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Regular research paper

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SCOTS PINE FORESTS OF THE *VACCINIO-PICEETEA* CLASS IN EUROPE: FOREST SITES STUDIED

ABSTRACT: The paper presents: a) the general differentiation of the pine forests of Europe, and b) the floristic differentiation of the ten study sites, located along the transect stretching between 50°28' and 70°09' N, as well as c) the relations between the geographical location and the climatic characteristics on the one hand, and the selected features of the richness and species diversity of the herb layer on the other.

One can observe a dependence ($p < 0.05$) between the temperature and latitude on the one hand, and the number of species from some groups on the other. For the vascular plants, the indicators of linear correlation amount to, respectively, 0.64 and -0.63 (the number of the vascular species of the herb layer increases with the warming of climate and the movement towards the South), and for the numbers of lichen species: -0.81 and 0.78 (the dependencies have the opposite directions to the previous ones).

The variability of the relative shares of the particular species groups is correlated with geographical location and climatic variables. Three basic patterns of spatial variability can in this context be identified. The first of these is represented by the share of the lignified *chamaephytes* (dwarfshrubs). In accordance with this pattern, the minimum shares are observed at the latitudes of Lithuania, Latvia, and Estonia.

The second pattern of variability is represented by the shares of *hemicryptophytes*. In accordance

with this pattern the maximum shares are observed between 53° and 56° N. The third pattern of variability is represented, in particular, by the share of the evergreen species which is proportional to the latitude.

KEY WORDS: Scots Pine, life forms, geographical variability

1. INTRODUCTION

1.1. THE EUROPEAN RANGE OF THE SCOTS PINE (*PINUS SILVESTRIS* L.)

The Scots pine (*Pinus silvestris* L.) belongs to the coniferous trees having the broadest range in the world. From West to East this range stretches from the Atlantic coast to the Okhotsk Sea at the coasts of East Siberia (equivalent to 165 longitude degrees, that is – more than 8,000 km) (Nikolov and Helmisaari, 1992). The northernmost range of the natural stands of Scots pine in Europe exceeds 71° N in Scandinavia, while in the South it reaches central Spain and the Balkans, at about 40° N (this distance being equivalent to the stretch of more than 30 degrees of latitude, that is – more than 3,500 km) (Fig. 1).

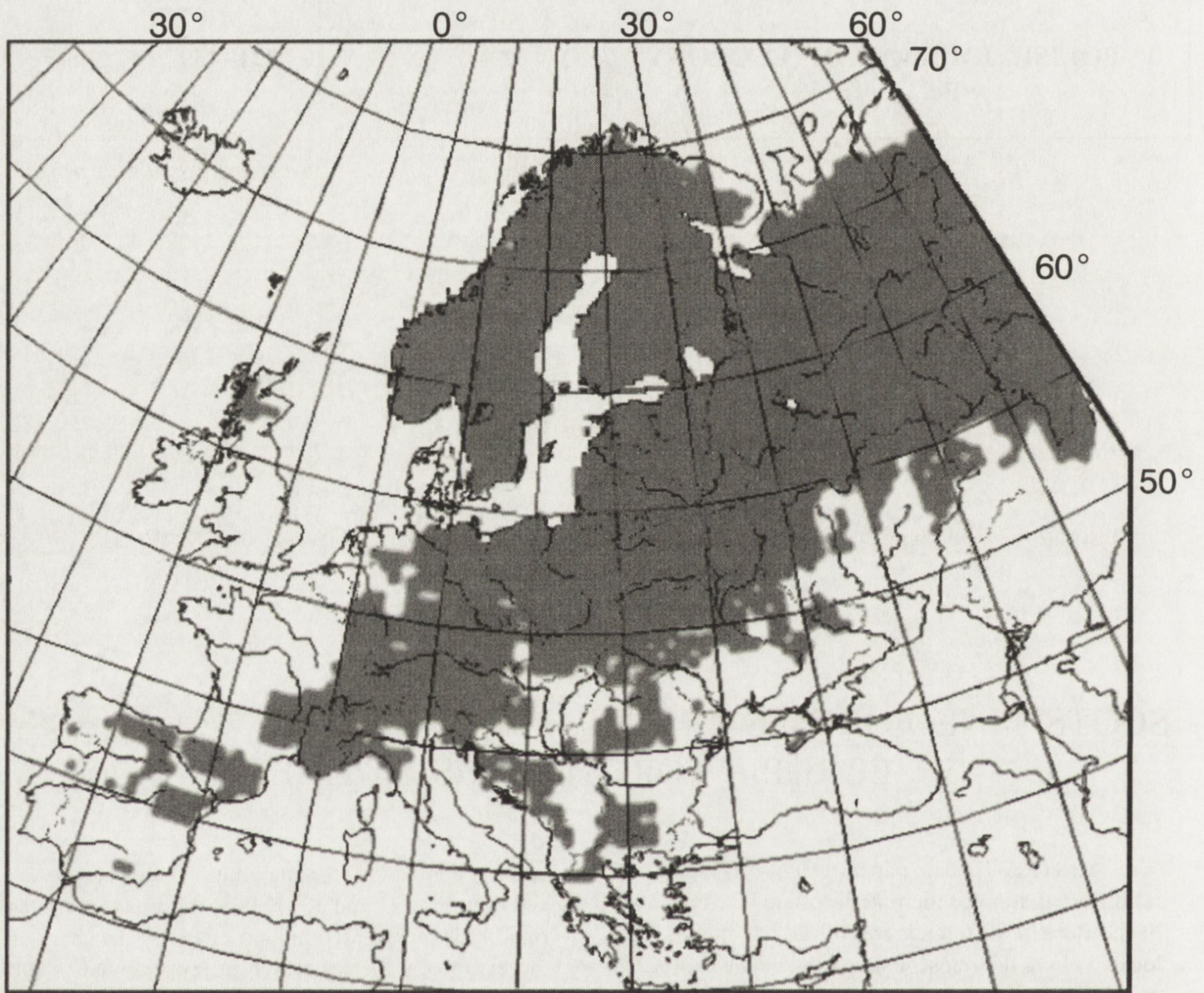


Fig. 1. Distribution of Scots pine (*Pinus silvestris*) in Europe (dark area) Elaborated on the basis of Jalas and Suominen, 1973, modified and simplified.

Within its entire geographical range pine is adapted to various climates. It occurs both in locations featuring annual precipitation exceeding 1700 mm, and in the dry climate, with annual precipitation about 200 mm (Kelly and Connolly, 2000). In Europe it grows in various climatic zones: oceanic, sub-oceanic, sub-continental, continental, mountain, and Mediterranean (Ellenberg, 1988). Pine can grow on various bedding and soils. In the northern part of the continent dominating are locations associated with acid sandy bedding and podzolic-earth soils, while in the South pine more frequent grows on the rocky carbonate soils. At the northern (Scandinavia) and western (Scotland) limits of the European range, as well as in the mountains, pine is also encountered on the shallow, young soils having developed from the acid granite rocks. It is quite common, although never over very large areas, to have

pine stands growing on the peat soils, having developed from the high and intermediate peat.

The distribution of the Scots pine in particular regions of Europe results from:

a) its high resistance to stress caused by the unfavourable habitat conditions (low temperatures, extremely acid or alkaline bedding, drought, etc.),

b) low competitive capacity with respect to other tree species, which push out pine from the more favourable habitats,

c) the history of climate changes and of the Holocene migrations.

It is assumed that pine is the species of continental nature. Some 10,000 years BP, after the continental ice cover had receded, the expansion of pine started from Central Europe in the northern and western directions. The maximum range, encompassing the entire northern Scotland and Ireland, took

place approximately 6,000 years BP (Kelly and Connolly, 2000). It is commonly held that there were two migration waves, from two different refuges (Sinclair *et al.*, 1998). Some 4,000 years ago the range started to shrink again. Pine disappeared from Ireland at about 1000 AD (Bradshaw and Browne, 1987), and at more or less the same time it also receded from the present-day territory of Belgium (Huntley and Prentice, 1993). The fluctuations of the range and the extinction on the local scale were taking place later on, as well, due to the climatic changes. The studies of Kullman (1986) imply that pine disappeared from central Sweden almost entirely until the year 1700, that is – in the period of the “little ice age”, and the re-colonisation of this area started only in the middle of the 18th century.

The present sites of the Scots pine stands on the Iberian Peninsula have the relic character. After the wave of expansion, which took place in the pre-boreal and partly boreal period (some 9–7 thousand years BP) the range of the cool forests with domination of *Pinus silvestris* started to shrink. This phenomenon intensified in the Atlantic period (approximately 7,500–4,500 years ago) when, along with the progressing warming and the increase of humidity, the deciduous forests, primarily based upon oaks and beeches, developed. The present distribution of the Scots pine in this region is associated with the topographic locations, which are too difficult for the other tree species to occupy (Martínez García and Montero, 2000).

1.2. THE DISTRIBUTION OF THE PINE FORESTS IN EUROPE

The wide geographical range and the possibility of existence within various habitats cause that the Scots pine is one of the most important forest forming and admixture species in many different types of forest communities of Europe. The classification of these units on the Europe-wide scale is a difficult task, and has not been accomplished entirely until today. Only the division into two groups is relatively distinct, called by Ellenberg (1988), respectively “the northern forests”, characterised by the low species diversity, and by the appearance on acid soils, and “the southern forests”, with a significant species richness. This kind of perception, of the ecological-physiognomic character, found its reflection also in the more recent

cartographic elaborates (see Bohn and Katenina, 1996), as well as in the characteristics concerning the NATURA 2000 system (*The Interpretation Manual...*, 1999).

From the point of view of the phytosociological classification the forests with domination of the Scots pine are assigned to two classes: *Erico-Pinetea* Horvat 1959, and *Vaccinio-Piceetea* Br.-Bl. 1939. Besides, the Scots pine occurs relatively frequently in the forest and shrub communities belonging to the classes of *Quercu-Fagetea* Br.-Bl. et Vlieg. 1937, *Quercetea robori-petraeae* Br.-Bl. et R. Tx. 1943, as well as *Pino-Juniperetea* Rivas-Martínez 1964.

The class of *Erico-Pinetea* encompasses very numerous xerothermic forest and shrub communities with domination of various pine species, including also the Scots pine, occurring on the limestone bedding within the particularly dry habitats, in the soil and topo-climatic terms, of the southern part of Europe, to the South of Czech, Slovakia and Germany, down to the Balkan Peninsula. These communities are floristically very rich, with a specific combination of the strongly xerothermic and lime-loving species of the Mediterranean type of range with the forest species of boreal-continental type of range.

The *Vaccinio-Piceetea* class encompasses the holarctic-boreal, acidophilic, oligo- and meso-trophic communities featuring the domination of the coniferous tree species, with the shrubs and the mesophilic mosses. This class encompasses in Europe the lowland and mountain spruce, pine and fir forests, the major part of the mixed forests, as well as the majority of the sub-alpine and sub-polar shrubs and dwarfshrub formations. Within this class the pine forests constitute the order of *Cladonio-Vaccinietalia* Kiell.-Lund 1967. This subdivision includes forest communities with domination of the Scots pine and/or the birch varieties among the trees, and the grassy-dwarfshrub and mossy herb layer, frequently with a significant share of the lichens.

The habitat area of the pine forests of Europe, belonging to the class of *Vaccinio-Piceetea* and the order *Cladonio-Vaccinietalia*, stretches meridionally between approximately 71° N in Scandinavia and approximately 50° N in Poland and Ukraine – that is, to the North of the Carpathian crescent. The isolated stands are encountered on the Balkans and in the Caucasus Mts., even at the latitude of roughly 42° N. In

the East-West direction these forests stretch between the Ural Mts. (60° E) and 12° E in southern Scandinavia (although isolated Scandinavian stands exist even at 8° E). The westernmost sites (at about 6° W) exist in Scotland (Fig. 2).

The proper pine forests belong to the *Cladonio-Vaccinietalia* order, and are differentiated into several ecological groups. In a very rough approximation we can divide them into dry, fresh, wet, and boggy forests.

The fresh pine forests, of interest to us here, are linked with the sandy areas, mainly with the outwash fields, the dune sands, and river terraces, occupying altogether in Europe more than 9% of total area. In only few cases they are encountered on the rocky bedding, like, for instance, in Scandinavia, in Scotland, and in the mountain areas (in south Poland, for instance, in Stołowe Mts.).

With respect to the phytogeographical differentiation four European regions of oc-

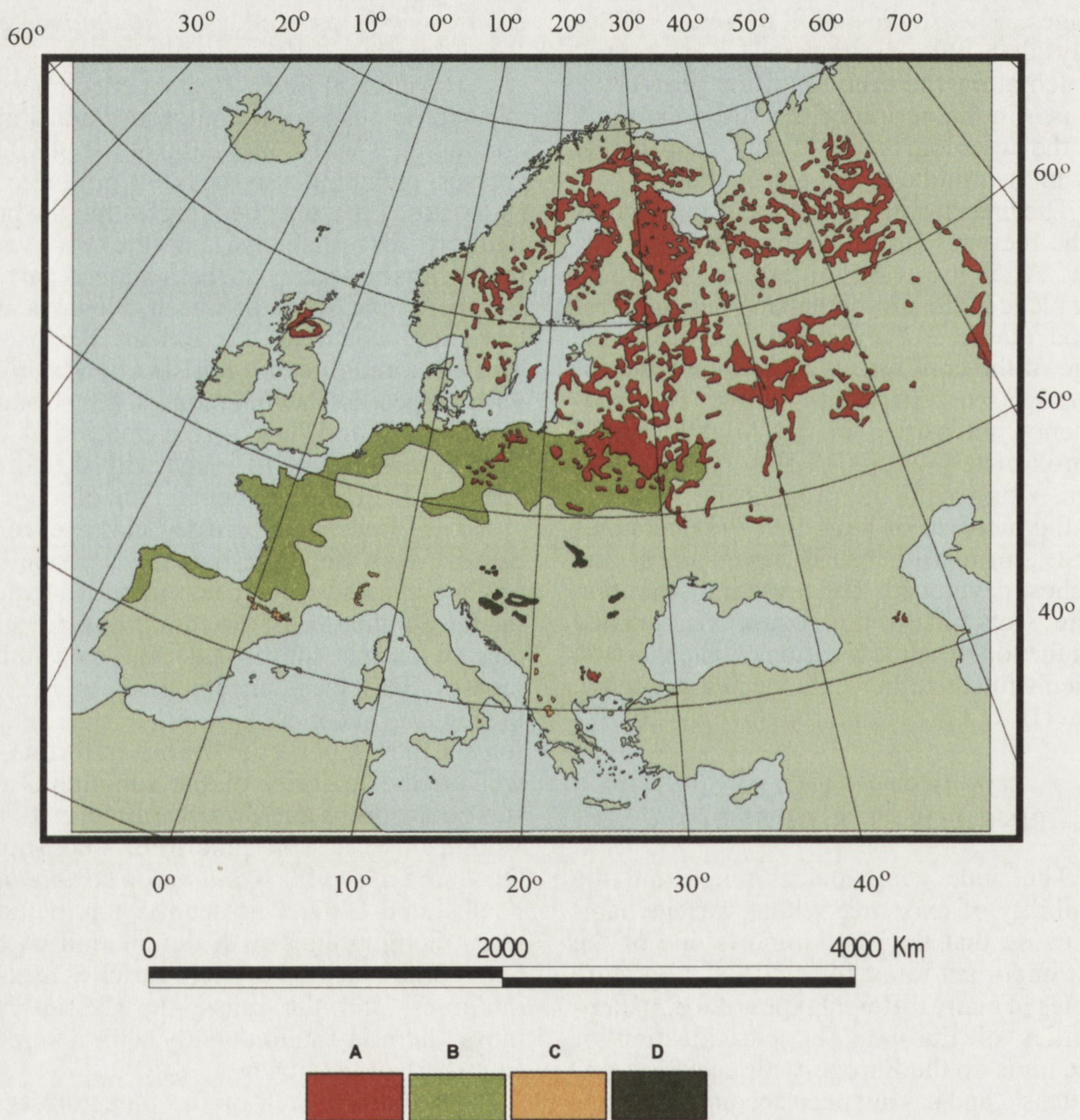


Fig. 2. Distribution of Scots pine forests in Europe (elaborated on the basis of Bohn and Katenina, 1996, modified and simplified). A – the main areas of occurrence of the Scots pine forests of the *Cladonio-Vaccinietalia* order; B – the general distribution of forests of *Quercetea roburi-petraeae*, *Erico-Pinetea* and *Pino-Juniperetea* classes with the occurrence of oaks and *Pinus sylvestris*, as well as of mixed oak-pine forests of the *Dicrano-Pinion* alliance; C – the isolated, south European stands of the Scots pine forests of the *Cladonio-Vaccinietalia* order; D – selected areas with *Pinus sylvestris* forests of *Erico-Pinetea* and *Pino-Juniperetea* classes.

currence of the fresh pine forests can be distinguished:

- a) Scandinavia,
- b) Central-Eastern Europe,
- c) North-Western Europe, and
- d) Southern Europe.

Conform to the traditional way of defining plant communities, applied to date (Cajander, 1921; Kujala, 1929; Ilvessalo, 1937), several types of pine forests are distinguished in Scandinavia. The most common is the *Pinus-Cladonia* type. It occurs over almost entire area, except for the mountain regions, in conditions of continental climate, with low precipitation. This type is characterised by a weak development of the shrub layer and a high share of lichens in the herb layer. In phytosociological terms this type is represented by the broadly conceived association known under a couple of names, like, for instance, *Cladonio-Pinetum boreale* Kielland-Lund 1967, or *Cladonio-Pinetum sylvestris* Olsson 1974.

Another widely occurring type is *Pinus-Calluna-Empetrum*. It occurs on cool areas with low evapotranspiration, up to the subalpine floor. It features a quasi-constant admixture of the birch *Betula pubescens ssp. czerepanovii*. Likewise, such species as *Calluna vulgaris*, *Empetrum hermaphroditum*, *Empetrum nigrum*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, and in the North also *Vaccinium uliginosum*, are persistently present. One of the forms of this type is represented by the association *Barbillophozio-Pinetum* Kielland-Lund 1981.

In the subalpine belt of western Norway, in conditions of the maritime climate, two specific types of pine forests occur. The first of them, *Pinus-Bazzania*, is characterised by the domination of the pine and a limited share of the birch. In accordance with the phytosociological classification it is represented by the association *Bazzanio-Pinetum* Kielland-Lund 1981. On the other hand, the second type, *Pinus-Epipactis*, is often a birch wood with a small share of pine. It is represented by the association *Epipacti atrorubentis-Betuletum* Björndalen 1980.

In central Sweden and northern Finland, in conditions of low precipitation and high temperature amplitudes, the type of *Pinus-Calamagrostis lapponica* occurs, characterised by the lack or low degree of heath (*Calluna vulgaris*) coverage.

In central and southern Scandinavia, on locations featuring relatively low precipita-

tion, most often on the bedding of the sandy moraines, the type of *Pinus-Vaccinium vitis-idaea* is widespread. In the majority of cases it can be identified with the association of *Vaccinio-Pinetum empetretosum* Olsson 1974.

The subsequent three types of pine forests occur on the southern extremes of Scandinavia, in places, which are relatively warmer, often with southern exposure and the more fertile bedding. Their species composition contains the species of the more southern or south-eastern distribution type. The first of the three is *Pinus-Convallaria*, encompassing pure pine forests, with domination of grasses and herbs in the herb layer floor. This type can be identified with such communities as *Saniculo-Pinetum* Björndalen 1980, *Convallario-Pinetum* Björndalen 1980, *Seslerio-Pinetum* Björndalen 1980, *Melico-Pinetum* Marker 1969. The two remaining types, *Pinus-Fragaria* and *Pinus-Lathyrus-Rubus saxatilis*, are characterised by a relatively high share of the deciduous trees, and the presence of numerous species from the family of *Fabaceae*.

The Central-Eastern Europe is the area of domination of two associations of regional character: *Leucobryo-Pinetum* Mat. (1962) 1973, and *Peucedano-Pinetum* Mat. (1962) 1973. The first of them is observed in the western part of the area, encompassing southern Poland (Matuszkiewicz, 2001), and the whole Germany, and reaching The Netherlands (Kelly and Connolly, 2000) as well as Austria (Mucina *et al.*, 1993). The second of the communities has a subcontinental character, and it occurs, in particular, in central and north-eastern Poland, in Lithuania and Belarus'. The associations mentioned do not exhaust the entire diversity of the Central-European fresh pine forests. Thus, for instance, the association *Festuco eggleri-Pinetum*, featuring a limited geographical range, is linked with the serpentinite bedding, while *Empetro nigri-Pinetum* occurs in the belt of coastal dunes of Poland and Germany. One should also pay attention to the fact that this area constitutes the origin of numerous other communities representing the fresh pine forests (like, for instance, *Dicrano-Pinetum*, *Myrtillo-Pinetum*, *Vaccinio vitis-idaeae-Pinetum*, *Cardaminopsio petraeae-Pinetum*, *Festuco supinae-Pinetum*, *Festuco-Pinetum serpentinum*, *Festuco ovinae-Pinetum* – Kelly and Connolly, 2000), although in their majority they

can be treated as synonymous names or the local variations of the two primary regional forms.

Pine forests occur in north-western Europe only in the North of Scotland, where they cover approximately 17,000 hectares, which constitutes roughly 1% of the probable original range (Rodwell, 1991). They are represented mainly by the association *Hylocomio-Pinetum* auct., and their patches frequently contain numerous forest generalists (Rodwell, 1991; Kelly and Connolly, 2000).

In southern Europe the pine forests from the class of *Vaccinio-Piceetea* are altogether rare, and their various classifications have only local validity. At least two different communities occur in Bulgaria, one with the domination of dwarfshrubs, and the other with a high share of *Calamagrostis arundinacea* in the herb layer. They occupy the poorest sites in the upper parts of the Rodepe, Pirin, and Rila mountains (Bondev, 1991). In Greece, the weakly pronounced pine woods of the *Vaccinio-Piceetea* class occur in the mountain and subalpine zones of the ranges of Pieria, Bermio, Aridea, Lailias and Orvilos (Dafis, 1976; Spanos *et al.*, 2000). In Spain, where there are relatively many forests with *Pinus silvestris*, only the association of *Veronico-Pinetum silvestris* Rivas-Martínez 1968, can be unambiguously classified in the *Vaccinio-Piceetea* class. The remaining communities represent most probably the associations belonging to other classes (Martínez García and Montero, 2000).

1.3. AIM OF STUDY

In the years 1991–2000 studies were conducted in the pine forests, with the primary aim of assessing the reaction of the forest ecosystems to climate changes. The decision was made to conduct these studies in the most common and at the same time economically most important pine forests, and to apply the method of transects, cutting across the various climatic zones of Europe (Breymer, 1997). The majority of results concerning the variability of the pine forests along the parallel transect (stretching along the latitude of 52° N) were already published (Breymer and Roo-Zielińska, 1998; Roo-Zielińska and Solon, 1997, 1998a, b, c; Solon and Roo-Zielińska, 1998; Solon, 1998). The results presented cur-

rently concern the forest study sites located along the N-S transect. The adopted approach in the analysis and presentation of results concerning the geo-botanical differentiation of the sites is analogous to the one applied in the studies devoted to the parallel transect (Roo-Zielińska and Solon, 1997, 1998a).

The purpose of the present paper is to show:

- a) the general differentiation of the pine forests of Europe, and, against this background,
- b) the floristic differentiation of the study sites, with the identification of their syntaxonomic position, and
- c) the determination of the relation between geographical location (which affects the macro-climatic differentiation and reflects the history of development of vegetation) and the climatic characteristics on the one hand, and the selected indicators of the species richness and diversity of the herb layer.

The subject of analysis is constituted by ten forest study plots, located along the transect stretching between 50°28' and 70°09' N, at which studies were conducted in the years 1997–2000 (see Fig. 1 in Breymer 2003a).

2. STUDY METHODS

The basis for the description of the ten study sites was constituted by the floristic characterisation of the vegetation patch, representing the given type of association, and recorded in the form of the phytosociological relevés (see Appendix 1 and 2). Each relevé contains the following information on the given vegetation patch: 1) species composition; 2) coverage (that is – the area shares of the particular species); 3) layer structure (the structural feature of the association, concerning its vertical aspect, with four layers usually being distinguished: trees – A, shrubs – B, herb layer – C, the ground adjacent layer – i.e. mosses and lichens – D). The majority of the phytosociological relevés were made in 1997, and for the Norwegian site – in 2000. Each relevé was made for the area of 400 m². The quantitative coverage characteristics of the species were evaluated according to the modified 12-point scale, in which “r”, “+”, “1” denote, respectively, 0.1%, 0.5%, and up

to 10%, while the remaining values from 2 to 10 denote the successive 10-per-cent intervals. The species of the vascular plants were distinguished on the basis of the key of Szafer, *et al.* (1969), and their names were conform to the elaboration of Rothmaler (1976). The mosses were distinguished by Ewa Fudali from the Academy of Agriculture in Wrocław, while lichens – by Wiesław Fałtynowicz from the University of Wrocław. The phytosociological relevés obtained were put together in the table.

On the basis of the floristic composition of the herb layer mutual similarities of the selected forest associations were calculated with the use of the Bray-Curtis distance measure, represented through the dendrogram obtained from the group average link algorithm of cluster analysis.

On the basis of information contained in each of the ten phytosociological relevés the numbers and the surface shares of the species representing the different Raunkiaer's life forms were determined, along with the types of persistence of leaves, and the types of anatomical structure. The detailed characterisations of the species were taken from the list of Ellenberg (1974). The interdependencies between the geographical location and the climatic characteristics (these two taken as

independent variables), and the shares of the species representing the particular ecological groups were determined on the basis of correlation and regression analysis. The climatic characteristics were composed of the long-term average of annual precipitation, long-term average of annual temperature (see Breymeyer, 2003a, b), as well as the Lang and Martonne indices. The index of Lang (Lang, 1915) is expressed as $L = (\text{annual precipitation} / \text{mean annual temperature})$, while the index of Martonne (Martonne, 1926) is defined as $M = [\text{annual precipitation} / (\text{mean annual temperature} + 10)]$.

3. RESULTS

3.1. FLORISTIC RICHNESS OF THE STUDY SITES

Appendix 1 presents the phytosociological relevés of the study sites. The plots analysed are relatively poor in terms of the numbers of herb layer species (between nine at FN1 and 24 at PL2), although altogether as many as 54 species appeared in all the relevés. Besides, the presence of six species of trees as well as 15 species of shrubs, and 26

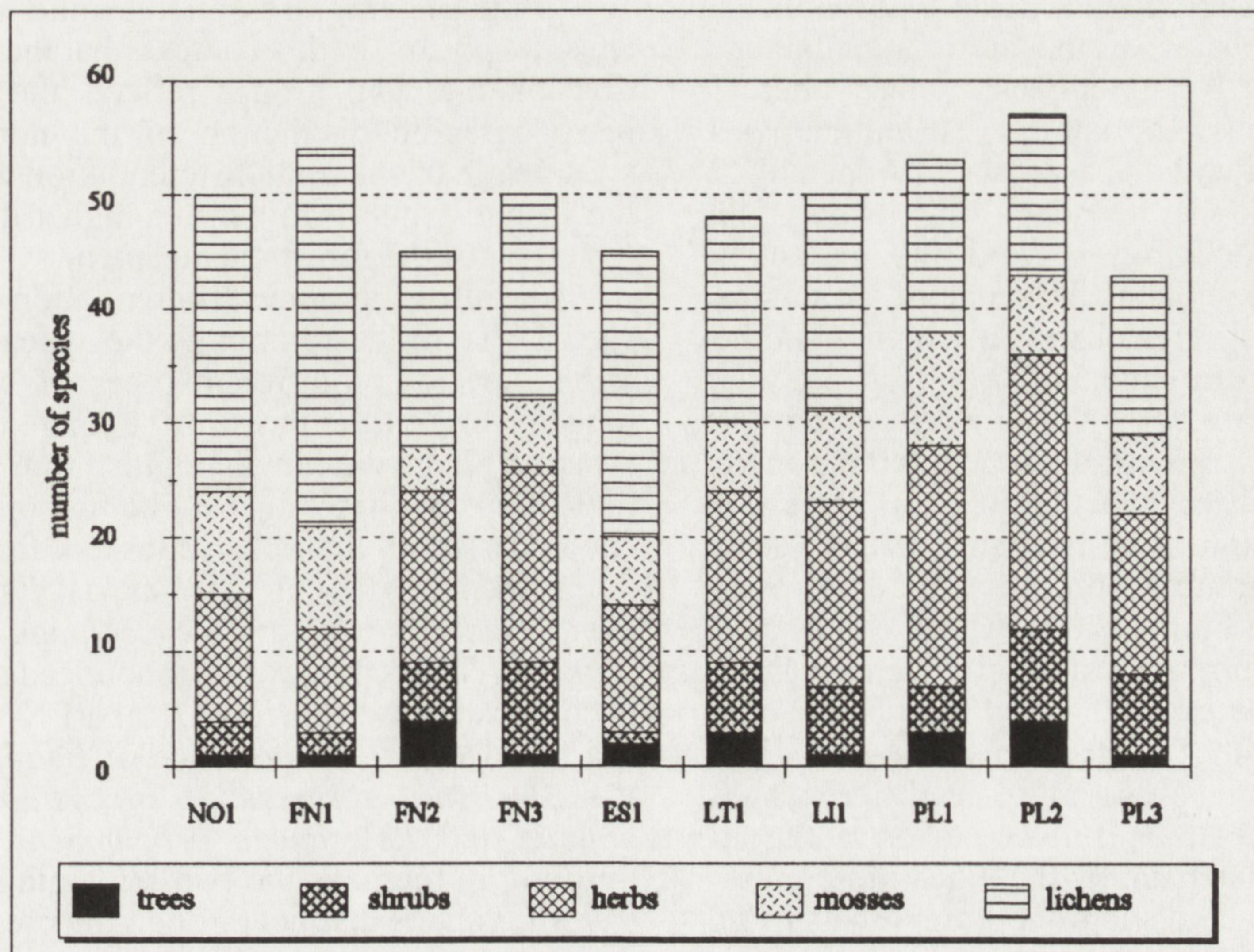


Fig. 3. The number of species on study sites.

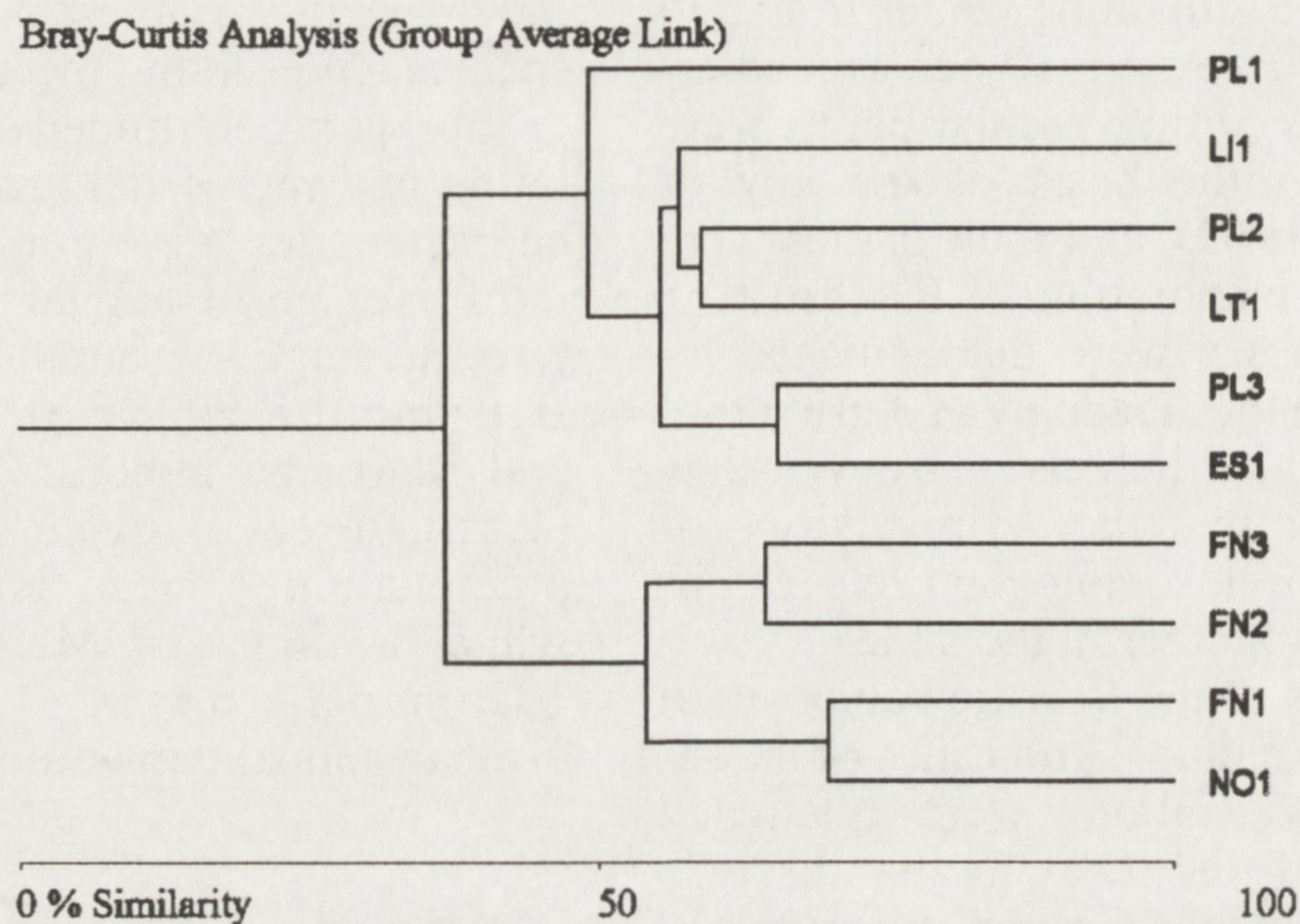


Fig. 4. The dendrogram of similarities among the species composition of the herb layer vascular plant species of the study sites (based on the species cover).

species of mosses (of which three were the northern species from the genus *Dicranum*: *D. brevifolium*, *D. drummondii* and *D. elongatum*) was registered.

Appendix 2 illustrates the differentiation of lichens on the sites studied. The total number of species registered on all the sites was 80. The largest number of lichens grew on wood (46) and on the bark of the trees (33), less on the ground (22), and only nine on the rock bedding. Particularly pronounced are the species of the arctic-mountainous, arctic-boreal-mountainous, and boreal-mountainous geographical distribution types, designated with the asterisks in Appendix 2.

Taking into account all the layers of the forest association, and all the systematic groups, one obtains the range of the number of all the species observed within a site between 43 (PL2) and 57 (PL2), (Fig. 3).

With respect to the similarity of the species composition of the vascular plants composing the herb layer the sites analysed can be classified into two distinct groups (Fig. 4). The first group encompasses the Norwegian and all the Finnish sites, with the sites NO1 and FN1 forming a subgroup well separated from the sites FN2 and FN3. The second group includes all the remaining sites. This second group is also internally differentiated. Thus, an isolated position is taken by the site PL1, characterised by the much more grassy herb layer. The subgroup composed of PL3 and ES1 distinguishes itself in a negative manner, namely by the lack of a certain group of the species of the sub-continental charac-

ter. The last subgroup, composed of the sites LT1, LI1 and PL2, is the most representative one for the sub-boreal pine forests.

The similarity of the sites with respect to the composition of the lichen flora has a different aspect (Fig. 5). A clearly isolated position is taken by the sites NO1 and FN1. Within the second group two sub-groups can be distinguished. The first one includes the sites FN2, FN3, LI1 and PL3. The second sub-group encompasses all the other study sites. It appears, in this context, that the basic division into two groups reflects the clear bio-geographic distinction of the northern sites, while the internal differentiation within the second group is rather to a higher degree the effect of the forest management.

The bio-geographic differentiation of the sites is also reflected through the appearance of the species of different types of spatial range. Thus, on the basis of the range of the vascular plants we can distinguish four separate groups of sites (Fig. 6). The first of them encompasses all the Polish sites and features the presence of such species as *Festuca ovina*, *Quercus robur* and *Peucedanum oreoselinum*. The second, well-pronounced group is composed of the sites NO1 and FN1. It is characterised by the presence of *Betula pubescens* ssp. *czerepanovii*, *Arcostaphylus alpinus* and *Loiseleuria procumbens*. The third group includes the two remaining Finnish sites and is distinct through the presence of *Linnaea borealis* and *Empetrum nigrum*, that is – the species, which occur also on the sites classified in the previous group. The

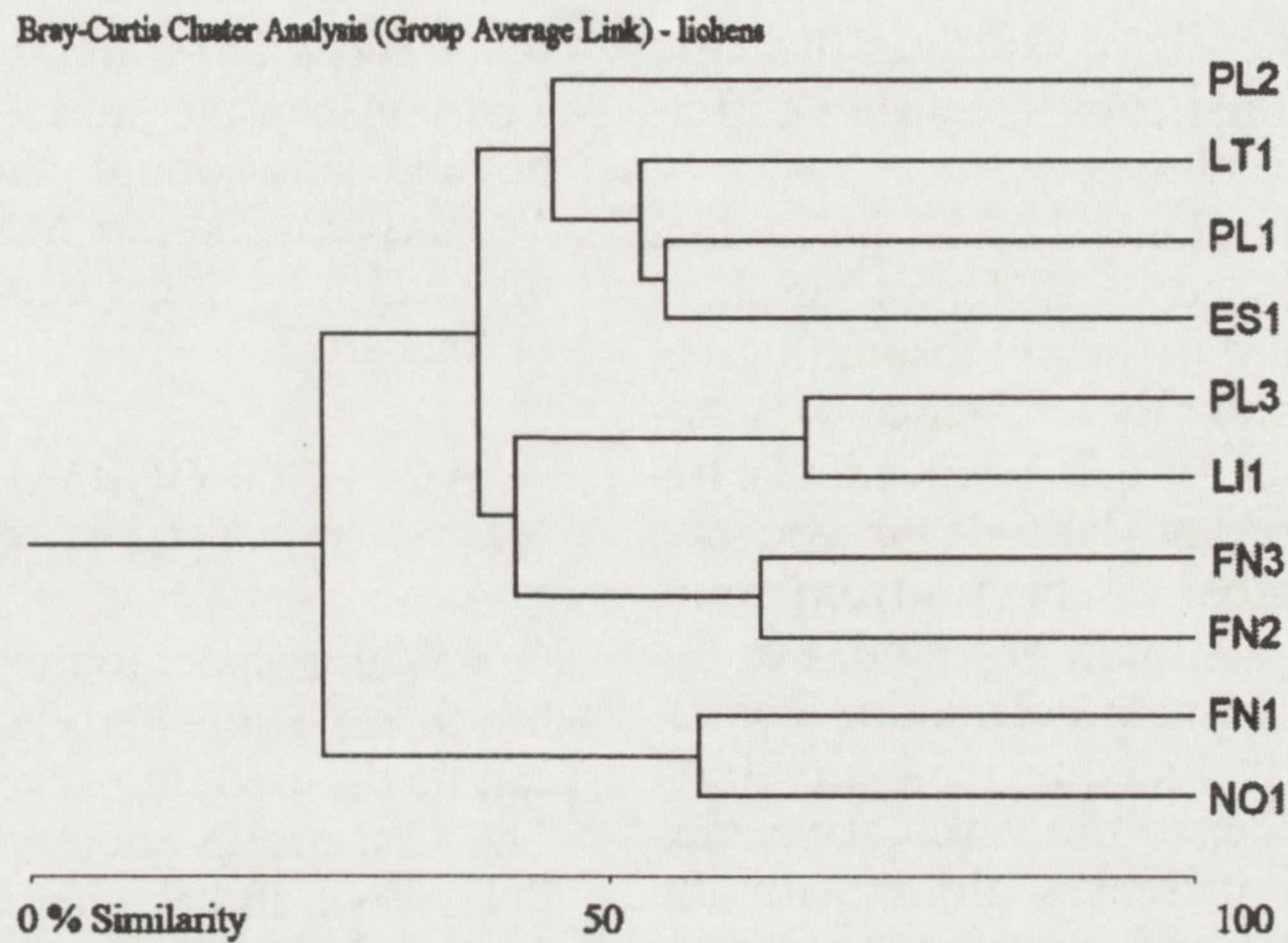


Fig. 5. The dendrogram of similarities among the species compositions of the lichen layer of the study sites (based on the species number).

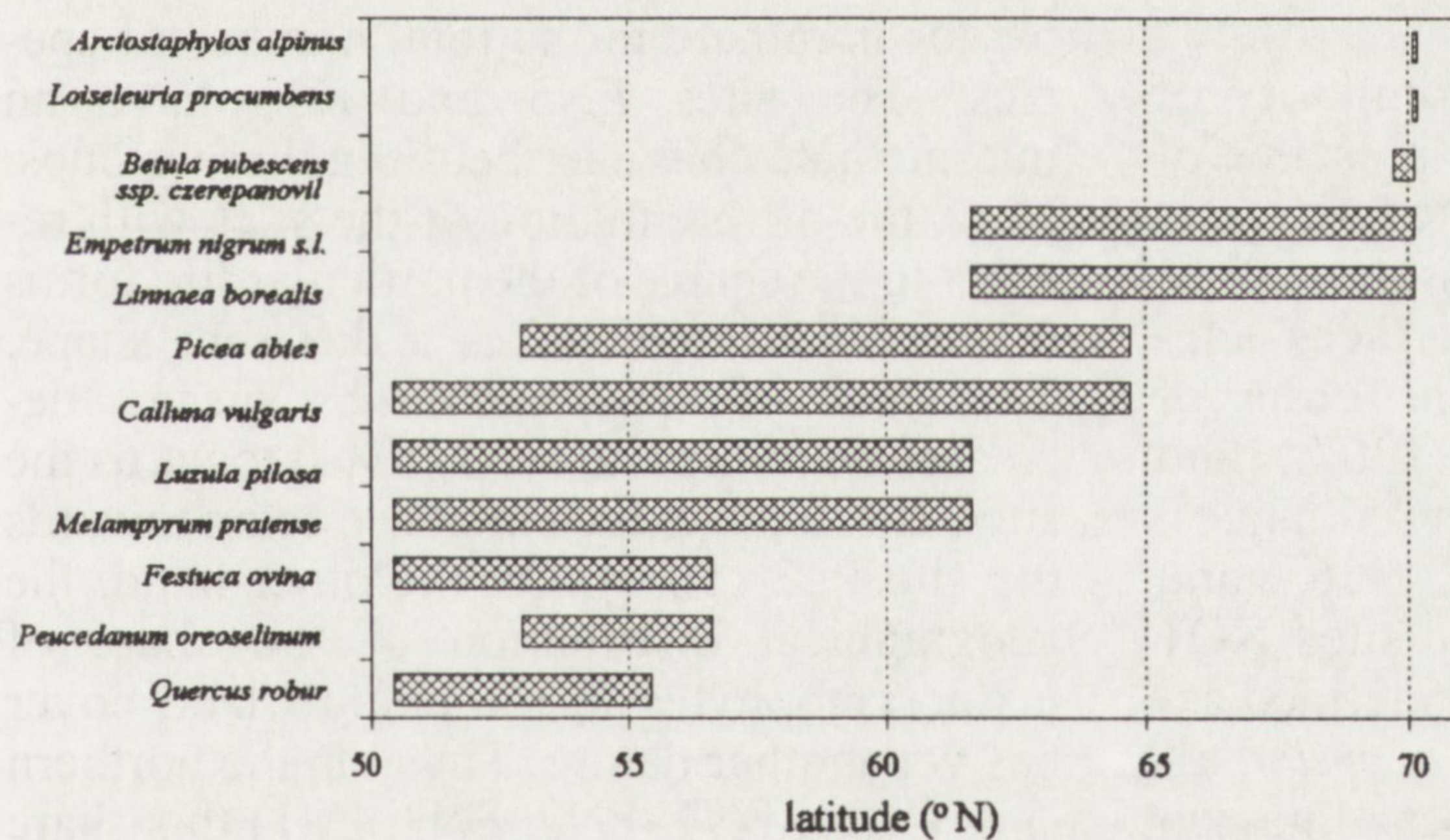


Fig. 6. The presence of selected vascular plant species along the N-S transect.

last, fourth site group, composed of the sites ES1, LT1, LI1, is characterised by the lack of two groups of species, namely those of the clearly northern type of range and the southern ones.

The differentiation of the sites with respect to the appearance of the definite lichen species is not so unambiguous (Fig. 7). Except for the distinctly different sites NO1 and FN1 the composition of the lichen flora in the remaining part of the transect changes in a relatively smooth manner. Attention might only be paid to

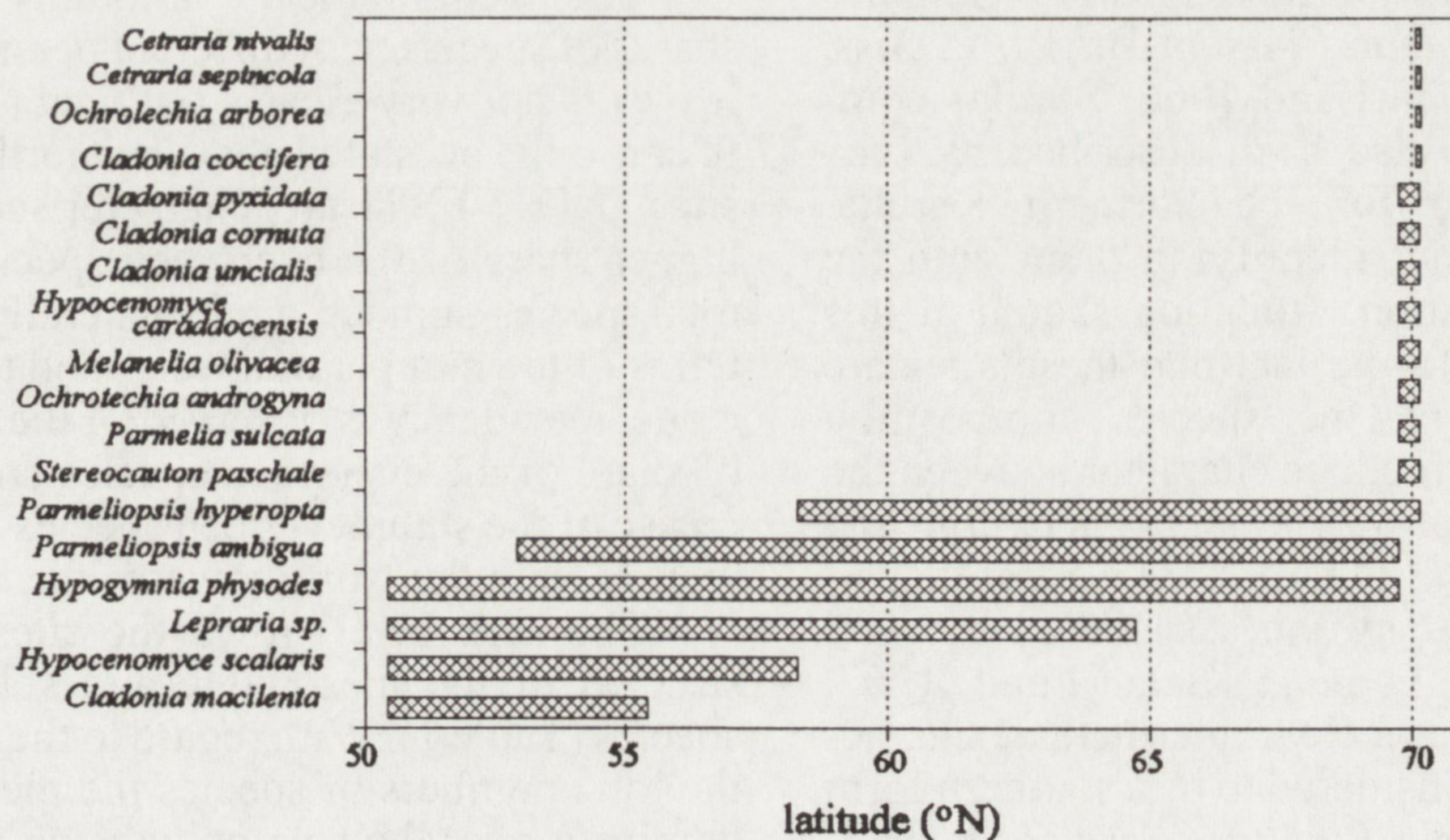


Fig. 7. The presence of selected lichen species along the N-S transect.

the fact that the site ES1 constitutes the limit of appearance of the lichen species of different types of spatial range.

As already mentioned before, individual sites are characterised by different numbers of species registered in the phytosociological relevé. In this context the existence of a statistically significant ($p < 0.05$) dependence between temperature and latitude on the one hand, and the number of species from some groups on the other should be noted. For the vascular plants the linear correlation coefficients are, respectively, equal 0.64 and -0.64 (that is – the number of the vascular species of the herb layer increases along with the warming of climate and with the movement towards the South), and for the numbers of the lichen species, respectively -0.81 and 0.78 (meaning that the tendency has the opposite direction).

The differentiation of the similarity of the species composition and the presence of species with a limited geographical range is reflected in the syntaxonomic assignment of the plant associations of the surfaces analysed. All of them represent the order of *Cladonio-Vaccinietalia* Lund 1967, and within its framework – two alliances: *Phyllodoco-Vaccinion* Nordh. 1936, and *Dicrano-Pinion* Libb. 1933. The sites NO1 and FN1 are represented by an undefined association from the *Phyllodoco-Vaccinion* alliance, corresponding, in the Scandinavian forest classification, to the *Pinus-Calluna-Empetrum* type. The sites FN2 and FN3 can be identified with the *Empetro-Pinetum fenoscandicum* W.Mat. 1962, association, or treated as a form of the association *Calamagrostio lapponicae-Pinetum* Br.-Bl. et Siss. 1939 em. Kielan-Lund 1966. Similar communities have also been described by Oksanen (1983) for the northern Karelia, although without identifying them with the known association. Attention should at this point be paid to the fact that these sites are characterised by the species composition having an intermediate character between the communities of *Phyllodoco-Vaccinion* and *Dicrano-Pinion*. The ES1 site is most plausibly represented by the association of *Vaccinio-Pinetum boreale* Kielan-Lund 1967. The LT1 site has a clear intermediate character. It can be considered to be a southern form of the *Vaccinio-Pinetum boreale* Kielan-Lund 1967, a separate association *Vaccinio vitis-idaeae-Pinetum* auct. (Bambe, 1999), or identified with the sub-boreal variant of

the *Peucedano-Pinetum* Mat. (1962) 1973. The consecutive sites – LI1, PI1, PL2 – are beyond any doubt the boreal variant of *Peucedano-Pinetum* Mat. (1962) 1973, while the site PL3 – of the *Leucobryo-Pinetum* Mat. (1962) 1973.

3.2. ECOLOGICAL STRUCTURE OF THE HERB LAYER

With respect to the differentiation of the life forms of the herb layer the sites analysed can be divided into several groups (Table 1). The first group encompasses the sites NO1, FN1, FN2 and is characterised by the clear domination of the number of the dwarfshrubs species in the total species numbers. The second group is composed of the sites LT1, LI1, PL1, PL2 and PL3, on which the hemicryptophytes dominate in the total number of species. The sites FN3 and ES1 have an intermediate character between these groups. Now, the differentiation of the sites with respect to the shares of the particular life forms in total land cover takes a different shape. The share of the dwarfshrubs species decreases from the site NO1 (83%) towards the site LI1 (30%), to then increase again towards the site PL3 (50%). On the other hand, the geographical distribution of the share of hemicryptophytes in the overall land cover has yet another nature. Thus, on the northern sites (NO1, FN1, FN2, FN3, ES1) this share ranges between roughly 4% and roughly 14%, while on the remaining sites it is contained in the approximate interval of 20% to 40%.

The geographical variability of the shares of species with different persistence of leaves is not very clearly outlined (Table 1). It can only be stated that the northernmost sites (NO1, FN1) are characterised by the higher share of the evergreen species in the total species number, while generally, both in terms of the number of species and their coverage, a tendency is observed of the decrease of share of the evergreen species and the increase of the summer-green species in the direction from the North towards the South.

The herb layer of all the sites is constructed of the mesophyte and sclerophyte species (Table 1). With regard to the shares in the total numbers of species the mesophytes dominate over the sclerophytes on eight out of ten sites, while in terms of the share in total cover – on seven sites the sclerophytes dominate.

Table 1. Percentage share of different ecological groups of the herb layer plants on study sites. A - according to species number, B - according to species cover.

		NO1	FN1	FN2	FN3	ES1	LT1	LI1	PL1	PL2	PL3
A - according to species number											
Raunkiaer's life forms											
	herb and grassy chamaephytes	9.09	22.22	13.33	17.65	9.09	13.33	18.75	14.29	16.67	14.29
	woody chamaephytes (dwarfshrubs)	54.55	55.56	46.67	23.53	36.36	13.33	25	9.52	16.67	21.43
	geophytes	9.09	0	20	17.65	0	13.33	6.25	14.29	20.83	0
	hemicryptophytes	18.18	11.11	20	29.41	27.27	46.67	37.5	52.38	41.67	42.86
	(nano)phanerophytes	9.09	11.11	0	5.88	18.18	6.67	6.25	4.76	0	14.29
	therophytes	0	0	0	5.88	9.09	6.67	6.25	4.76	4.17	7.14
persistence of leaves											
	evergreen species	54.55	77.78	46.67	35.29	45.45	33.33	37.5	23.81	16.67	42.86
	summergreen species	36.36	22.22	40	47.06	45.45	46.67	50	47.62	54.17	35.71
	overwintering green species	9.09	0	13.33	17.65	9.09	20	12.5	28.57	29.17	21.43
anatomical structure											
	sclerophytes	36.36	66.67	46.67	35.29	36.36	40	56.25	33.33	41.67	50
	mesophytes	63.64	33.33	53.33	64.71	54.55	60	43.75	61.9	58.33	50
	higrophytes	0	0	0	0	0	0	0	4.76	0	0
	helophytes	0	0	0	0	9.09	0	0	0	0	0
B - according to species cover											
Raunkiaer's life forms											
	herb and grassy chamaephytes	2.78	8.33	24.89	27.62	12.9	13.76	22.22	12.42	14.17	16.67
	woody chamaephytes (dwarfshrubs)	83.33	83.33	54.75	46.96	51.61	36.7	29.63	31.06	44.53	50
	geophytes	2.78	0	6.79	6.08	0	5.05	1.85	12.42	6.88	0
	hemicryptophytes	8.33	4.17	13.57	13.81	9.68	25.69	40.74	34.78	26.32	20
	(nano)phanerophytes	2.78	4.17	0	2.76	6.45	0.46	1.85	3.11	0	10
	therophytes	0	0	0	2.76	19.35	18.35	3.7	6.21	8.1	3.33
persistence of leaves											
	evergreen species	69.44	87.5	76.92	63.54	41.94	44.04	40.74	27.95	28.34	53.33
	summergreen species	27.78	12.5	20.36	28.18	54.84	49.08	50	50.31	57.49	33.33
	overwintering green species	2.78	0	2.71	8.29	3.23	6.88	9.26	21.74	14.17	13.33
anatomical structure											
	sclerophytes	61.11	83.33	83.71	63.54	38.71	53.67	70.37	31.68	44.94	56.67
	mesophytes	38.89	16.67	16.29	36.46	58.06	46.33	29.63	65.22	55.06	43.33
	higrophytes	0	0	0	0	0	0	0	3.11	0	0
	helophytes	0	0	0	0	3.23	0	0	0	0	0

Table 2. Coefficients of linear correlations between latitude and climatic characteristics (independent variables) and structural characteristics of herb layer ($p < 0.05$; ns - not significant).

	precipitation	temperature	Lang index	latitude
	share according to species number			
herb and grass chamaephytes	ns	ns	-0.74	ns
woody chamaephytes (dwarfshrubs)	-0.69	-0.87	ns	0.89
hemicryptophytes	ns	0.9	ns	-0.9
therophytes	0.9	0.78	ns	-0.76
evergreen species	ns	-0.83	ns	0.77
summergreen species	0.66	0.74	ns	-0.64
overwintering species	ns	0.8	ns	-0.78
mesophytes	ns	ns	0.68	ns
share according to species cover				
woody chamaephytes (dwarfshrubs)	-0.8	-0.84	ns	0.83
hemicryptophytes	ns	0.72	ns	-0.73
terophytes	0.8	ns	ns	ns
evergreen species	-0.69	-0.89	ns	0.84
summergreen species	0.75	0.82	ns	-0.75
overwintering species	ns	0.77	ns	-0.79
sclerophytes	ns	-0.69	ns	ns
mesophytes	ns	0.71	ns	ns

The spatial variability of the shares of particular species groups is often correlated with geographical location and climatic variables. Out of 130 potential interrelations (26 dependent variables and five independent variables) there are 33, which display statistically significant linear correlation (Table 2). It must be emphasised that this group of sig-

nificant correlation contains mostly those referring to average annual temperature, while none of the dependent variables is correlated with the Martonne index.

It can be assumed that in many cases the correlation with latitude sufficiently well describes the spatial variability of the features selected. This fact becomes especially pronounced when non-linear regression models are applied. In this context, there are three basic patterns of the spatial variability of the structural characteristics of the herb layer. The first pattern of variability corresponds to the share of the lignified chamaephytes (dwarfshrubs), (Fig. 8). In accordance with this type the minimum shares of dwarfshrubs are observed at the latitudes of Lithuania, Latvia, and Estonia.

The second type of variability is represented by the share of hemicryptophytes (Fig. 9). Conform to this pattern the maximum shares of the respective plants are observed between 53° and 56° N, that is – on the sites PL2, PL1, LI1, LT1. It should be emphasised at

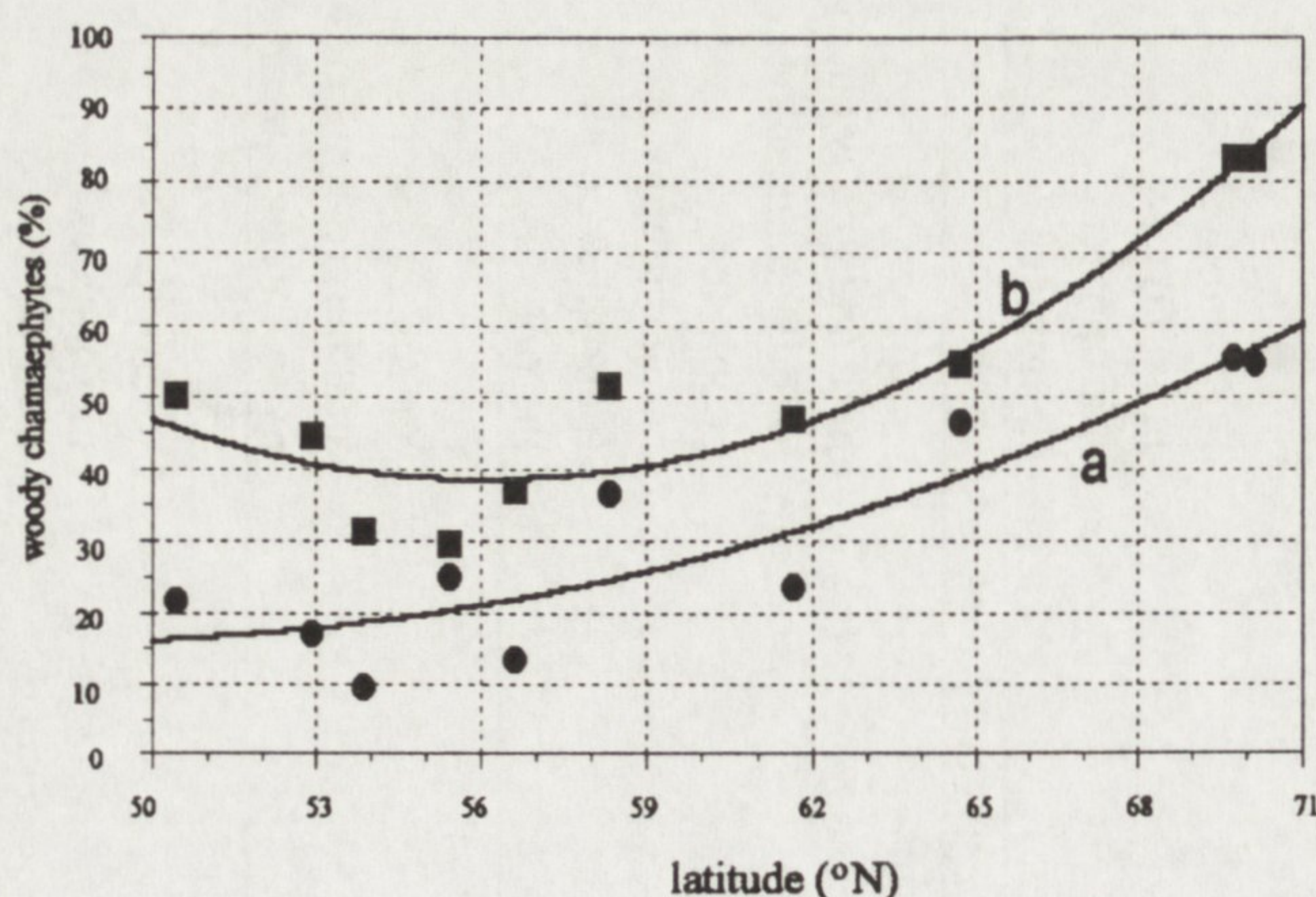


Fig. 8. Regression lines for the share of woody chamaephytes (dwarfshrubs) against the latitude: a – according to the species number, ($y = a + bx + cx^2$, $a = 214.0$; $b = -8.23$; $c = 0.09$; correlation coefficient 0.91); b – according to the species cover, ($y = a + bx + cx^2$, $a = 768.74$; $b = -26.07$; $c = 0.23$; correlation coefficient 0.95).

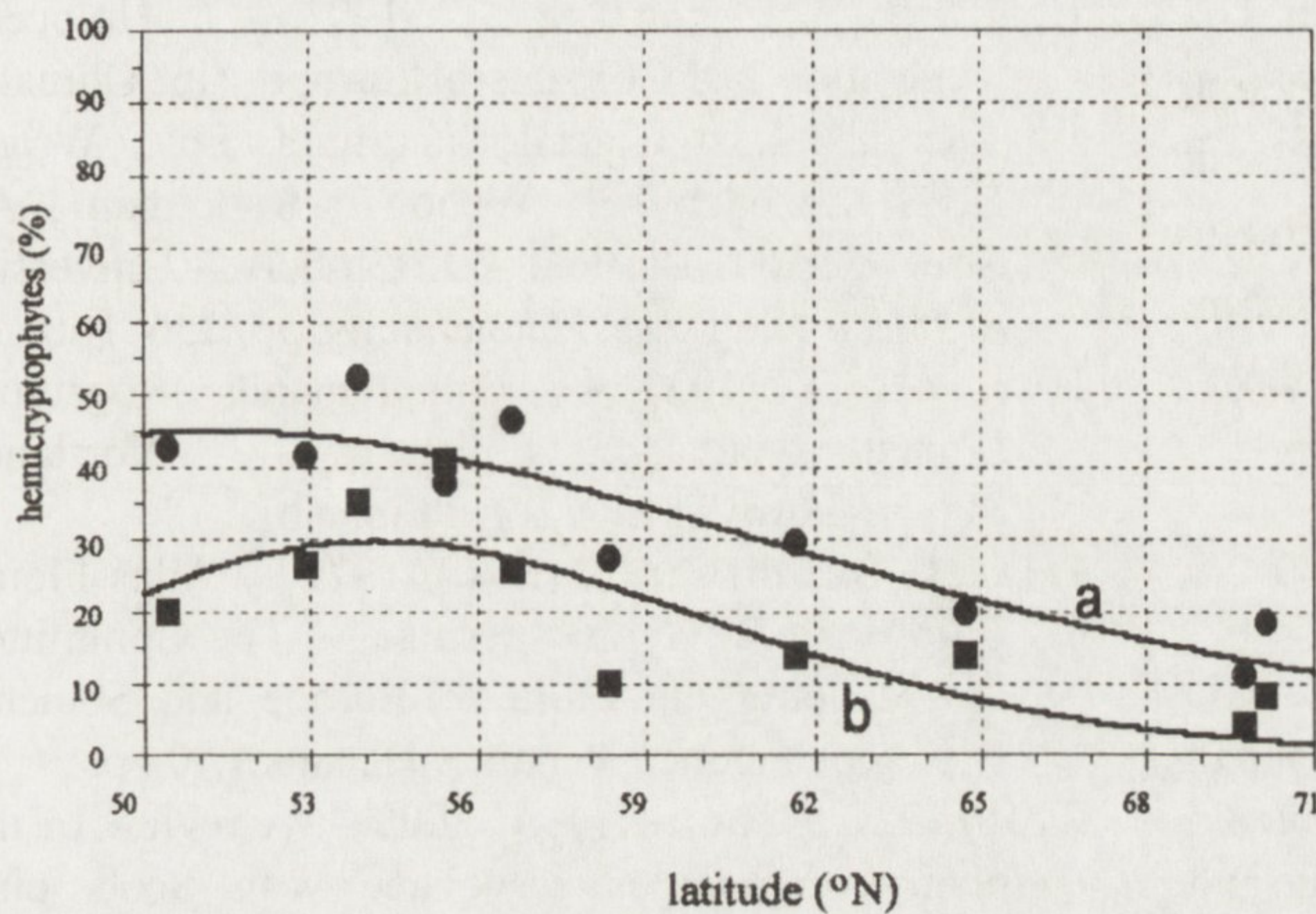


Fig. 9. Regression lines for the share of hemicryptophytes against the latitude: a – according to the species number, ($y = \exp(a + b/x + \ln(x))$, $a = 145.08$; $b = -1467.0$; $c = -28.61$; correlation coefficient 0.91); b – according to the species cover, ($y = \exp(a + b/x + \ln(x))$, $a = 435.92$; $b = -4691.0$; $c = -86.65$; correlation coefficient 0.81).

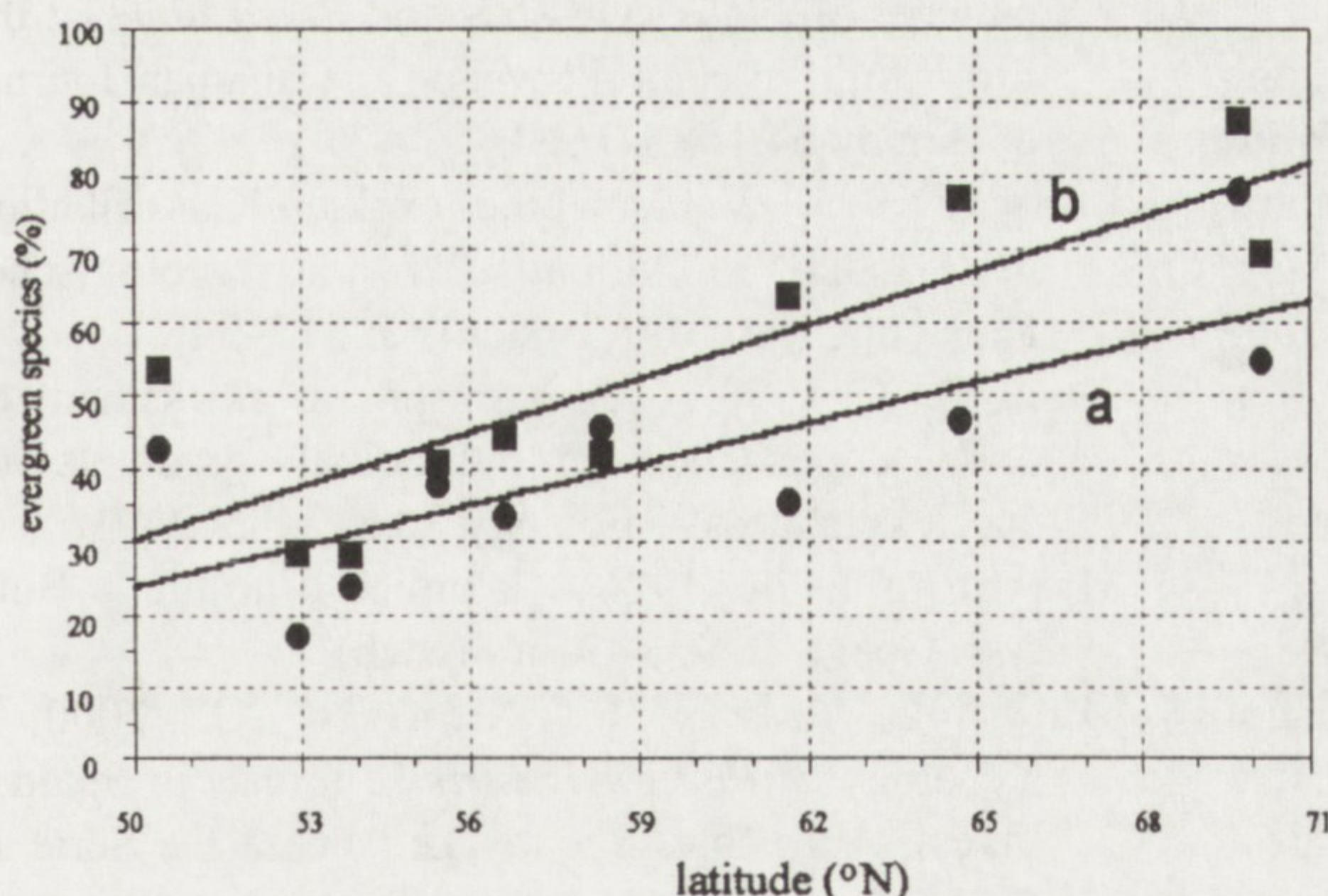


Fig. 10. Regression lines for the share of evergreen species against the latitude: a – according to the species number, ($y = a + bx$, $a = -69.61$; $b = 1.87$; correlation coefficient 0.77); b – according to the species cover, ($y = a + bx$, $a = -92.66$; $b = 2.46$; correlation coefficient 0.84).

this point that in the instances quoted the tested models of non-linear regression, accounting for latitude as the independent variable, give a better approximation of the actual variability of the shares of particular species groups in comparison with the same type of models, in which climatic characteristics were adopted as the independent variable.

The third pattern of variability is represented by, in particular, the share of the evergreen species (Fig. 10). In accordance with this model, the share of the species is proportional to the latitude.

4. CONCLUSIONS

Distinct changes of the floristic composition are observed within the pine forests located along the North-South transect. The primary factor of the spatial geographic variability of the floristic composition of the fresh pine forests is the differentiation of the ranges of particular plant species, which – at least theoretically – find in this type of vegetation the appropriate life conditions. It should be emphasised that the sites ES1 and LT1 have an intermediate character between the well-discriminated Scandinavian pine forests and the Central-European ones.

The geographical differentiation of the study sites is reflected in the most pronounced manner at the level of the herb layer, while being less visible in the lichen flora. One observes in this context a statistically significant ($p < 0.05$) dependence between the latitude and the numbers of species from some groups. For the vascular plants the linear correlation coefficient is at -0.64 (the number of vascular plant species increases southward), and for the lichens it is equal 0.78 (the dependence has an opposite direction). Similar relations between the number of species and latitude have been described for many types of ecosystems and the selected systematic groups of plants and animals (Lyons, 1999). It appears, moreover, that the differentiation of lichens is influenced to a much higher degree by the local conditions, including the land use history, than by the macro-environmental factors.

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Appendix 1. Floristical differentiation of the study sites (symbols of cover - see text).

Trees – A, shrubs – B, herb layer – C, the ground adjacent layer – i.e. mosses and lichens – D

plot	NO1	FN1	FN2	FN3	ES1	LT1	LI1	PL1	PL2	PL3
latitude (°N)	70,15	69,746	64,724	61,662	58,337	56,623	55,431	53,874	52,922	50,447
longitude (°E)	24,788	27,022	26,03	29,282	24,986	24,888	26,018	23,308	23,619	22,94
cover A (%)	50	50	50	60	50	70	50	70	60	80
cover B (%)	5	40	5	5	5	20	20	20	5	5
cover C (%)	90	55	90	70	90	80	90	80	60	90
cover D (%)	90	90	95	95	90	90	80	70	80	70
number of species: A layer	1	1	4	1	2	3	1	3	4	1
number of species: B layer	3	2	5	8	1	6	6	4	8	7
number of species: C layer	11	9	15	17	11	15	16	21	24	14
number of species: D layer - mosses	9	9	4	6	6	6	8	10	7	7
number of lichen species	26	33	17	18	25	18	19	15	14	14
A layer										
<i>Pinus sylvestris</i>	4	4	4	6	5	6	4	6	5	7
<i>Picea abies</i>			1			2		3	3	
<i>Populus tremula</i>			(+)							
<i>Betula pendula</i>			(+)			+		+	+	(+)
<i>Betula pubescens pubescens</i>					(+)					
<i>Quercus robur</i>									+	
B layer										
<i>Betula pubescens czerepanovii</i>	+	4								
<i>Pinus sylvestris</i>	1	+	+						+	+
<i>Juniperus communis</i>			+	+		+	1	1	+	+
<i>Picea abies</i>			+	+	+	1	1	1	+	
<i>Populus tremula</i>			(+)	+						
<i>Betula pendula</i>			(+)	+		1	+		+	+
<i>Sorbus aucuparia</i>	+			+			+	+	+	+
<i>Betula pubescens</i>				+		+				
<i>Alnus incana</i>				+						
<i>Salix sp.</i>				+		+				
<i>Frangula alnus</i>						+	+		+	
<i>Quercus robur</i>							1	r	+	+
<i>Quercus rubra</i>										+
<i>Padus serotina</i>										+
<i>Pyrus communis</i>									+	
C layer										
<i>Agrostis tenuis</i>									+	
<i>Avenella flexuosa</i>	1	+	(+)		+	1		+		+
<i>Arctostaphylos alpinus</i>	(+)									
<i>Calamagrostis sp.</i>			2	+		+	2	+	+	
<i>Calluna vulgaris</i>			5	4	2	2	4	1	2	2
<i>Carex montana</i>							+			+
<i>Chamaecytisus ratisbonensis</i>									+	
<i>Chimaphilla umbellata</i>							+			+
<i>Convallaria majalis</i>			(+)	+		r		1	+	
<i>Diphasiastrum complanatum</i>		(+)	+	(+)			1		+	
<i>Dryopteris carthusiana</i>								+	+	
<i>Empetrum nigrum s.l.</i>	6	4	4	3						
<i>Epilobium angustifolium</i>				(+)					+	
<i>Equisetum pratense</i>				(r)						
<i>Festuca ovina</i>						3	5	+	2	+
<i>Festuca rubra</i>									+	
<i>Fragaria vesca</i>								+		+
<i>Genista tinctoria</i>									+2	
<i>Goodyera repens</i>					(+)	(+)				
<i>Hieracium pilosella</i>						(+)		+		
<i>Hieracium cfr. umbellatum</i>			+							

plot	NO1	FN1	FN2	FN3	ES1	LT1	LI1	PL1	PL2	PL3
<i>Ledum palustre</i>			+		+					
<i>Lembotropis nigricans</i>										1
<i>Linnaea borealis</i>		+	(+)	+						
<i>Loiseleuria procumbens</i>	(+)									
<i>Luzula pilosa</i>				+	+	+	2	1	+	+
<i>Lycopodium annotinum</i>	+					1				
<i>Maianthemum bifolium</i>			(+)							
<i>Lycopodium clavatum</i>		+					1		+	+
<i>Melampyrum pratense</i>				+	3	4	1	1	2	+
<i>Molinia caerulea</i>					+					
<i>Monotropa hypopitys</i>				+					r	
<i>Orobanche sp.</i>							+			
<i>Peucedanum oreoselinum</i>						r	1	r	+	
<i>Picea abies</i>								+		
<i>Pinus sylvestris</i>	+	+		+	+	r	+			+
<i>Poa compressa</i>										+
<i>Polygonatum multiflorum</i>								+		
<i>Polygonatum odoratum</i>						+			+	
<i>Pteridium aquilinum</i>									r	
<i>Pulsatilla patens</i>								+		
<i>Pulsatilla vernalis</i>				(+)						
<i>Rubus saxatilis</i>			r							
<i>Rumex acetosella</i>								(+)	+	
<i>Scorzonera humilis</i>									+	
<i>Solidago virgaurea</i>	(+)		+	(+)		+	+	+	+	
<i>Sorbus aucuparia</i>					+					
<i>Thymus serpyllum</i>								+		
<i>Trientalis europaea</i>	+		(+)			1				
<i>Vaccinium myrtillus</i>	2	(+)	+	2	4	2	3	3	6	3
<i>Vaccinium uliginosum</i>	2	1	+	+	+		(+)			
<i>Vaccinium vitis-idaea</i>	4	4	6	3	3	6	4	2	4	4
<i>Veronica officinalis</i>				+				+	+	
<i>Viola riviniana</i>								+		
D layer - Mosses										
<i>Amblystegium serpens</i>								+		
<i>Andraea rupestris</i>		+								
<i>Brachythecium oedipodium</i>								+		
<i>Brachythecium salebrosum</i>							+			
<i>Caliergonella cuspidata</i>								+		
<i>Ceratodon purpureus</i>						+				
<i>Dicranum affine</i>	+									
cfr. <i>Dicranum brevifolium</i>				+						
<i>Dicranum drummondii</i>	+	+								
<i>Dicranum elongatum</i>		+								
<i>Dicranum polysetum</i>	+	1	1	+	2	2	2	3	2	1
<i>Dicranum scoparium</i>	1			1	1	1	1			3
<i>Herzogiella seligeri</i>										+
<i>Hylocomium splendens</i>	2		1	1	+	+	1	1	2	
<i>Hypnum cupressiforme</i> fo. <i>filiforme</i>									+	
cfr. <i>Lepidozia reptans</i>		+								
<i>Leucobryum glaucum</i>										+
<i>Lophocolea heterophylla</i>									+	
<i>Orthodicranum montanum</i>						+				
<i>Pleurozium schreberi</i>	6	7	8	9	8	7	7	5	6	5
<i>Pohlia nutans</i>	1	1		+	+		1	1	+	+
<i>Polytrichum formosum</i>									+	+
<i>Polytrichum juniperinum</i>	1	1					+	+		
<i>Polytrichum longisetum</i>								+		
<i>Ptilidium ciliare</i>	+	+	+							
<i>Ptilium crista-castrensis</i>					+		+	+		

Appendix 2. The presence of lichens on the study sites: a - occurrence on the ground; b - occurrence on the lying dead wood; c - occurrence on rocks and stones; d - occurrence on the bark of standing trees. Asterisk (*) is given for the species of arctic-alpine, arctic-boreal-alpine and boreal-alpine types of geographical distribution.

plot	NO1	FN1	FN2	FN3	ES1	LT1	LI1	PL1	PL2	PL3
latitude (°N)	70,15	69,746	64,724	61,662	58,337	56,623	55,431	53,874	52,922	50,447
longitude (°E)	24,788	27,022	26,03	29,282	24,986	24,888	26,018	23,308	23,619	22,94
<i>*Arctoparmelia centrifuga</i> (L.) Hale		c								
<i>Bryoria fuscescens</i> (Gyelnik) Brodo & D. Hawksw.			d							
<i>Bryoria simplicior</i> (Vain.) Brodo & D. Hawksw.		d								
<i>Bryoria</i> sp.	b									
<i>Buellia griseovirens</i> (Turner. & Borrer ex Sm.) Almb.				d				d		
<i>*Cetraria hepatizon</i> (Ach.) Vain.		c								
<i>Cetraria islandica</i> (L.) Ach.						a				
<i>*Cetraria nivalis</i> (L.) Ach.	b									
<i>Cetraria sepincola</i> (Ehrh.) Ach.	d									
<i>Chaenotheca ferruginea</i> (Turner ex Sm.) Migula					d			d		
<i>Chaenothecopsis</i> sp.					d					
<i>Cladonia arbuscula</i> (Wallr.) Flotow subsp. <i>arbuscula</i>	ab	abc	a	ab			a			a
<i>Cladonia cenotea</i> (Ach.) Schaerer	b	ab	b	b				b		
<i>Cladonia chlorophaea</i> s.l. (Flk. ex Sommerf.) Sprengel	b	ab	b	b	bd	b	ab	abd	a	ab
<i>Cladonia coccifera</i> (L.) Willd.	a									
<i>Cladonia coniocraea</i> (Flk.) Vainio					b			d	b	
<i>Cladonia cornuta</i> (L.) Hoffm.	b	ab								
<i>Cladonia deformis</i> (L.) Hoffm.	b	a		b						
<i>Cladonia digitata</i> (L.) Hoffm.	b	ab		b	abd	bd			b	
<i>Cladonia fimbriata</i> (L.) Fr.		b	b		a					b
<i>Cladonia furcata</i> (Huds.) Schrader							a			
<i>Cladonia glauca</i> Flk.						b		ab		
<i>Cladonia gracilis</i> (L.) Willd.	ab					a	a			
<i>Cladonia macilenta</i> Hoffm. subsp. <i>macilenta</i>							b		b	b
<i>Cladonia ochrochlora</i> Flk.					a	b		b		
<i>Cladonia phyllophora</i> Hoffm.							a			
<i>Cladonia pleurota</i> (Flk.) Schaerer	b	b					a			
<i>Cladonia pyxidata</i> (L.) Hoffm.	b	c								
<i>Cladonia rangiferina</i> (L.) Weber	ab	a	a	a	a	a	a			a
<i>Cladonia rangiformis</i> Hoffm.		b								
<i>Cladonia stellaris</i> (Opiz) Pouzar & Vězda			a			a				
<i>Cladonia sulphurina</i> (Michx.) Fr.			b							
<i>Cladonia uncialis</i> (L.) Weber	a	a								
<i>Cladonia</i> sp.										d
<i>Dimerella diluta</i> (Ach.) Vězda									b	
<i>Hypocenomyce caradocensis</i> (Leight. Ex Nyl.) P. James & G. Schneid.	ko	ko								
<i>Hypocenomyce scalaris</i> (Ach.) Choisy					d		bd	d	b	d
<i>*Hypogymnia bitteri</i> (Lyngé) Ahti			b							
<i>Hypogymnia physodes</i> (L.) Nyl.		d	b	bd	bd	bd	b	bd	b	d
<i>Hypogymnia tubulosa</i> (Schaerer) Havaas					d					
<i>*Hypogymnia vittata</i> (Ach.) Parrique		d	bd	d						
<i>Imshaugia aleurites</i> (Ach.) Fricke Meyer	d	d		d	d		d			d
<i>Lecania naegelii</i> (Hepp) Diederich & P. Boom					d					
<i>Lecanora conizaeoides</i> Nyl. in Crombie										d
<i>Lecanora pulicaris</i> (Pers.) Ach. subsp. <i>pulicaris</i>					d	d				
<i>Lecanora</i> sp.							b			
<i>Lepraria</i> sp.			d	d	d	bd	bd	bd	b	bd

