne w porządkowaniu pośrednim (CCA) były niższe niż w porządkowaniu bezpośrednim (DCA), co wskazuje, że badane czynniki nie wyczerpują przyczyn zmienności runa leśnego.

Zaobserwowano wyraźny związek występowania *Rubus hirtus* z prześwietleniem, wzrost bogactwa gatunków na powierzchniach w dnach wąwozów i ich korelację ze zwiększoną zawartością badanych czynników, a także wpływ zaburzeń – małe powodują wzrost ilości gatunków, duże prowadzą do dominacji jednego (rys. 6–9). Rozpatrywano także optima ekologiczne wybranych gatunków w gradiencie wilgotności gleb oraz amplitudy ekologiczne (rys. 10). Interesującym zjawiskiem była specjalizacja oportunistyczna między *Oxalis acetosella* i *Ficaria verna* związana ze zmiennością czasową. Bogactwo gatunkowe i wskaźnik Shannona zmieniają się istotnie podczas sezonu wegetacyjnego oraz zależą od typu siedliska. Wskaźnik Shannona wykazał, że największa różnorodność gatunków charakterystyczna jest dla wczesnego lata, natomiast wiosną zaznacza się dominacja *Ficaria verna* (Circaeo-Alnetum) i *Anemone nemorosa* (Tilio-Carpinetum), a jesienią *Galeobdolon luteum*. Wskaźnik równomierności nie podlegał istotnym statystycznie zmianom zarówno podczas sezonu wegetacyjnego, jak również w obrębie typu siedliska (rys. 11).

Wyniki analiz glebowych potwierdziły ogólne zakwaszenie i zubożenie gleb płowych Pogórza Wielickiego.

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ANNEX

The list of Latin names of plant species used in figures

| | |
|---------------|-------------------------------------|
| <i>Ad mos</i> | <i>Adoxa mochatellina</i> |
| <i>Ae pod</i> | <i>Aegopodium podagraria</i> |
| <i>Aj rep</i> | <i>Ajuga reptans</i> |
| <i>An nem</i> | <i>Anemone nemorosa</i> |
| <i>As eur</i> | <i>Asarum europaeum</i> |
| <i>At fil</i> | <i>Athyrium filix-mas</i> |
| <i>Ca ama</i> | <i>Cardamine amara</i> |
| <i>Ca bri</i> | <i>Carex brizoides</i> |
| <i>Ca pal</i> | <i>Caltha palustris</i> |
| <i>Ca pil</i> | <i>Carex pilosa</i> |
| <i>Ch alt</i> | <i>Chrysosplenium alternifolium</i> |
| <i>Ci lut</i> | <i>Circaea lutetiana</i> |
| <i>Co sol</i> | <i>Corydalis solida</i> |
| <i>Cr pal</i> | <i>Crepis paludosa</i> |
| <i>Dr fil</i> | <i>Dryopteris filix-mas</i> |
| <i>Eq hie</i> | <i>Equisetum hiemale</i> |
| <i>Fe gig</i> | <i>Festuca gigantea</i> |
| <i>Fi ver</i> | <i>Ficaria verna</i> |
| <i>Fi ulm</i> | <i>Filipendula ulmaria</i> |
| <i>Ga apa</i> | <i>Galium aparine</i> |
| <i>Ga lut</i> | <i>Galeobdolon luteum</i> |
| <i>Ga pub</i> | <i>Galeopsis pubescens</i> |

| | |
|---------------|--------------------------------|
| <i>Ge rob</i> | <i>Geranium robertianum</i> |
| <i>He hel</i> | <i>Hedera helix</i> |
| <i>Im nol</i> | <i>Impatiens noli-tangere</i> |
| <i>Im par</i> | <i>Impatiens parviflora</i> |
| <i>Lu pil</i> | <i>Luzula pilosa</i> |
| <i>Ly nem</i> | <i>Lysimachia nemorum</i> |
| <i>Ma bif</i> | <i>Majanthemum bifolium</i> |
| <i>Me rub</i> | <i>Melandrium rubrum</i> |
| <i>Ox ace</i> | <i>Oxalis acetosella</i> |
| <i>Po mul</i> | <i>Polygonatum multiflorum</i> |
| <i>Po nem</i> | <i>Poa nemoralis</i> |
| <i>Pe ela</i> | <i>Primula elatior</i> |
| <i>Pu obs</i> | <i>Pulmonaria obscura</i> |
| <i>Ru hir</i> | <i>Rubus hirtus</i> |
| <i>So dul</i> | <i>Solanum dulcamara</i> |
| <i>Ur dio</i> | <i>Urtica dioica</i> |
| <i>Vi riv</i> | <i>Viola riviniana</i> |

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