Phytogeographical boundary between the Pannonicum and Hercynicum: a multivariate analysis of landscape in the Podyjí/Thayatal National Park, Czech Republic/Austria

Fytogeografická hranice mezi Panonikem a Hercynikem: mnohorozměrná analýza krajiny v Národním parku Podyjí/Thayatal

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The phytogeographical boundary between two major Central European floristic regions is analysed at the landscape scale in the border area between the Czech Republic and Austria. A database of floristic records, potential natural vegetation types, selected environmental variables, and mean Ellenberg indicator values was compiled for a grid of 172 quadrats of approximately 1.2 ×1.1 km. The data on flora and vegetation were subjected to detrended correspondence analysis to reveal the main gradients, and to cluster analysis to suggest a regional land classification. The patterns revealed by these analyses were related to environmental variables, and cluster analysis of environmental variables was used to produce an environmental land classification. The results indicate that the Pannonicum and Hercynicum are separated by a transitional zone, located on the prominent deforested slope at the edge of the Bohemian Massif. Floristically, this zone is more closely related to the Hercynicum, but according to the environmental land classification it rather belongs to the Pannonicum. This zone possesses some additional unique features not shared with the two main regions, e. g. a low proportion of nitrophilous species and occurrence of several species restricted to it. The Dyje/Thaya river valley, which runs roughly perpendicular to the main phytogeographical boundary, does not influence the regional phytogeographical subdivision and belongs to the same phytogeographical region as the adjacent landscape.

Keywords: Cluster analysis, detrended correspondence analysis, Ellenberg indicator values, flora, grid map, land classification, potential natural vegetation

Introduction

The Pannonicum and Hercynicum have long been commonly accepted phytogeographical regions of Central Europe (Drude 1902, Hayek 1923). According to the classification and terminology of Meusel et al. (1965), the Pannonicum is a Province within the Pontic-South Siberian Region, and the Hercynicum is a Sub-Province of the Central European Province within the Middle European Region. Various phytogeographical land classification maps show a high degree of agreement in the location of the boundary between these two major areas (Dostál 1957, 1960, Niklfeld 1964, Meusel et al. 1965). This boundary generally follows the geological dividing line between the Bohemian Massif in the northwest (with higher altitudes, lower temperatures, higher precipitation, ancient siliceous bedrock, and a landscape mosaic of forest tracts and treeless areas) and the outer depressions of the Carpathians and the Alps in the southeast (with lower altitudes, a warmer and drier climate, Tertiary and Quaternary sediments, and a landscape largely deforested since prehistoric times). However, at a more detailed scale (e. g. 1:500,000 and larger) there are often more options for drawing the dividing line, and regional land classification schemes may differ accordingly.

The present paper focuses on phytogeographical land classification at the landscape scale. Podyjí/Thayatal National Park, located on the border between the Czech Republic and Austria, was selected along with some adjacent areas as a study site (Fig. 1). All the existing phytogeographical land classification schemes agree that the boundary between the Pannonicum and Hercynicum runs through this area. The gently undulating landscape of the national park is divided by the deeply incised, V-shaped valleys of the Dyje/Thaya river and its tributary from the right, the Fugnitz rivulet. Similar valleys, oriented roughly perpendicular to the geological dividing line between the Bohemian Massif and the Tertiary outer depressions of the Carpathians, are a typical feature of the landscape in the border area between the Pannonicum and Hercynicum (e. g. Svratka, Jihlava, Jevišovka, and Kamp valleys).

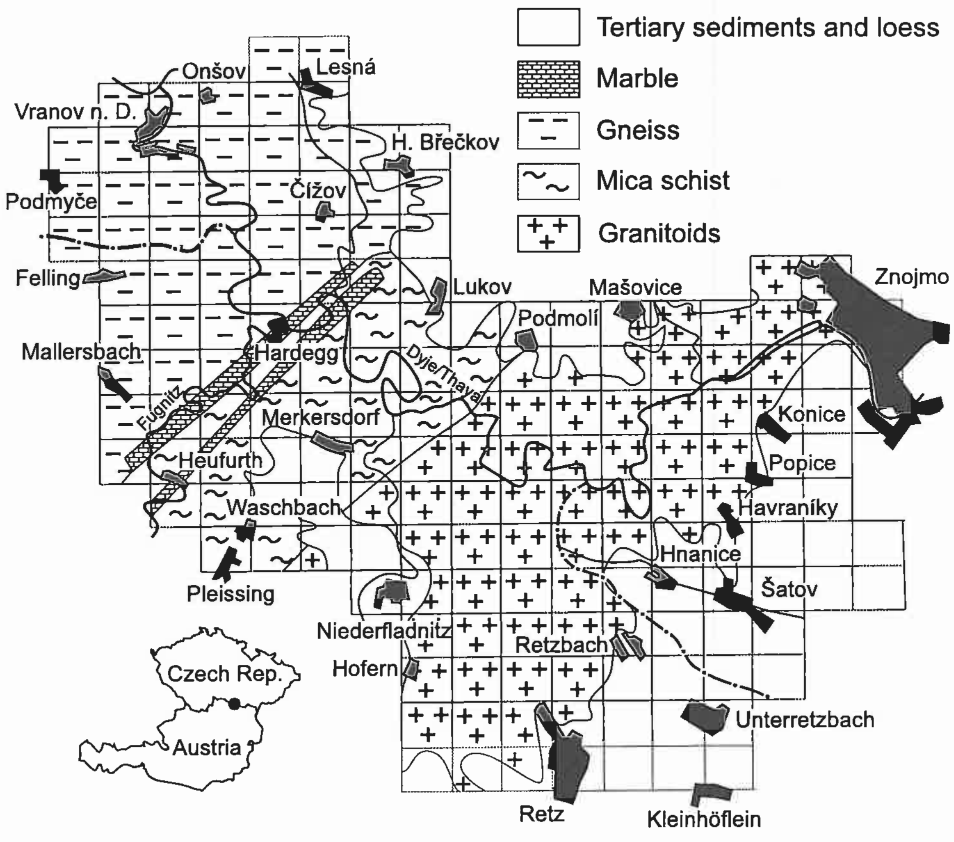

Fig. 1. – Map of the study area with the distribution of the main bedrock types.

The problems with determining the main phytogeographical boundary in this area are best shown in the Biogeographical Land Classification of the Czech Republic (Culek 1996, see Fig. 7). This classification scheme uses a concept of well-defined cores of the biogeographical regions that are separated by transitional or atypical zones. Low-altitudinal eastern and south-eastern parts of the study area with Tertiary and Quaternary sediments are classified as the core of the Lechovice region which belongs to the Pannonicum. The adjacent belt to the northwest, which runs SW-NE, is considered to be a transitional zone assigned to the Lechovice region. It comprises the prominent slope at the edge of the Bohemian Massif and an adjacent area of Tertiary deposits. The bedrock is predominantly acidic (granitoids, siliceous sand and gravel), but similarly to the Pannonian lowlands, the landscape has been deforested for several centuries. This zone combines thermophilous and continental plant species of the Pannonicum with acidophilous species of the Hercynicum. The central and western part of the study area, with a gently undulating landscape on siliceous bedrock, locally overlaid by superficial deposits, and with the river valleys, is largely forested and belongs to the core of the Jevišovice region within the Hercynicum.

The phytogeographical land classification used in the Flora of the Czech Republic (Skalický 1988, see Fig. 7) defines all regions with crisp boundaries without transitional zones. This scheme locates the main boundary farther west, so that the Pannonicum also includes the SW-NE stretch of the Dyje valley, in the central-eastern part of the study area. The rationale for this was probably the occurrence of Pannonian flora on the sunny upper slopes of the valley.

Niklfeld (1993) suggests that the transitional zone on the Bohemian Massif edge slope belongs to the Pannonicum and supports this view with the fact that vineyards are common in this zone, similarly to the core of the Pannonicum. This corresponds to the traditional Lower Austrian land classification, reflected in vernacular term "Weinviertel" (vine region) used for the Pannonicum, as opposed to the "Waldviertel" (forest region) for the Hercynicum.

A possible alternative approach to the regional phytogeographical land classification of this area would have the main division line roughly paralleling the edge of the Bohemian Massif as in the schemes of Culek (1996) and Skalický (1988), but with a promontory of the Pannonicum running up along the Dyje/Thaya river valley. The rationale for this approach is in the occurrence of Pannonian thermophilous flora in the river valleys, notably on some south-facing slopes isolated from the core of the Pannonian region. In the phytogeographical land classification by Skalický (1988), this solution was accepted in a similar landscape in the nearby Jihlava river valley. If this scheme was applied in the Podyjí/Thayatal National Park, the promontory of the Pannonicum would probably reach the area around the mouth of the Fugnitz, where Pannonian flora and vegetation is supported on marble, which is imbedded in siliceous bedrock.

Recent research activities in the Podyjí/Thayatal National Park, namely detailed grid mapping of flora (Grulich 1997) and potential natural vegetation mapping (Chytrý & Vicherek 1995), make it possible to analyse the phytogeographical patterns in the area quantitatively and to check the regional land classification schemes based on expert knowledge. The aim of this paper is to detect and hierarchize the principal floristic and vegetational gradients and to propose phytogeographical boundaries in this area.

Material

The basic dataset included vascular plant records from 172 contiguous quadrats arranged in a grid derived from the Central European grid for phytogeographical mapping. Each quadrat measured 1' of longitude and 0.6' of latitude, i. e. approximately 1.2 × 1.1 km. The grid covered the territory of the bilateral Podyjí/Thayatal National Park in the Czech Republic and Austria and some adjacent areas, particularly in the south and east (Fig. 1). Original data were published as grid maps in the "Distribution Atlas of the Vascular Plants in the Podyjí/Thayatal National Park" (Grulich 1997). As several maps in this atlas are summary maps for groups of closely related species and some of these species are mapped again separately, we excluded the following species to avoid overlaps: all species of *Alchemilla* except *Alchemilla vulgaris* agg.; all species of *Callitriche* except *Callitriche palustris* agg.; *Galium valdepilosum;* all species of *Rubus* except *Rubus caesius, R. fruticosus* agg., *R. idaeus* and *R. saxatilis; Silene vulgaris* subsp. *antelopum* and subsp. *vulgaris*; *Veronica vindobonensis.* Hybrids were excluded as well. Species aggregates were used unless precise data on distribution of their component species were available. In spite of the fact that the aggregates often included several species with different ecology and local distribution, each of the aggregates possessed certain ecological and distributional range within the study area. Therefore, for the analysis of local phytogeographical patterns, distributional data for aggregates were considered as valuable as distributional data for species. The resulting dataset included 1193 species, subspecies or species aggregates (referred to as species throughout this paper). The number of species per quadrat ranged from 108 to 565. Species names follow Ehrendorfer (1973) and Grulich (1997).

For supplementary analyses, information on potential natural vegetation and environmental factors was compiled for each quadrat. The percentage cover of 23 potential vegetation types included in the "Map of Potential Natural Vegetation of the Podyjí/Thayatal National Park" (Chytrý & Vicherek 1995) was calculated for 128 quadrats from the digitized version of this map in the ARC/INFO geographical information system. This information was not compiled for the 44 marginal quadrats, because they were only partly covered by vegetation mapping.

Environmental data for each quadrat included: (1) maximum altitude; (2) altitudinal range, i. e. the difference between the highest and lowest altitude within a quadrat, derived from a digital elevation model in ARC/INFO; (3) percentage forest cover, calculated from a digitized forest cover map in ARC/INFO; (4–9) mean indicator values for light, temperature, continentality, moisture, soil reaction and nutrients, according to Ellenberg et al. (1992).

Mean indicator values were calculated by averaging the indicator values of the species occurring in each grid square. The species which are missing in Ellenberg tables (9.1 % of all species) were not considered in the calculations. Out of these, 3.5 % were eastern and southeastern species not occurring in Germany, i. e. the area for which Ellenberg et al. compiled the indicator values (e. g. *Aconitum anthora, Carex pediformis, Seseli osseum*), 3.1 % were cultivated species or species escaped from cultivation (e. g. *Aesculus hippocastanum, Calendula officinalis, Papaver somniferum*), 1.4 % were taxonomically problematic or recently described species (e. g. *Achillea pratensis, Senecio germanicus, Veronica triloba*), and 0.9 % were rare alien species (e. g. *Commelina communis*). Due to their limited number, the effects of the missing species on indicator value patterns were probably negligible, although some of these species showed a distinct distributional pattern. Many species included in Ellenberg tables were also not considered in the analysis, because their indicator values are not given due to species wide tolerance or poor indicator capacity for a particular environmental factor. This is especially important for temperature and soil reaction where the indicator values were not indicated for about 35 % of the species included in Ellenberg tables (continentality, moisture, and nitrogen values were missing for 15–20 %).

For 115 quadrats in the northern part of the area, where a phenological map was available (Chytrý & Tichý 1998), mean values of the local stage of spring phenological development were calculated. These values provide a rough estimate of the delay in spring phenological events, with value 1 representing the most advanced and value 5 the most delayed areas. Spatial variation in the environmental variables over the study area is shown in Figs. 2 and 3.

Data analysis

Ordination

Major floristic and vegetational gradients in the study area were revealed by detrended correspondence analysis, DCA (Hill 1979), using the CANOCO 4.0 package (ter Braak & Šmilauer 1998) which includes the debugged version of the DECORANA program with strict convergence criteria (Oksanen & Minchin 1997). DCA axes, which were extracted from a matrix of quadrats and species or quadrats and vegetation types, correspond to major floristic and vegetational gradients, respectively. Importance of the axes and underlying gradients is inversely related to their numerical ranking. The gradients associated with individual axes are uncorrelated, and the relative importances of the respective axes are proportional to their eigenvalues. These properties of DCA were used to detect several different floristic and vegetational gradients and to rank them by their relative importance.

DCA was applied to a flora data matrix of 1193 species by 172 quadrats, and to a vegetation data matrix of 23 potential natural vegetation types by 128 quadrats. The former included presence/absence data, the latter percentages which were log-transformed in order to increase importance of rare vegetation types. The first three axes were used for interpretation. Quadrat scores on these axes were standardized to unit range and both positive and negative half of the gradient were mapped separately onto the grid, using symbols the size of which was proportional to the quadrat scores (DMAP program, A. Morton, ined.). Correlation coefficients of the quadrat scores with environmental variables were calculated with the SPSS package (SPSS Inc. 1998) so that the variation in flora and vegetation could be related to environmental gradients.

Classification

The complete linkage algorithm of the cluster analysis, implemented in the package SYNTAX 5 (Podani 1993), was applied to (1) the floristic data matrix (1193 x 172); (2) the vegetation data matrix (23 x 128); (3) the matrix of environmental variables 1–9 as described above. Prior to analysis, vegetation data matrix was log-transformed, and environmental variables were centered around variable means and standardized by standard deviation in order to remove the effect of different measuring units. The Jaccard coefficient was used as a distance measure in the floristic data analysis, and the chord distance in the analyses of vegetational and environmental data.

The upper parts of the dendrograms resulting from the cluster analysis were used to divide the quadrats into 4–6 groups. Groups defined on the basis of floristic data were parametrized by environmental variables, and the differences in these variables between the groups were tested with the Tukey multiple range test (SPSS Inc. 1998).

To define differential species of the groups of quadrats based on the floristic classification, the *u*-value (Bruelheide 1995, Bruelheide & Jandt 1995) was calculated for each species within each group. This value is a test parameter derived from the Gaussian distribu-

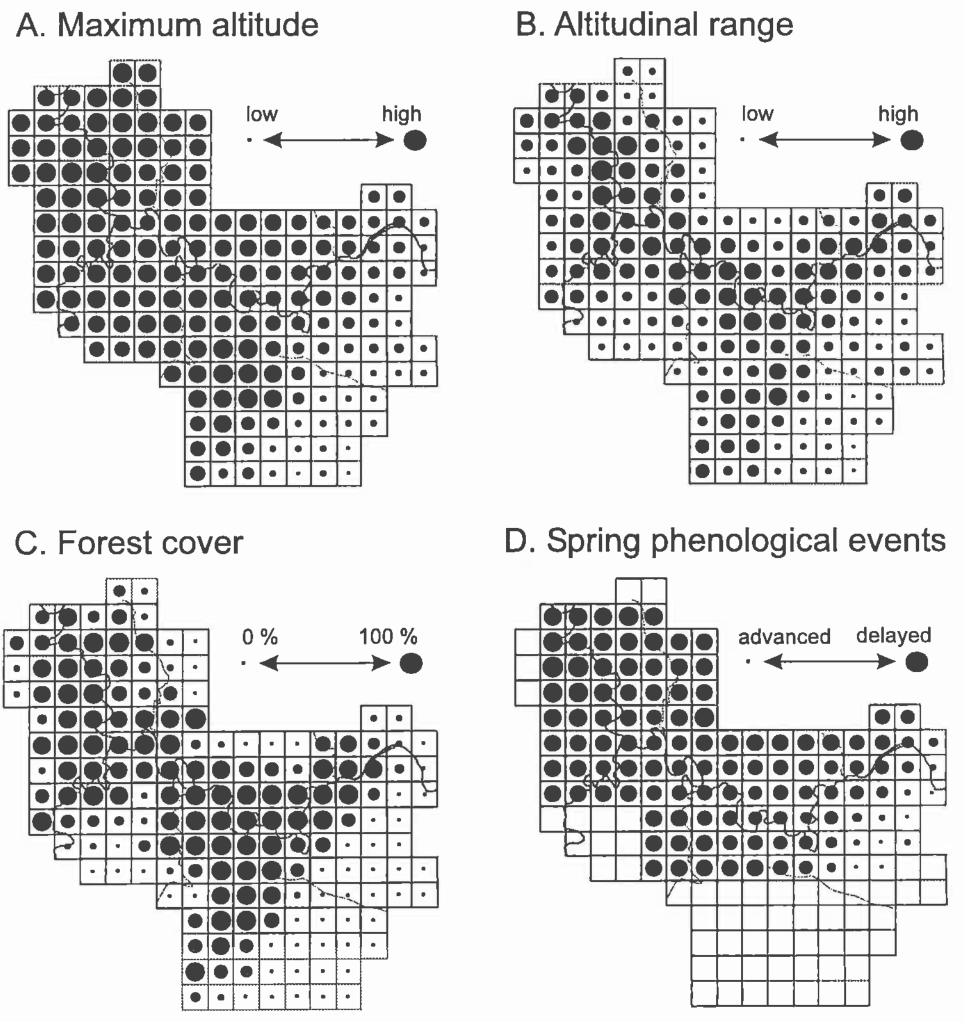

Fig. 2. – Patterns of selected environmental variables in the study area. Values are standardized to unit range.

tion which was originally developed as a measure of species fidelity in phytosociological tables. In the current study, it was used as a measure of species occurrence concentration in particular groups of quadrats. Basically, *u*-value calculation includes comparison between the species occurrence frequency in the given group of quadrats and in the quadrats not belonging to this group, but it also considers the total number of quadrats and the proportion between number of quadrats belonging to the given group and the total number of quadrats. High *u*-value of a species in a particular group indicates that the species occurs in most of the quadrats of this group, but is absent in most of the quadrats of the other groups. On the other hand, *u*-value close to zero indicates that frequency of a species in quadrats of the given group does not differ from frequency of this species in the other quadrats. Thus the groups which include many species with high *u*-value are well defined in floristic terms, whereas groups whose species have low *u*-values are poorly differentiated.

Results

Indicator value patterns

Ellenberg indicator value analysis yielded striking differentiation patterns for all of the six investigated ecological factors. Light values (Fig. 3A) tended to be higher in deforested areas, especially in the Tertiary depression in the southeast, and near the NE and SW edges of the study area. A relatively high proportion of the heliophilous species is also found in the river valleys, where these species are mostly confined to canopy openings on south-facing slopes and to alluvial meadows.

The temperature and continentality patterns (Figs. 3B, 3C) are very similar to each other. The highest values (i. e. most thermophilous and most continental plants) are found in the southeast. The Dyje river valley is also characterized by relatively high values than the adjacent gently undulating landscape at an altitude of approximately 400–500 m. However, average values alone may be somewhat misleading, for temperature in particular. Therefore, standard deviations of temperature values were calculated in addition to averages (not shown), and these were higher in the valley than in the adjacent landscape. This agrees with the observation that at some sites within the valley, such as the lower parts of north-facing slopes, species with low temperature demands are frequently found, whereas on south-facing slopes, and often also in alluvial meadows, thermophilous species are common. Warmer habitats usually support higher species richness than cooler habitats; therefore thermophilous species prevail for the valley as a whole. In the landscape outside the valley, higher temperature and continentality values were found in the deforested areas, where higher temperature extremes may be expected. It is possible that the differentiation in continentality would be slightly more pronounced if the species with eastern or southeastern distribution missing in the Ellenberg tables were also included.

The moisture pattern (Fig. 3D) is roughly inverse to temperature and continentality. It reflects the precipitation gradient from the drier southeast to the wetter northwest (Vesecký et al. 1958). Higher moisture values in the extreme southeast and east are obviously due to deeper and heavier soils with a higher water-holding capacity.

Soil reaction (Fig. 3E) is mainly dependent on bedrock type. The most acidic areas are found in quadrats where gneiss (western part) or granitic bedrock (southeast-central part)

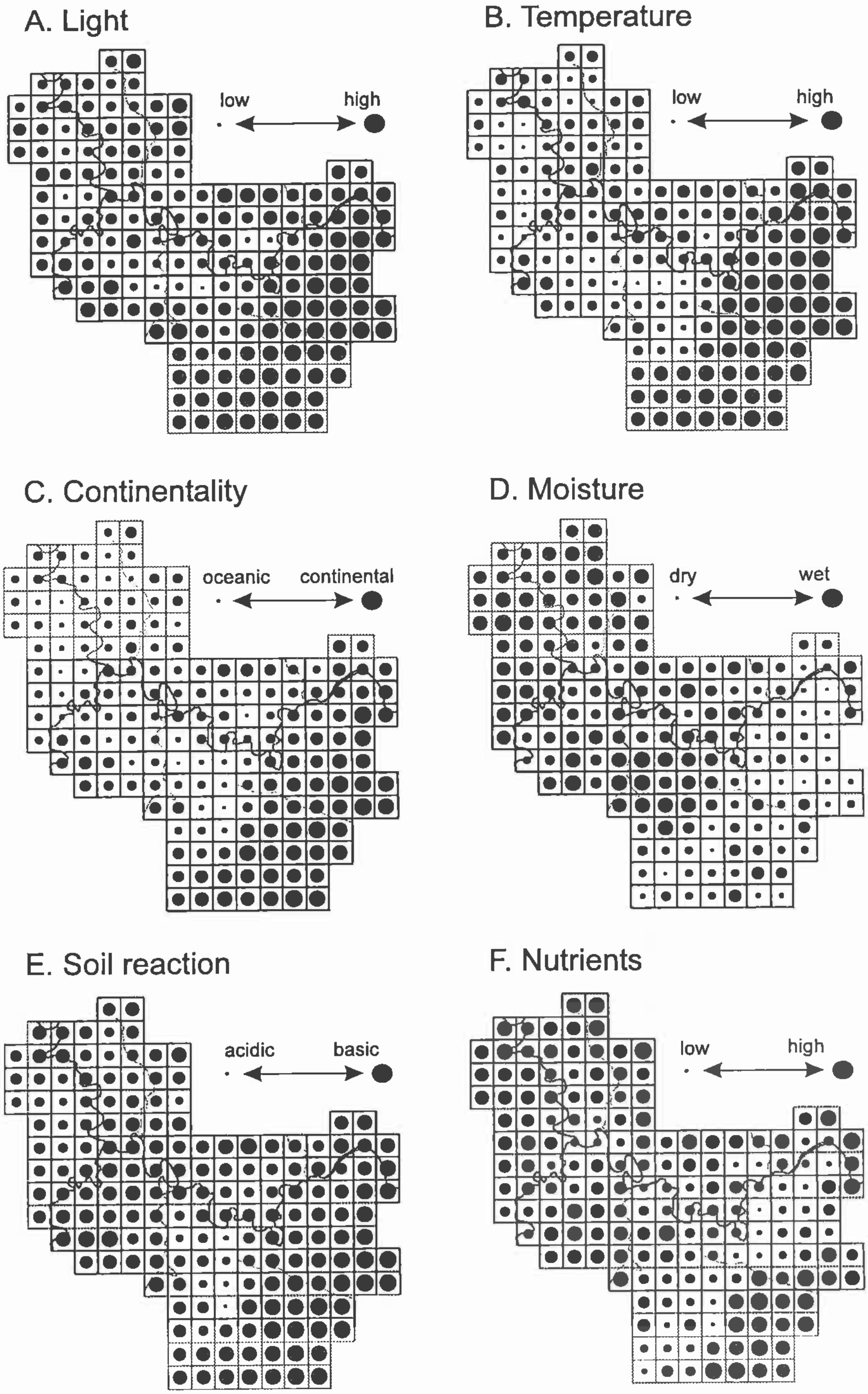

Fig. 3. – Patterns of mean Ellenberg indicator values in the study area. Values are standardized to unit range. Actual ranges are the following: light 5.6–7.5, temperature 5.4–6.2, continentality 3.6–5.0, moisture 3.9–6.0, reaction 5.1–7.5, nutrients 4.1–5.9.

prevail (Batík 1992); these areas match very well the areas with the highest moisture values. This indicates that leaching, in addition to the base status of the initial bedrock, is probably involved in forming acidic soils. On the other hand, more basic conditions are indicated in the areas where Tertiary sediments or loess prevail, notably in the east and southeast, but also in the central-western part where marble occurs in narrow strips and gneiss and granitoids are replaced by mica schist. Mica schist itself is not more basic than gneiss or granitoids, but weathers into loamy soils with a higher cation exchange capacity.

The pattern of nutrients (Fig. 3F) is similar to that of moisture. Higher values are encountered on deeper soils, such as in the extreme east and southeast, and in forested areas. The SW-NE belt with low nutrient values in the eastern part of the study area corresponds to the dry and largely deforested slope on the Bohemian Massif edge, over granitic bedrock. Low moisture status (due to low precipitation and good draining of shallow soils over granitoids) probably accounts for lower productivity in this area and a slower rate of nutrient accumulation and turnover. In addition, past land use including grazing and bed-raking has probably caused considerable nutrient depletion. Comparatively low nutrient values are found in the river valleys too, but also in this case, standard deviation is high, because the valleys include both the nutrient-poor habitats of upper slopes and nutrient-rich habitats of ravine forests, lower slopes etc.

Ordination and main gradients in the study area

In the ordination of floristic data, the variance explained by the first three axes was rather low, but these axes had a straightforward ecological interpretation (Table 1, Fig. 4). The most important floristic gradient in the Podyjí/Thayatal National Park, associated with DCA axis 1, is the one between the upland forested areas over ancient hard bedrock of the

Table 1. – Correlations of the DCA ordination axes with environmental variables. Floristic ordination and potential natural vegetation ordination are presented separately. Light, temperature, continentality, moisture, reaction and nutrient values are calculated according to Ellenberg. Phenology is measured on a scale from 1 (areas with most advanced spring phenological development) to 5 (with most delayed development). *** $P<0.001$, ** $P<0.01$, * $P<0.05$, n.s. – not significant.

Dataset	Flora			Potential natural vegetation		
DCA axis	1	2	3	1	2	3
Eigenvalue	0.240	0.126	0.057	0.731	0.193	0.149
Cumulative % variance	8.6	13.0	15.1	26.4	33.9	39.3
Maximum altitude	–0.867***	–0.270***	0.164*	–0.824***	–0.190*	0.092 n.s.
Altitudinal range	–0.604***	0.553***	0.197***	–0.365***	0.557***	0.324***
Percentage forest cover	–0.797***	0.267***	0.361***	–0.536***	0.291**	0.331***
Light value	0.932***	0.073 n.s.	–0.126 n.s.	0.746***	0.014 n.s.	0.062 n.s.
Temperature value	0.881***	0.466***	–0.077 n.s.	0.779***	0.302***	0.001 n.s.
Continentality value	0.932***	0.265**	–0.211**	0.777***	0.186*	–0.115 n.s.
Moisture value	–0.617***	–0.683***	–0.125 n.s.	–0.597***	–0.396***	–0.004 n.s.
Reaction value	0.828***	0.181*	–0.575***	0.545***	0.183*	–0.347***
Nutrient value	0.284***	–0.588***	–0.512***	–0.047 n.s.	–0.292**	–0.363***
Phenology	–0.722***	–0.503***	–0.189*	–0.788***	–0.252*	–0.292**

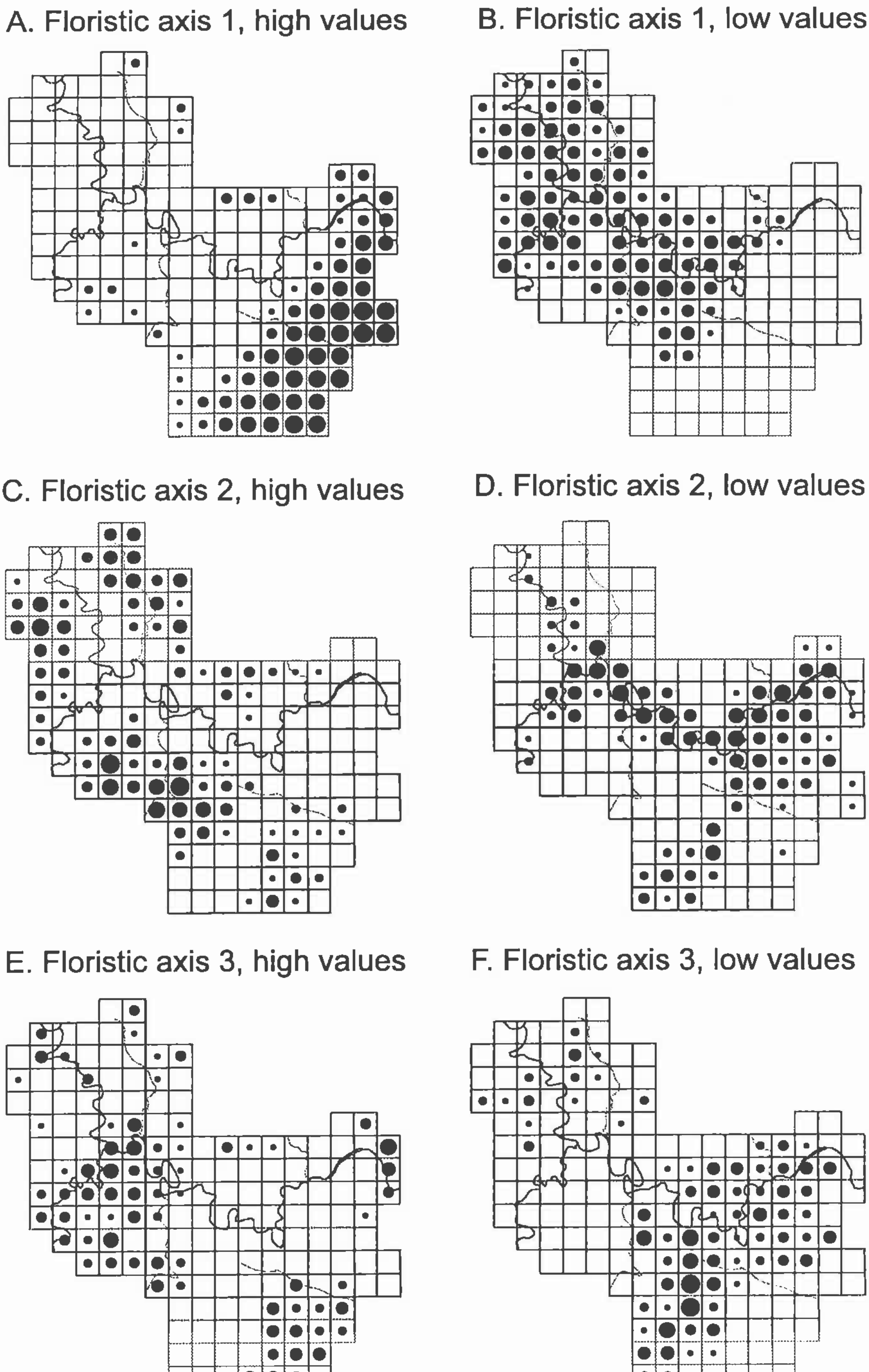

Fig. 4. – DCA ordination of the floristic data. Quadrat scores on ordination axes are standardized to unit range from 0 to 1. On the left, quadrats with high scores on particular axes are indicated by circles (0.55 – smallest circles, 1 – largest circles); on the right, circles indicate quadrats with low scores (0.45 – smallest circles, 0 – largest circles). Quadrats, which are empty in both left and right figures, have scores from 0.45 to 0.55, and occupy central part of the gradient represented by particular axis.

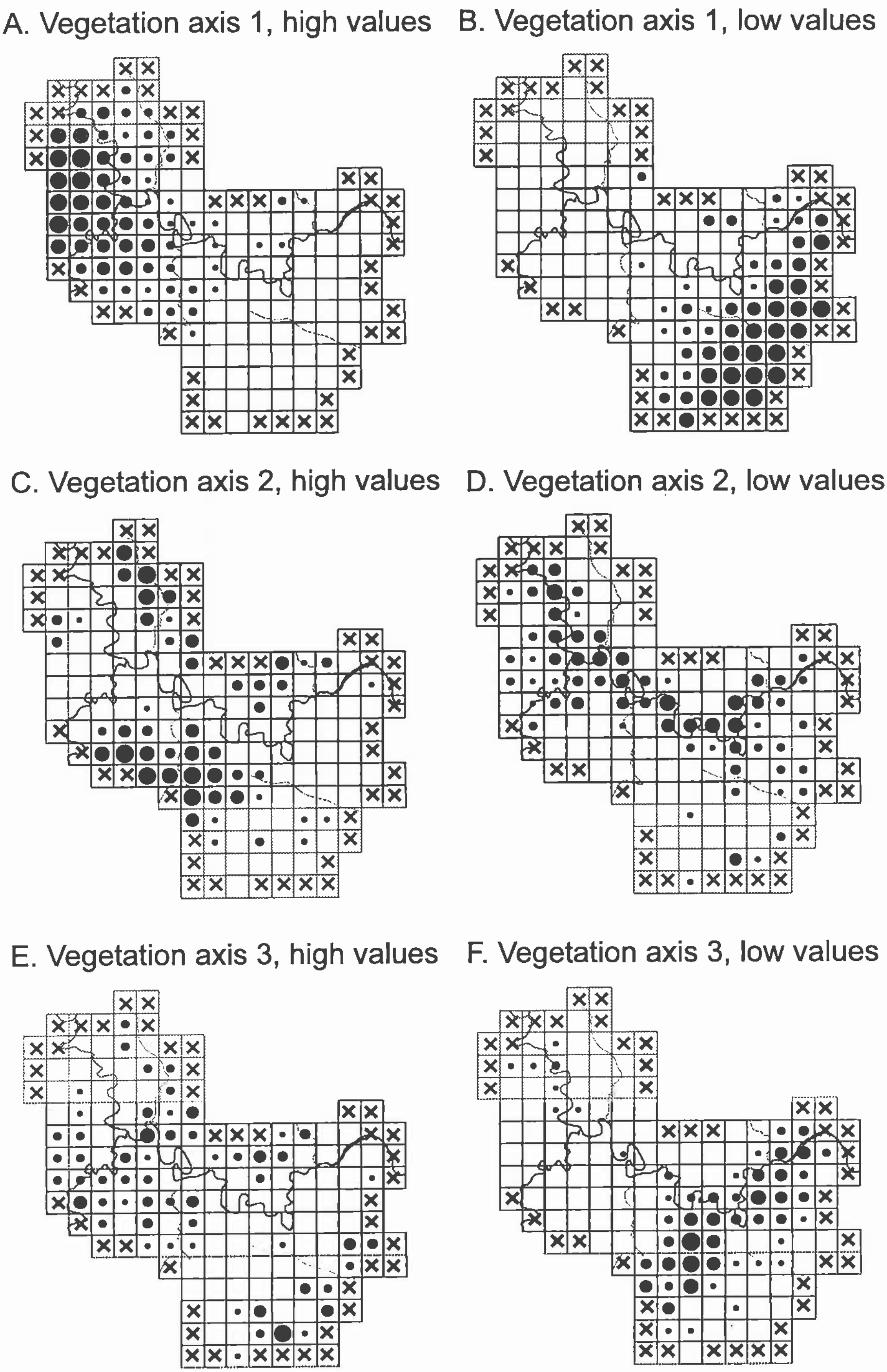

Fig. 5. – DCA ordination of the vegetation data. Quadrat scores on ordination axes are standardized to unit range from 0 to 1. On the left, quadrats with high scores on particular axes are indicated by circles (0.55 – smallest circles, 1 – largest circles); on the right, circles indicate quadrats with low scores (0.45 – smallest circles, 0 – largest circles). Quadrats, which are empty in both left and right figures, have scores from 0.45 to 0.55, and occupy central part of the gradient represented by particular axis. Vegetation data are missing for the quadrats indicated by crosses.

Bohemian Massif (western and central part, with lower temperatures and higher precipitation), and the deforested Tertiary depressions (southeastern part, with a warmer and drier climate).

The second most important floristic gradient (DCA axis 2) is between dry, warm areas with nutrient-poor soils, and deforested areas with wetter, cooler climate and rich soils. Significant correlation of the second axis with altitudinal range suggests that soil erosion and runoff on steeper slopes are probably the main underlying factors responsible for the differentiation in moisture and nutrient status. This gradient separates the river valleys and granitic hillocks in the south, from the areas with wet meadows and rich alder forests on the flatland.

The third floristic gradient (DCA axis 3) reflects the differentiation of areas with nutrient- and base-rich soils on the one hand, and poor soils on the other. Rich end of this gradient is represented by the marble outcrops in the valleys of the western-central part of the study area, together with areas on Tertiary/Quaternary sediments in the eastern and southeastern part, whereas on the poor end, soils on granitic bedrock predominate.

Vegetation data ordination (Table 1, Fig. 5) yielded results similar to the floristic ordination, with nearly the same gradients, arranged in an identical hierarchy. The relative importance of the first gradient increased, as its eigenvalue was almost four times higher than the second eigenvalue. As this ordination is based on the potential natural vegetation, the first axis does not represent a gradient between the forested and deforested areas, although it is significantly correlated with the forest cover. More clearly than in the floristic ordination, this gradient reflects the altitudinal pattern of vegetation belts along co-varying gradients of temperature and moisture.

Land classification

Environmental classification based on the maximum altitude, altitudinal range, forest cover and mean Ellenberg values (Fig. 6A) divided the area into the forested and deforested part at the highest hierarchical level. In the forested part, quadrats in the gently undulating landscape (Group A in Fig. 6A) were distinguished from the quadrats in the river valleys and on the Bohemian Massif edge slope (Group B). The deforested part was divided into the quadrats of the cooler and wetter central and western areas (Groups C, D) and the quadrats of the warmer and drier east and southeast (Groups E, F). Further division of the deforested areas in the central and western part lacks ecological interpretation, whereas the division in the eastern-southeastern part follows the moisture and nutrient pattern.

Floristic classification (Fig. 6B) also separated forested and deforested areas at the highest hierarchical level. In the further branching of the dendrogram, a small group of quadrats on the most acidic soils and with the most oceanic climate (Group B) was separated from the rest (Group A) of the forested quadrats. The deforested areas were divided into those in the cooler and wetter part of the area (Group C), those on nutrient-poor granitic bedrock in the warmer and drier part (Group D), and those on nutrient-rich Tertiary/Quaternary bedrock in the warmer and drier part (Group E). Environmental parameters of each of these groups are summarized in Table 2.

Species with the highest concentrations in particular groups of the floristic classification, i. e. the species with the strongest capacity to discriminate particular group from the others, are summarized in Table 3. Group A is clearly characterized by species of deciduous broad-leaved forests on mesic soils. Very low u-values in Group B indicate that this group is very poorly defined floristically, being more or less negatively differentiated; even cultivated species or species escaped from cultivation with one or two occurrences in the study area, such as *Hieracium aurantiacum* and *Fraxinus pensylvanica* are ranked among the 25 most concentrated species, which indicates that many of the species listed in Table 3 are very poor indicators of this group. In spite of this, many species of Group B may be characterized as species of acidophilous oak forests. Group C has also comparatively low u-values, but there is a clear differentiation by the species of wet meadows. A few species of weeds (*Ranunculus arvensis, Galium spurium, Veronica persica*) indi-

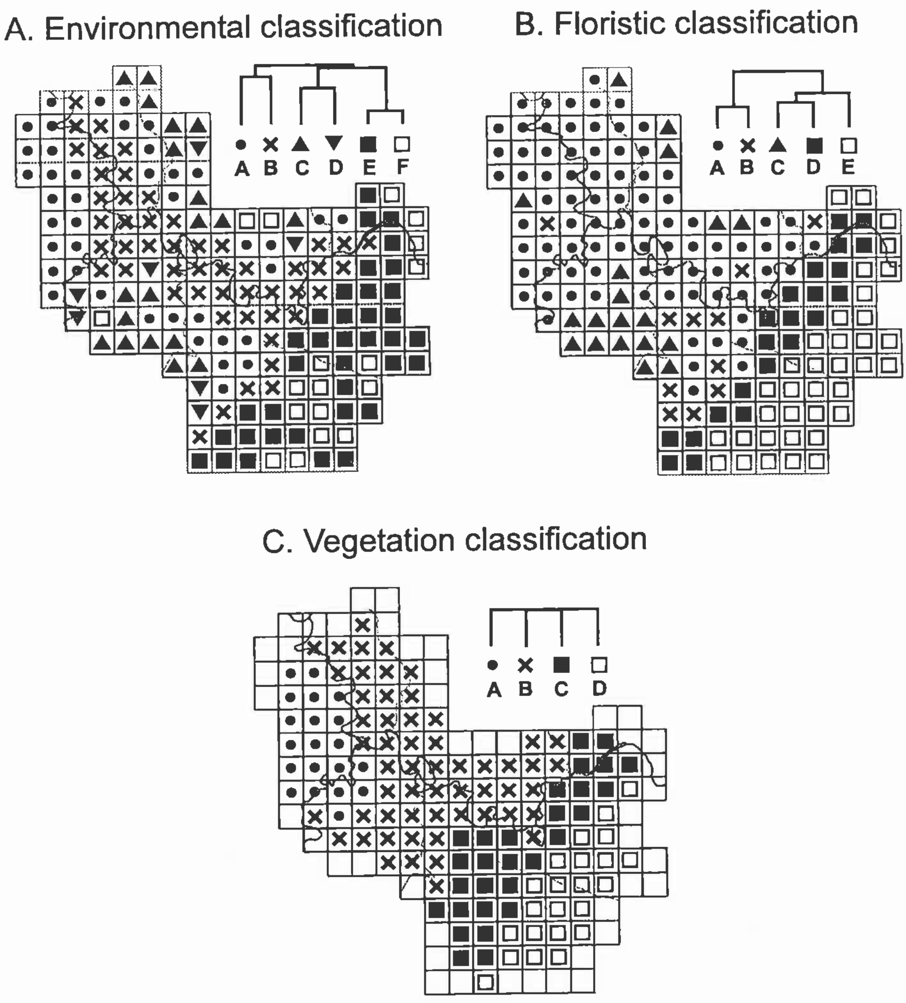

Fig. 6. – Classification of the study area based on environmental variables, floristic data, and potential natural vegetation (cluster analysis, complete linkage). Upper parts of the dendrograms are shown, and groups of quadrats defined by these dendrograms are mapped using different symbols. Vegetation data are missing for empty quadrats in Figure C.

cate that besides the wet meadows, arable land is a typical habitat in the quadrats of this group. Groups D and E are very well differentiated floristically (note the high *u*-values), being characterized by the species of dry grasslands over siliceous bedrock (Group D) and by thermophilous weeds and synanthropic species (Group E). The fact that all the groups of quadrats (perhaps except Group B) are characterized by ecologically uniform groups of indicator species suggests that the floristic land classification produced by cluster analysis is ecologically reasonable.

Classification based on the potential natural vegetation (Fig. 6C) clearly reflects the overriding importance of the first gradient detected in the ordination. Vegetation zonation from the west to the southeast includes beech forests (Group A), Hercynian oak-hornbeam forests (Group B), acidophilous oak forests associated with thermophilous oak forests (Group C), and Pannonian oak-hornbeam forests associated with thermophilous oak forests (Group D).

Table 2. – Environmental characteristics of five groups of quadrats defined by cluster analysis of floristic data (see Fig. 6B). Means ± standard deviations are indicated. Values in a row with different letters are significantly different (Tukey, $P<0.05$).

Group	A	B	C	D	E
Number of quadrats	84	11	19	22	36
Maximum altitude (m a.s.l.)	451±35 c	448±36 c	442±20 c	364±35 b	287±26 a
Altitudinal range (m)	120±50 b	107±42 b	53±23 a	108±33 b	49±24 a
Percentage forest cover	71±31 d	88±20 d	15±24 b	42±33 c	2±7 a
Light value	6.4±0.2 a	6.3±0.4 a	6.7±0.3 b	7.0±0.2 c	7.2±0.2 d
Temperature value	5.7±0.1 a	5.6±0.2 a	5.7±0.1 a	6.0±0.1 b	6.1±0.1 b
Continentality value	4.0±0.1 b	3.9±0.2 a	4.1±0.1 c	4.3±0.1 d	4.6±0.2 e
Moisture value	5.0±0.3 b	5.0±0.4 b	5.1±0.4 b	4.3±0.2 a	4.5±0.3 a
Reaction value	6.3±0.2 b	5.9±0.4 a	6.6±0.3 c	6.6±0.2 c	7.2±0.2 d
Nutrient value	5.0±0.3 b	5.0±0.4 b	5.3±0.3 c	4.5±0.2 a	5.4±0.4 c
Phenology	4.1±0.6 c	3.9±0.2 c	4.3±0.2 c	2.8±0.6 b	1.9±0.8 a

Discussion

Phytogeographical boundaries, detected for other regions in quantitative studies based on similar data and analysed by similar methods as in the present paper, were usually associated with climatic patterns, the distribution of different bedrock types, and possibly also with the difference between coastal and inland areas (McLaughlin 1986, 1989, Pedersen 1990, Hill 1991, Wheeler et al. 1992, Myklestad 1993, Myklestad & Birks 1993, Andersson & Weimarck 1996, Wohlgemuth 1996a, 1996b, Kadmon & Danin 1997). Unlike these studies, which analysed comparatively large areas, the present paper focuses on the landscape scale, for which similar studies are extremely rare. Heikkinen et al. (1998) carried out a study on a nearly identical scale (1 km^2 grid), but in a very different environment of subarctic open landscape. They revealed a major floristic gradient from elevated alpine areas to the river valleys with moist forests and cliffs. Abundance of mires was also an important factor influencing the floristic pattern.

Climatic and geological gradients were also important for the floristic differentiation in the Podyjí/Thayatal National Park, but the main floristic discontinuity was found between forested and deforested areas (Fig. 4A–B, Table 1). This kind of floristic differentiation, however, is not suitable for phytogeographical land classification, as it would tend to produce mosaics of forested and deforested patches. An appropriate solution to this problem seems to be in assigning floristic Group C (Fig. 6B, Table 2) which is a subgroup of the deforested group, to the forested Groups A and B, because these three groups are spatially connected and all of them are characterized by species more typical of the Hercynicum (Table 3). Group B cannot be separated from Group A due to its poor positive differentiation. Thus we arrive at a regional subdivision which is very close to that proposed by Culek (1996), with a joint Group A+B+C, Group D and Group E, corresponding in turn to the Jevišovice region, transitional zone, and the core of the Lechovice region. Group D is transitional in terms of all the environmental characteristics except Ellenberg nutrient value which is lower compared to both Group A+B+C and Group E. In terms of floristic composition, it is characterized by several species which have a striking concentration in the quadrats of this group (Table 3). This indicates that Group D represents a self-contained phytogeographical unit rather than a pure transitional zone.

Table 3. – Floristic indicators of five regions (groups of quadrats) defined by cluster analysis of floristic data. Species are ranked according to the decreasing concentration in each region which is proportional to *u*-value. For each region, 25 species with highest *u*-value are listed and the range of *u*-value between the 1st and 25th species is given. Species with higher *u*-values have a better capacity to differentiate the given region from other regions. Regions with higher *u*-values of their indicator species are better positively characterized in floristic terms.

Code of region with *u*-range of indicator species in brackets				
A (6.99–6.02)	B (3.17–0.87)	C (5.63–2.17)	D (9.09–5.61)	E (8.17–5.01)
Bromus benekenii	*Carex canescens*	*Carex appropinquata*	*Odontites lutea*	*Podospermum canum*
Cyclamen purpurascens	*Holcus mollis*	*Trollius europaeus*	*Helichrysum arenarium*	*Lycium barbarum*
Sambucus racemosa	*Nardus stricta*	*Eriophorum angustifolium*	*Silene otites*	*Sclerochloa dura*
Cardamine impatiens	*Hieracium aurantiacum*	*Ranunculus arvensis*	*Rosa pimpinellifolia*	*Atriplex oblongifolia*
Carex pilosa	*Galium rotundifolium*	*Polygonum bistorta*	*Fumaria rostellata*	*Lathyrus tuberosus*
Impatiens noli-tangere	*Gnaphalium sylvaticum*	*Equisetum palustre*	*Rosa jundzillii*	*Reseda lutea*
Calamagrostis arundinacea	*Spergularia rubra*	*Carex cespitosa*	*Achillea setacea*	*Cardaria draba*
Galium odoratum	*Vaccinium myrtillus*	*Senecio rivularis*	*Pulsatilla grandis*	*Inula britannica*
Cirsium palustre	*Athyrium filix-femina*	*Salix rosmarinifolia*	*Armeria elongata*	*Onopordon acanthium*
Oxalis acetosella	*Carex leporina*	*Carex davalliana*	*Hieracium echioides*	*Asperugo procumbens*
Campanula rotundifolia	*Veronica officinalis*	*Crepis mollis*	*Avenochloa pratensis*	*Tragopogon dubius*
Daphne mezereum	*Epilobium angustifolium*	*Juncus inflexus*	*Petrorhagia prolifera*	*Salvia nemorosa*
Asarum europaeum	*Prunella vulgaris*	*Caltha palustris*	*Androsace elongata*	*Hordeum murinum*
Sanicula europaea	*Carex elata*	*Carum carvi*	*Cytisus procumbens*	*Malva pusilla*
Galium sylvaticum	*Fraxinus pensylvanica*	*Carex gracilis*	*Festuca pallens*	*Atriplex tatarica*
Senecio germanicus	*Mycelis muralis*	*Taraxacum palustre* agg.	*Aster linosyris*	*Euphorbia virgata*
Primula elatior	*Sagina procumbens*	*Ranunculus auricomus* agg.	*Carex supina*	*Atriplex acuminata*
Hepatica nobilis	*Dryopteris carthusiana*	*Valeriana dioica*	*Biscutella laevigata*	*Panicum milliaceum*
Dentaria bulbifera	*Luzula luzuloides*	*Iris pseudacorus*	*Chondrilla juncea*	*Mercurialis annua*
Chaerophyllum aromaticum	*Senecio viscosus*	*Cardamine pratensis*	*Lotus borbasii*	*Kochia scoparia*
Carex digitata	*Juncus tenuis*	*Galium spurium*	*Veronica spicata*	*Sisymbrium loeselii*
Melica uniflora	*Senecio sylvaticus*	*Carex panicea*	*Quercus pubescens*	*Bromus japonicus*
Hypericum hirsutum	*Rubus idaeus*	*Cirsium canum*	*Gagea bohemica*	*Bryonia alba*
Fagus sylvatica	*Stellaria alsine*	*Veronica persica*	*Hieracium umbellatum*	*Veronica polita*
Mercurialis perennis	*Danthonia decumbens*	*Colchicum autumnale*	*Melampyrum arvense*	*Allium sativum*

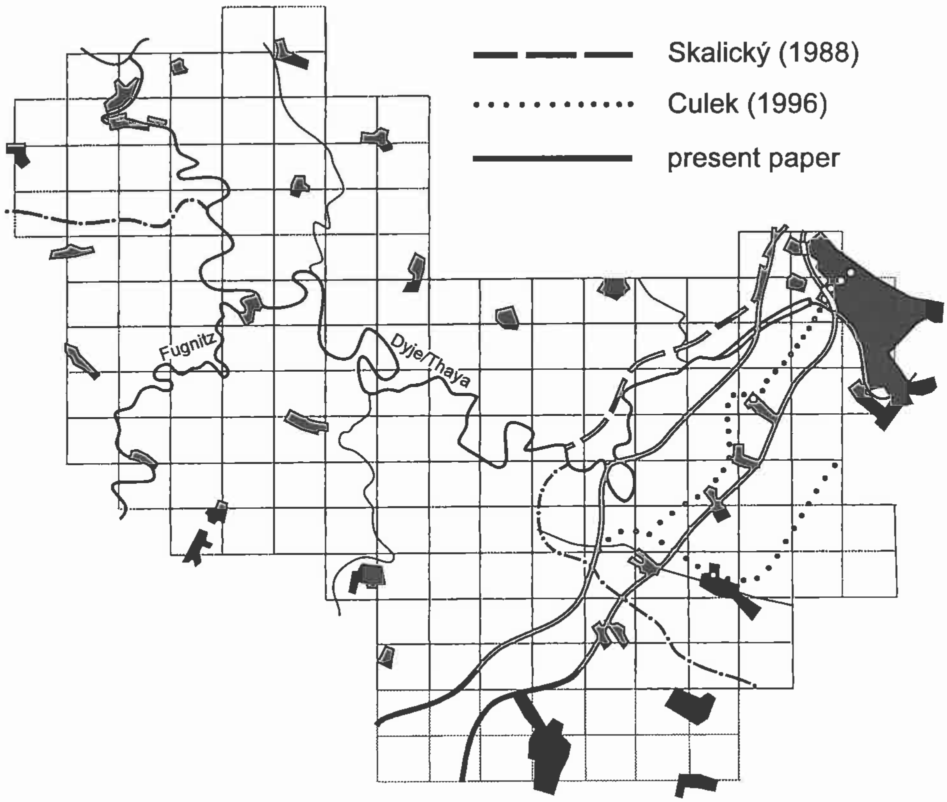

Fig. 7. – Location of phytogeographical boundaries suggested in earlier studies and tentative boundaries of the transitional zone between the Pannonicum and Hercynicum detected by multivariate analyses in the present paper.

Land classification based on the potential natural vegetation yielded four zones roughly paralleling the presumed main phytogeographical boundary. Unfortunately, this classification is of little use for the definition of this boundary, as the cluster analysis failed to hierarchize the zones. Another problem is that the potential natural vegetation does not reflect the flora and vegetation of secondarily treeless habitats. In the modern cultural landscape of Central Europe, however, large-scale deforestations have to be taken into account in phytogeographical considerations as well.

River valleys were detected as a separate landscape unit in the environmental land classification (Fig. 6A) but not in the floristic or in the vegetation classifications (Figs. 6B, 6C). In the floristic classification, it was obviously due to the overriding importance of the gradient of forest cover that assigned the quadrats of the predominantly forested river valleys to other forested quadrats. Further subdivision of forested quadrats followed the gradient of soil reaction rather than the composite gradient of altitudinal range, temperature, continentality and nutrients that would lead to the separation of the river valley from the other forested areas. River valleys were not detected in vegetation classification either, even though they support a higher number of different vegetation types than the adjacent landscape (Chytrý & Vicherek 1995). The reason is that the vegetation types dominating in the adjacent landscape are nearly always present in the valleys and often form a landscape matrix there. Therefore, the boundary between the Pannonicum and Hercynicum with a promontory running up the river valley is not plausible for the study area.

Conclusion

The results of multivariate analyses are closest to the Biogeographical Land Classification by Culek (1996), in which a transitional zone is introduced between the central and western upland part of the study area (predominantly forested, on siliceous bedrock with a cooler and wetter climate – Hercynicum), and the low-altitudinal depressions in the eastern and southeastern part (largely deforested, on Tertiary sediments and loess, with a warmer and drier climate – Pannonicum). This transitional zone shares several species with each of the two major regions and possesses intermediate values of environmental variables, but it has some unique features as well, e. g. low proportion of nitrophilous species and occurrence of several species restricted to it. Fig. 7 shows tentative boundaries of this zone, roughly following the results of the current analyses based on quadrats, but adjusted to actual positions of geological, topographical and land-use boundaries. Compared to Culek (1996), the position of the transitional zone must be slightly moved to the west, so that it includes the largely deforested area on the granitic bedrock of the prominent slope on the edge of the Bohemian Massif. Towards the southeast it does not extend much beyond the limits of the granitic bedrock. In the floristic classification, the transitional zone appears to be slightly closer to deforested areas of the Hercynicum rather than to the Pannonicum (see the dendrogram in Fig. 6B). Closer relationships of the transitional zone to the Hercynicum are also supported by almost identical position of the boundary between this zone and the core area of the Pannonicum in the floristic and vegetation classification, whereas the boundary between the transitional zone and the core area of the Hercynicum is different in these two classifications; the former boundary should be therefore considered more important in phytogeographical considerations. On the other hand, the abiotic environment of the transitional zone is closer to the Pannonicum (Fig. 6A). The analyses do not support the concept of the main phytogeographical boundary with a promontory of the Pannonicum in the Dyje/Thaya river valley.

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Souhrn

Průběh fytogeografické hranice mezi panonskou a hercynskou oblastí je analyzován v krajině Národního parku Podyjí a přilehlého území v Rakousku (obr. 1). Pro 172 síťových kvadrátů o přibližné velikosti 1,2 × 1,1 km byla sestavena databáze s floristickými záznamy o výskytu cévnatých rostlin (Grulich 1997), údaji o potenciální přirozené vegetaci (Chytrý & Vicherek 1995), hodnotami vybraných proměnných prostředí (maximální nadmořská výška, rozsah nadmořských výšek, lesnatost a nástup jarních fenofází, obr. 2) a s Ellenbergovými indikačními hodnotami, vypočítanými jako průměr hodnot pro druhy vyskytující se v jednotlivých kvadrátech. Ellenbergovy hodnoty umožnily charakterizovat prostorovou variabilitu hlavních ekologických faktorů: světla, tepla (teploty), kontinentality, vlhkosti, půdní reakce a dostupnosti živin (obr. 3).

Ordinační metodou detrendované korespondenční analýzy byly určeny hlavní gradienty ve složení flóry a potenciální přirozené vegetace (obr. 4, 5, tab. 1). Nejvýznamnější floristický gradient probíhá od nižších, teplých a suchých oblastí s třetihorními a čtvrtohorními sedimenty Dyjsko-svrateckého úvalu na jihovýchodě k vyšším, chladnějším a vlhčím oblastem na tvrdých horninách Českého masívu ve střední a severozápadní části území. Tento gradient je současně i gradientem mezi odlesněnými a lesnatými částmi území. Druhý nejvýznamnější gradient, na prvním nezávislý, odděluje odlesněné plošiny v chladnější a vlhčí oblasti, s půdami živinami bohatými, od suchých a teplých oblastí s půdami chudými. Na tomto gradientu jsou výrazně diferencovány plošiny v oblasti Českého masívu na jedné straně od údolí Dyje a Fugnitz a okrajového svahu Českého masívu na straně druhé. Třetí floristický gradient odděluje oblasti s půdami bohatými na báze a živiny (např. krystalické vápence v okolí Hardeggu a mladé sedimenty Dyjsko-svrateckého úvalu) od oblastí s chudými půdami. Prakticky shodné tři hlavní gradienty byly zjištěny také při ordinaci vegetačních dat, tj. údajů o poměrném zastoupení jednotek potenciální přirozené vegetace v jednotlivých síťových kvadrátech.

Po zjištění hlavních gradientů byla provedena regionalizace území klasifikační metodou shlukové analýzy (obr. 6). První klasifikace vycházela pouze z dat o abiotickém prostředí (včetně Ellenbergových indikačních hodnot) a rozlišila tři hlavní územní jednotky: Dyjsko-svratecký úval včetně odlesněného okrajového svahu Českého masívu, zalesněné území v Českém masívu a odlesněné území v Českém masívu. V rámci zalesněného území v Českém masívu se dále oddělila údolí Dyje a Fugnitz od plošin. Další klasifikace území vycházela z floristických dat a rozlišila pět územních jednotek, a to dvě jednotky zalesněných plošin v Českém masívu včetně říčních údolí, odlesněnou plošinu v Českém masívu, okrajový svah Českého masívu a Dyjsko-svratecký úval. Všech pět floristických územních jednotek bylo charakterizováno průměrnými hodnotami faktorů abiotického prostředí (tab. 2) a rostlinnými druhy, které danou jednotku svým výskytem diferencují od jednotek ostatních (tab. 3). Pro hodnocení míry koncentrace druhů v jednotlivých územních jednotkách se ukázal jako vhodný statistický koeficient u (Bruelheide 1995). Třetí klasifikace území byla založena na potenciální přirozené vegetaci, a proto neodrážela vliv odlesnění krajiny. Tato klasifikace rozlišila od západu k jihovýchodu územní jednotku bučin, jednotku hercynských dubohabřin, jednotku acidofilních doubrav a jednotku panonských dubohabřin s teplomilnými doubravami. Ani klasifikace flóry, ani klasifikace vegetace nerozlišily říční údolí jako samostatnou jednotku.

Výsledky podporují koncepci vyhraněné přechodné zóny mezi Panonikem a Hercynikem na odlesněném okrajovém svahu Českého masívu, která přibližně odpovídá přechodné zóně v Biogeografickém členění České republiky (Culek 1996), je však oproti ní mírně posunutá k západu (obr. 7). Tato zóna je floristicky nepatrně bližší Hercyniku, z hlediska abiotické klasifikace krajiny však patří spíše do Panonika, a navíc má některé jedinečné rysy, odlišující ji od obou hlavních oblastí. Kromě výskytu většího množství druhů pro tuto zónu specifických (tab. 3) zde např. roste méně nitrofilních druhů. Hranice termofytika a mezofytika ve fytogeografickém členění pro Květenu ČR (Skalický 1988) je nerealisticky posunutá až za Dyji v jejím úseku od místa, kde opouští státní hranici, po Znojmo. Údolí Dyje by mělo být ve studovaném území řazeno do stejné fytogeografické oblasti jako navazující krajina a nemělo by mít větší vliv na regionální fytogeografické členění.

References

Andersson P.-A. & Weimarck G. (1996): Floristic patterns and phytogeography of Skåne, S Sweden. – Symb. Bot. Ups. 31: 239–264.

Batík P. (1992): Geologická mapa Národního parku Podyjí (Geological map of the Podyjí National Park). – Český geologický ústav, Praha.

Bruelheide H. (1995): Die Grünlandgesellschaften des Harzes und ihre Standortsbedingungen. Mit einem Beitrag zum Gliederungsprinzip auf der Basis von statistisch ermittelten Artengruppen. – Diss. Bot. 244: 1–338.

Bruelheide H. & Jandt U. (1995): Survey of limestone grassland by statistically formed groups of differential species. – Coll. Phytosoc. 23: 319–338.

Chytrý M. & Tichý L. (1998): Phenological mapping in a topographically complex landscape by combining a field survey with an irradiation model. – Appl. Veget. Sci. 1: 225–232.

Chytrý M. & Vicherek J. (1995): Lesní vegetace Národního parku Podyjí/Thayatal. Die Waldvegetation des Nationalparks Podyjí/Thayatal. – Academia, Praha.

Culek M. (ed.) (1996): Biogeografické členění České republiky (Biogeographical land classification of the Czech Republic). – Enigma, Praha.

Dostál J. (1957): Fytogeografické členění ČSSR (Phytogeographical land classification of Czechoslovakia). – Sborn. Čs. Společ. Zeměp. 62: 1–18.

Dostál J. (1960): The phytogeographical regional distribution of the Czechoslovak flora. – Sborn. Čs. Společ. Zeměp. 65: 193–202.

Drude O. (1902): Der herzynische Florenbezirk. – W. Engelmann, Leipzig.
Ehrendorfer F. (1973): Liste der Gefäßpflanzen Mitteleuropas. Ed. 2. – G. Fischer, Stuttgart.
Ellenberg H., Weber H. E., Düll R., Wirth W., Werner W. & Paulißen D. (1992): Zeigerwerte von Pflanzen in Mitteleuropa. Ed. 2. – Scr. Geobot. 18: 1–258.
Grulich V. (1997): Atlas rozšíření cévnatých rostlin Národního parku Podyjí/Thayatal. Verbreitungsatlas der Gefäßpflanzen des Nationalparks Podyjí/Thayatal. – Masarykova univerzita, Brno.
Hayek A. (1923): "Pontische" und "pannonische" Flora. – Österr. Bot. Z. 72: 231–235.
Heikkinen R. K., Birks H. J. B. & Kalliola R. J. (1998): A numerical analysis of the mesoscale distribution patterns of vascular plants in the subarctic Kevo Nature Reserve, northern Finland. – J. Biogeogr. 25: 123–146.
Hill M. O. (1979): DECORANA. A Fortran program for detrended correspondence analysis and reciprocal averaging. – Cornell University, Ithaca.
Hill M. O. (1991): Patterns of species distribution in Britain elucidated by canonical correspondence analysis. – J. Biogeogr. 18: 247–255.
Kadmon R. & Danin A. (1997): Floristic variation in Israel: a GIS analysis. – Flora 192: 341–345.
McLaughlin S. P. (1986): Floristic analysis of the southwestern United States. – Great Basin Nat. 46: 46–65.
McLaughlin S. P. (1989): Natural floristic areas of the western United States. – J. Biogeogr. 16: 239–248.
Meusel H., Jäger E. & Weinert E. (1965): Vergleichende Chorologie der zentraleuropäischen Flora. Vol. 1. – G. Fischer, Jena.
Myklestad A. (1993): The distribution of *Salix* species in Fennoscandia – a numerical analysis. – Ecography 16: 329–344.
Myklestad A. & Birks H. J. B. (1993): A numerical analysis of the distribution patterns of *Salix* species in Europe. – J. Biogeogr. 20: 1–32.
Niklfeld H. (1964): Zur xerothermen Vegetation im Osten Niederösterreichs. – Verh. Zool.-Bot. Ges. Wien 103/104: 152–181.
Niklfeld H. (1993): Pflanzengeographische Charakteristik Österreichs. – In: Mucina L., Grabherr G. & Ellmauer T. (eds.), Die Pflanzengesellschaften Österreichs I. Anthropogene Vegetation, p. 43–75, G. Fischer, Jena/Stuttgart/New York.
Oksanen J. & Minchin P. R. (1997): Instability of ordination results under changes in input data order: explanations and remedies. – J. Veget. Sci. 8: 447–454.
Pedersen B. (1990): Distributional patterns of vascular plants in Fennoscandia: a numerical approach. – Nord. J. Bot. 10: 163–189.
Podani J. (1993): SYN-TAX-pc. Computer programs for multivariate data analysis in ecology and systematics. Version 5.0. – Scientia Publishing, Budapest.
Skalický V. (1988): Regionálně fytogeografické členění (Phytogeographical land classification). – In: Hejný S. & Slavík B. (eds.), Květena České socialistické republiky 1 (Flora of the Czech Socialistic Republic), p. 103–121, Academia, Praha.
SPSS Inc. (1998): SPSS[R] Base 8.0. – SPSS Inc., Chicago.
ter Braak C. J. F. & Šmilauer P. (1998): CANOCO reference manual and user's guide to Canoco for Windows. Software for Canonical Community Ordination (version 4). – Centre for Biometry, Wageningen.
Vesecký A., Petrovič Š., Briedoň V. & Karský V. (eds.) (1958): Atlas podnebí Československé republiky (Climatic atlas of the Czechoslovak Republic). – Ústřední správa geodesie a kartografie, Praha.
Wheeler G. A., Cushing E. J., Gorham E., Morley T. & Ownbey G. B. (1992): A major floristic boundary in Minnesota: an analysis of 280 taxa occurring in the western and southern portions of the state. – Can. J. Bot. 70: 319–333.
Wohlgemuth T. (1996a): Ein floristischer Ansatz zur biogeographischen Gliederung der Schweiz. – Bot. Helv. 106: 227–260.
Wohlgemuth T. (1996b): Biogeographical regionalization of Switzerland based on floristic data: How many species are needed? – Biodiv. Lett. 3: 180–191.

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