Environmental control of the vegetation pattern in deep river valleys of the Bohemian Massif

Vliv faktorů prostředí na vegetaci hlubokých říčních údolí Českého masivu

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The pattern of natural vegetation on non-calcareous soils in two deep river valleys of the Bohemian Massif (Vltava and Dyje rivers, Czech Republic) was analyzed in order to determine the main topographic and soil variables affecting the composition of the vegetation. Vegetation data together with topographic and soil variables were collected along transects down the slope from the upper edge to the bottom of the valley. The distribution of vegetation types within the valleys was described using cluster analysis and non-metric multidimensional scaling (NMDS). Effects of topographic and soil variables were compared using a set of canonical correspondence analyses (CCAs) with explanatory variable selection based on the Akaike information criterion (AIC). In order to describe the non-linear interaction between the two topographic variables, elevation and aspect, a new method (moving window CCA) was introduced. This method assessed the explanatory power of aspect at various elevations above the valley bottom. Results show that main vegetation coenoclines are correlated with two complex environmental gradients: the moisture-nutrient-soil reaction and light-temperature-continentality gradients. Soil variables are slightly better predictors of vegetation composition than topographic variables. Altogether, these variables explain 18.8–21.6% of the total inertia. Although soil development depends on topography, the variation jointly explained by both groups of variables is only 3.9–5.2%, indicating that each of these two groups of variables influences vegetation pattern in a different way. Variables selected by the most parsimonious model for the Vltava valley are aspect, soil pH, soil type fluvisol and soil depth. For the Dyje valley the same variables as in Vltava valley were selected except for soil depth, which was replaced by soil type cambisol. Aspect has a strong effect on vegetation on the middle slopes but not on the lower slopes of the valleys. The results of all analyses are similar between the two valleys, suggesting that similar patterns may also occur in other deep river valleys of mid-altitudes of the Bohemian Massif.

K e y w o r d s : canonical correspondence analysis, cluster analysis, deep river valleys, non-metric multidimensional scaling, moving window CCA, vegetation-environment relationships

Introduction

In the gently undulating landscape of the Bohemian Massif, which occupies a large part of the Czech Republic and adjacent areas of Germany and Austria, deep river valleys are a distinct topographic feature. Compared to other valley types, these are narrow, V-shaped valleys with steep slopes, large meanders and a narrow, discontinuously developed floodplain. They are sharply incised in the flat or hilly landscapes, predominantly formed of granite or gneiss bedrocks. These valleys are mainly found at middle altitudes between 200 and 700 m. All river valleys of this type are of Quaternary age, when the uplift of the

Bohemian Massif increased the erosion power of rivers and caused the deepening of previously shallow and broad valleys into deep and narrow ones (Kopecký 1996).

Botanical diversity of deeply incised river valleys in the Bohemian Massif has the same general characteristics as other river corridors, such as high species richness (Gould & Walker 1999), linear plant migration (Naiman et al. 1993, Burkart 2001, Mouw et al. 2003) and sensitivity to alien plant invasions (Pyšek & Prach 1993, Planty-Tabacchi et al. 1996). Additionally, these valleys possess some other characteristics, in particular a high beta diversity of the plant communities on hillsides, caused by high topographic, geological and mesoclimatic diversity (Chytrý & Tichý 1998). There are sharp environmental gradients within relatively small areas, some of which are large enough to include both extreme as well as intermediate values of environmental factors (e.g. different moisture in the floodplain and on the south-facing upper parts of the valley slopes, or soil pH on outcrops of siliceous and calcareous bedrocks). Consequently, deep river valleys represent local biodiversity hotspots in an otherwise rather uniform landscape in the middle altitudes of the Bohemian Massif.

The high biotic diversity in the Bohemian Massif deep river valleys is coupled with limited human impact in some places. This feature also sharply contrasts with the adjacent landscape, which is dominated by an intensively managed mosaic of arable fields and secondary forest plantations. Because of the limited accessibility due to the steep valley slopes, there are complete zonations of near-natural vegetation types, predominantly forests, in several sections of the valleys.

Strong topographic gradients in the river valleys affect the variation in several environmental variables, which directly affect plant growth, e.g. moisture, nutrient availability and pH. Thus, topography strongly co-varies with vegetation pattern, and at some scales, topographic variables can be robust predictors of vegetation patterns. Such relationships are clear in river valleys with broad floodplains (e.g. Sagers & Lyon 1997, Gould & Walker 1999, van Coller et al. 2000, Goebel et al. 2006), but may be accentuated in deep river valleys due to the complex topography of the slopes adjacent to the floodplain.

Specific features of the vegetation pattern of these deep river valleys were summarized under the heading "river phenomenon" in the descriptions provided by Czech vegetation scientists in the 1960s (Blažková 1964, Jeník & Slavíková 1964). The "river phenomenon" concept describes how topographic and mesoclimatic features of the deeply incised river valleys of the Bohemian Massif affect their vegetation diversity. Of the abiotic factors, this concept stresses the sharp contrast between the deep river valleys and adjacent gently undulating landscape, the pronounced effect of exposed rocks occurring on steep slopes on the vegetation, the contrast between the sunny and warm south-facing slopes and shaded and cold north-facing slopes, high diversity of various extreme habitats situated next to each other and specific mesoclimatic conditions causing temperature inversions. Of the vegetation features, the "river phenomenon" concept emphasizes (1) the high biodiversity in deep river valleys, (2) non-random distribution of vegetation types and species richness within the valleys, (3) concentration of relict species, resulting from the fact, that deep river valleys probably served as a Pleistocene refuges for plant and animal species, and (4) migration of plants and animals along the rivers, connecting mountains with lowlands. Although there are several published local descriptions of plant communities in the Bohemian Massif deep river valleys (Blažková 1964, Türk 1994, Chytrý & Vicherek 1995, 1996, 2003, Kolbek et al. 1997, 1999–2003), there are no quantitative studies that test the predictions of the "river phenomenon" concept (Blažková 1964, Jeník & Slavíková 1964) and summarize the general features of vegetation patterns and their driving environmental factors.

The aim of this study is to produce a quantitative description of the vegetation-environment relationships in deep river valleys of the Bohemian Massif, focusing on the patterns occurring in a cross-section of the valleys. To avoid the effect of local idiosyncrasies on the results, we studied two valleys, Vltava and Dyje, differing markedly in both climatic and floristic characteristics. Specifically, we analyzed correlations between vegetation pattern and topographic variables, measured soil factors and species indicator values, in order to reveal the most important factors determining the pattern of vegetation in deep river valleys.

Methods

Study sites

One study site is a part of the Vltava river valley in S Bohemia, N of Český Krumlov (Fig. 1). The section of valley studied is situated between Zlatá Koruna (48°51' N, 14°22' E) and Boršov nad Vltavou (48°55' N, 14°26' E), with an altitudinal range of 400–540 m a.s.l. and maximum valley depth of around 100 m. Climate in this area is moderately warm, with mean January temperatures –3 to –1 °C and mean July temperatures 16–17 °C. Average annual precipitation is 550–600 mm (Tolasz 2007). Phytogeographically this area belongs to the Hercynian floristic region with some components of the forest flora of the Alps and continental thermophilous flora of Central Bohemia. Bedrock types include mainly acidic gneiss and granulite, with patchy occurrence of crystalline limestone (marble), serpentine and amphibolite (Chábera 1985).

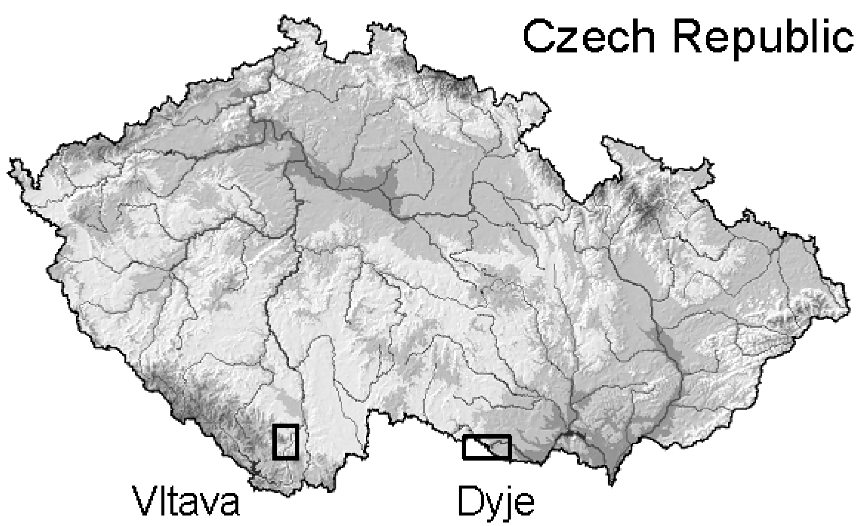

Fig. 1. – Location of the studied sections of the Vltava and Dyje valleys in the Czech Republic.

The other site is located in the Dyje (in German Thaya) river valley in the Podyjí/Thayatal National Park on the border between the Czech Republic and Austria (Fig. 1). The studied section of this river valley is between the towns of Vranov nad Dyjí (48°54' N, 15°49' E) and Znojmo (48°52' N, 16°03' E) on the Czech and Austrian sides of the national border, respectively. Altitudinal range is 220–536 m a.s.l. and maximum valley depth almost 200 m. Climate in this area is generally warmer and more continental than at the previous site, with mean January temperatures ranging between –3 and –2 °C, mean July temperatures 18–19 °C and mean annual precipitation 550–600 mm (Tolasz 2007). This site is located close to the boundary of the Hercynian and Pannonian floristic regions (Chytrý et al. 1999) and therefore has a significant proportion of thermophilous and continental species. Geological characteristics are similar to those of the previous site. Predominant bedrocks include acidic gneiss and granite, with some restricted occurrences of crystalline limestone (Batík 1992).

Data sampling

Fieldwork was conducted in 1992–1993 by M. C. (Dyje valley) and 2001–2003 by D. Z. (Vltava valley). The standardized sampling protocol (Chytrý 1995) was applied in both valleys. Vegetation was sampled along transects from the upper edge to the bottom of the valley in places where there was no artificial or human-disturbed vegetation. Transect sites were selected to include the maximum diversity of habitat types occurring in the valleys. Along these transects, vegetation and environmental data were collected in plots of 10 × 15 m (with longer axis situated along the isohypse) placed equidistantly every 30 m in the Vltava valley and 40 m in the Dyje valley, which reflects the greater depth of the Dyje valley. In each plot, all the vascular plants were recorded, plus an estimate of the cover based on the nine-degree Braun-Blanquet scale (Westhoff & van der Maarel 1978). Nomenclature of plant taxa follows Kubát et al. (2002).

Various topographic and soil factors were either measured directly, estimated or calculated (Table 1). Of them, heat index (Parker 1988) measures relative differences in the solar energy arriving at the different sites. It is calculated from the slope and aspect, using the formula heat index = cos (aspect – 202.5°) × tg (slope), where 202.5° represents the warmest SSW aspect. Although in theory solar irradiance in the northern hemisphere peaks at solar noon and a 180° aspect, delayed ground heating is responsible for the fact that the highest diurnal heat load is experienced on SW–SSW facing slopes (Geiger 1966). Aspect, due to its circular nature, was not used per se, but calculated as the deviance of the measured plot aspect from 22.5° (NNE), thus reaching the highest value of 180° on SSW slopes.

Within each plot, five measurements of soil depth were made using a metal gouge auger with an operational length of 70 cm and a diameter of 1.5 cm; the five values were averaged and used as an estimate of soil depth (note that the actual soil depth may be underestimated when the auger is used in stony soils). Due to a strongly skewed distribution, this variable was log-transformed before further analyses. At each plot, five soil samples from the A-horizon (depth 0–10 cm after litter removal) were collected from different places, mixed together and used to measure soil pH in water solution (dried samples were placed in distilled water for 24 hours; weight ratio of soil/water = 0.4). For each plot, soil types according to ISSS-ISRIC-FAO (1998) were recorded, using a simplified categorization of the following four broadly conceived classes: fluvisol – soils directly affected by a river

Table 1. – Explanatory variables used in the study.

Topographic variables (quantitative and ordinal variables):	
Elevation	relative elevation above the valley bottom (range 0–1, 0 for the valley bottom, 1 for the upper edge)
Aspect	aspect, expressed as deviation of plot aspect from 22.5° (NNE); it reaches the highest value for the supposedly warmest SSW aspect
Slope	slope inclination (°); observed range: Vltava 0–88°, Dyje 5–77°
Heat index	heat index = cos (aspect – 202.5°) × tg slope
Surface SL	landform shape in the downslope direction (three-degree ordinal scale: –1 concave, 0 flat, 1 convex)
Surface ISO	landform shape along an isohypse (three-degree ordinal scale: –1 concave, 0 flat, 1 convex)
Soil variables and soil types (quantitative and categorical variables):	
pH	active soil pH measured in water solution
Soil depth	soil depth, expressed as log [soil depth (cm)]
Fluvisol	fluvisols (water-influenced soils formed from alluvial deposits)
Skeletic	skeletic and hyperskeletic leptosols (stony soils on scree accumulations)
Cambisol	cambisols (well-developed zonal soils)
Lithic	lithic leptosols (shallow soils near rock outcrops)

water regime, with fluvic soil material (inspected using the auger); skeletic – skeletic and hyperskeletic leptosols on steep scree slopes, containing various proportions of gravel or coarse stones; cambisol – deeper and matured cambisols on slight slopes; lithic – shallow and undeveloped lithic leptosols on and near to rocky outcrops. As most plots were on acidic bedrock, data from transects containing plots on calcareous soils were removed from the data set (3 plots in the Vltava and 22 in the Dyje valley). These plots, representing vegetation types sharply different from those on acidic soils, might produce an undesirable outlier effect. The data set used for the analyses included 94 plots situated along 26 transects in the Vltava valley and 82 plots from 14 transects in the Dyje valley.

Classification and indirect ordination

To identify the main vegetation types, plots were classified by cluster analysis, performed separately on the data sets from each valley. Several pilot analyses with various combination of clustering methods and distance measures were calculated. For presentation, the relative Euclidean (chord) distance and Ward's clustering algorithm based on square-root transformed percentage cover data were used, because they best reflected the pattern of vegetation differentiation as judged by expert knowledge. The resulting classifications were projected onto an ordination diagram using non-metric multidimensional scaling (NMDS; Minchin 1987) performed on a matrix of Bray-Curtis dissimilarities between relevés, together with passively projected Ellenberg indicator values (EIV; Ellenberg et al. 1992) calculated as non-weighted averages of the values for all species in merged vegetation layers. NMDS was calculated using the advanced algorithm proposed by Minchin (1987). It includes several random calculations in order to search for a robust global solution and post-analysis rotation of NMDS axes based on principal components analysis so that the variance of points is maximized on the first dimension (for more details see Oksanen et al. 2006). Polarity of axes in resulting diagrams was adjusted in order to unify the directions of EIV and signs of correlations with axes in both valleys. Clusters obtained for each valley were ordered along the moisture gradient (according to cluster median EIV for moisture) from the driest (Cluster 1) to wettest (Cluster 5) to ensure that in both valleys the clusters with the same numbers represent analogous vegetation types. Interpretation of particular clusters in terms of vegetation types was based on expert judgement, supported by the list of diagnostic, constant and dominant species identified for each cluster (not shown; diagnostic species were determined using the phi coefficient of association, corrected for even group sizes according to Tichý & Chytrý 2006).

Correlation among explanatory variables and Ellenberg indicator values

Correlation matrix of all explanatory variables and EIV was calculated, using Spearman rank coefficients for all variables except the relationships between binary variables (soil types); these were calculated using contingency tables, with significance derived from Pearson's chi-square test with Yates's continuity correction (Sokal & Rohlf 1995). Correlations between explanatory variables were based on data merged from both valleys, while correlations of explanatory variables and EIV were made separately for each valley in order to detect local differences in observed patterns.

Variation partitioning between topographic and soil variables

Relationships between vegetation composition and environmental variables were analyzed using canonical correspondence analysis (CCA; ter Braak 1986), a method modified to handle unimodal species responses. In the first step, models based only on topographic (model *V.topo* for Vltava and *D.topo* for Dyje valley, respectively) and only on soil variables (models *V.soil* and *D.soil*) were developed for each valley in order to assess the amount of variation explained by each of these two types of explanatory variables. Models were built using a stepwise algorithm, combining forward and backward selection of explanatory variables. Evaluation of models' parsimony was based on the Akaike information criterion (AIC; Akaike 1973) as implemented in the R package Vegan (Oksanen et al. 2006). Conditional and shared effects of selected topographic and soil variables were calculated by partial CCA, using topographic variables as explanatory variables and soil variables as covariables (models *V.topo.cond* and *D.topo.cond*) and vice versa (*V.soil.cond* and *D.soil.cond*). In order to quantify the amount of variation explained by the model, the ratio of the sum of the constrained eigenvalues to total inertia was used. Like Økland (1999), this ratio was not interpreted as the proportion of the explained variation, but as the fraction of the total inertia explained by the model. A stepwise algorithm was used also to build a parsimonious model that combined both topographic and soil variables.

Moving window CCA: quantifying interaction between aspect and elevation

Preliminary analyses indicated that species composition mainly varies along two gradients, directly influenced by the topographic position in the valley – relative elevation above the valley bottom and aspect. However, aspect may have a different effect on vegetation in deeper, shaded parts of the valley, where it plays a less important role than in the upper parts, where the contrast in irradiation between north-facing and south-facing slopes is much more pronounced. To test this hypothesis, we proposed a method inspired by the moving window regression analysis (e.g. Walker et al. 2003, Palmer 2006), which was originally designed to detect changes in vegetation composition along transects. However, our analysis did not employ linear regression, but CCA with one explanatory variable, which analyzed the changes in explanatory power of this variable along a gradient of another variable. We call this method "moving window CCA". In our case, the method was used to quantify changes in the explanatory power of aspect when moving from the bottom to the upper edge of the valley. Plots were sorted by their relative elevation above the valley bottom (from 0 to 1) and a virtual moving window was set at the beginning of this series. The window then moved by steps of constant length toward the opposite end of the relative elevation interval (elevation). In each step, CCA analysis of the plots included in the window, with aspect as an explanatory variable, was calculated to quantify the amount of variation explained by aspect at particular elevations above the valley bottom, measured by the fraction of total inertia explained by the first axis of CCA. The size of the window and hence the gradient length was kept constant in all steps, which resulted in different numbers of plots being included in the window in particular steps. However, to make the analyses of all steps comparable (in the sense of variation explained by aspect), it was essential to keep constant the number of plots in each analysis. This was done by random selection (without replacement) of a constant number of plots in each particular step within the virtual window. This random selection was repeated 20 times and averaged fractions of total inertia together with confidence intervals were plotted against the relative elevation. Generally, the shape of the analyzed relationship depends on the gradient length (or size of the window) analyzed in each step, which corresponds to the scale of the studied relationship. To make the results comparable, this parameter was kept the same in both valleys. After several pre-analysis runs, the size of the window was set to 0.35 units of relative elevation, the number of steps of the window towards the end of the elevation gradient to 20 and number of plots randomly selected per window and used in CCA in a particular step to 17 in both valleys. To visualize the trend, the averages of the explained variation were smoothed by a curve fitted using a general additive model with three degrees of freedom (Hastie & Tibshirani 1990).

Software

TURBOVEG 2 database program (Hennekens & Schaminée 2001) was used for storing vegetation data, JUICE 6.3 (Tichý 2002) for data editing and calculation of Ellenberg indicator values and PC-ORD 4 (McCune & Mefford 1999) for processing cluster analysis. The calculation routine for moving window CCA analysis was written in R language and run in R software (R Development Core Team 2005) with Vegan package (Oksanen et al. 2006). R software was used also for calculating and drawing NMDS and CCA ordinations.

Results

Vegetation types and their ecological relationships

Differentiation of the vegetation types in the river valleys is illustrated in Fig. 2, which combines the results of cluster analysis and NMDS ordination with passively projected Ellenberg indicator values (see Table 2 for explanation of vegetation types). Number of

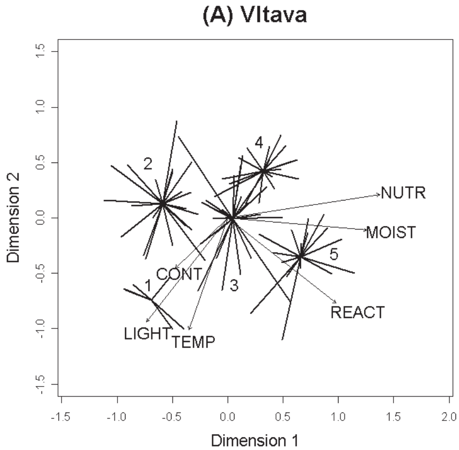

Fig. 2. – Non-metric multi-dimensional scaling (NMDS) ordination diagrams of vegetation plots from the Vltava and Dyje valleys with projected cluster membership (1–5; see Table 2 for cluster descriptions). Each spider connects individual plots with the average score for plots belonging to the same cluster. Ellenberg indicator values for LIGHT, TEMPerature, CONTinentality, MOISTure, soil REACTion and NUTRients are passively projected onto these ordination diagrams.

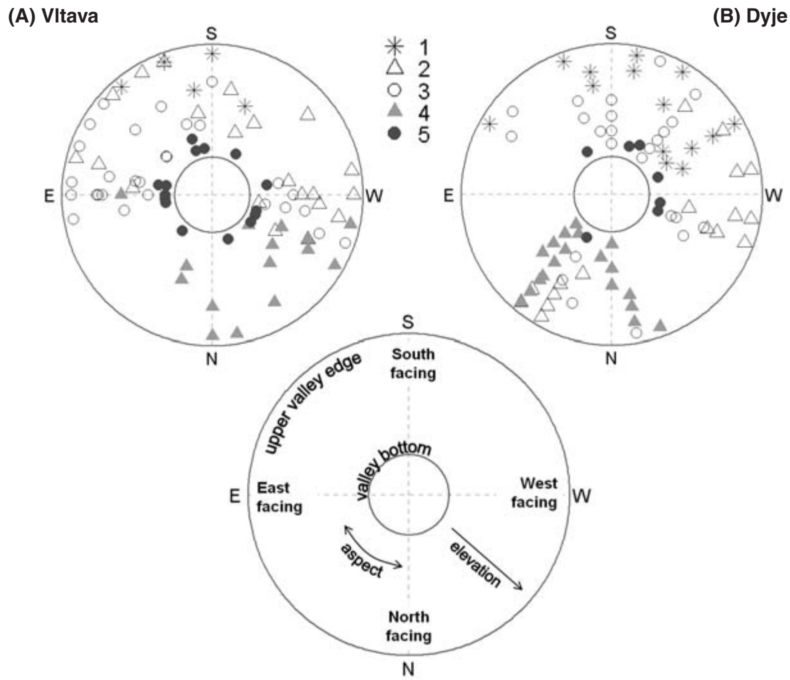

Fig. 3. – "Iris diagrams" showing distribution of particular vegetation types (clusters) in idealized space of the deep river valleys. Diagrams combine aspect and relative elevation above the valley bottom in the following way: central circle represents valley bottom, outer margin represents upper edge of the valley and the direction from the centre represents the direction, in which the slopes face (see the scheme in the middle). Point types refer to the vegetation types described in Table 2.

Table 2. – Brief description of clusters derived from cluster analysis of the Vltava and Dyje vegetation plot data, including number of plots in each cluster, average values ± S.D. of selected environmental variables (slope, soil pH, soil depth) and two most frequently occurring soil types (see Table 1 for abbreviations).

Cluster	Vegetation characteristics	No. of plots	Slope (°)	pH	Soil depth (cm)	Two most frequent soil types
Vltava						
1	thermophilous oak forests (*Quercus petraea, Q. robur*)	6	35±8	4.4±0.5	22±8	cambisol/lithic
2	acidophilous pine and oak forests (*Pinus sylvestris, Quercus petraea*)	24	41±18	3.8±0.2	16±9	cambisol/lithic
3	ravine and oak-hornbeam forests (*Acer, Tilia, Quercus petraea*)	29	39±10	4.2±0.4	23±8	cambisol/skeletic
4	fir forests (*Abies alba*)	18	35±8	4.1±0.3	32±10	cambisol/skeletic
5	alluvial alder forests (*Alnus glutinosa*)	17	26±25	4.6±0.4	33±17	fluvisol/skeletic
Dyje						
1	thermophilous oak forests (*Quercus petraea*)	14	36±8	4.5±0.4	21±9	cambisol/lithic
2	acidophilous pine and oak forests (*Pinus sylvestris, Quercus petraea*)	17	39±13	4.1±0.2	22±14	cambisol/lithic
3	ravine and oak-hornbeam forests (*Acer, Tilia, Carpinus betulus, Quercus petraea*)	25	35±12	5.0±0.7	28±16	cambisol/skeletic
4	beech forests (*Fagus sylvatica*)	19	33±6	5.0±0.5	40±9	cambisol/skeletic
5	alluvial alder forests (*Alnus glutinosa*)	7	10±6	5.2±0.6	65±27	fluvisol/skeletic

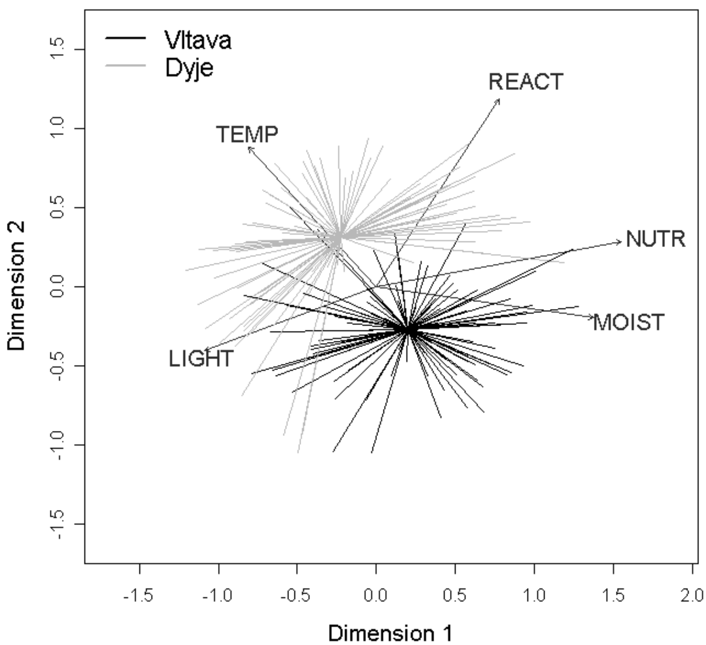

Fig. 4. – Joint NMDS ordination of all plots from the Vltava and Dyje valleys. Each spider connects individual plots with the average score for plots from each valley. Ellenberg indicator values are passively projected onto this ordination diagram (for abbreviations see Fig. 2).

clusters was arbitrarily set to five in both valleys. There are corresponding patterns in both valleys, with major vegetation types similarly scattered in the ordination diagrams. The first axes show strong correlations with EIV for moisture, nutrients and soil reaction, whereas the second axes correlate with light, temperature and continentality (although not so clearly in the Dyje valley). Central position in both ordination diagrams is occupied by ravine and oak-hornbeam forests (Cluster 3). The most dry, nutrient-poor, light and warm habitats are occupied by thermophilous oak forests (Cluster 1). More acidic and cooler habitats support acidophilous pine and oak forests (Cluster 2). The opposite part of the ordination diagrams, with wet and nutrient-rich habitats, is occupied by alluvial forests (Cluster 5). The vegetation in the coolest and most shady habitats, on the north-facing slopes, is in Cluster 4 and occupies similar habitats in both valleys, but with different species composition: in the Vltava valley, this cluster includes ravine forest dominated by fir with the tall forb *Lunaria rediviva* dominating the herb layer, whereas in the Dyje valley it is represented by beech forests. The spatial pattern of the distribution of particular vegetation types in idealized space of river valley is presented in "iris diagrams" (Fig. 3). The difference between the vegetation in the two valleys is shown in Fig. 4, with the Dyje valley being generally warmer.

Correlations among explanatory variables and Ellenberg indicator values

Distribution of soil types strongly depends on topographic features (Table 3): fluvisols and (hyper)skeletic leptosols are found in the lower and bottom parts of the valleys, while lithic leptosols and cambisols are confined to the middle and upper slopes. Lithic leptosols are shallow soils with low pH and are restricted to steep, upward convex and sun-exposed slopes. Fluvisols in the floodplain are deeper and less acid and together with hyperskeletic leptosols of stony screes occupy concave landforms. Elevation is strongly associated with soil reaction, with base-rich soils in the lower parts of the valleys. Slope is also negatively correlated with pH, with more acidic soils found on steeper slopes.

Correlations between Ellenberg indicator values and explanatory variables were (in contrast to the correlation of explanatory variables with one another) calculated for separate data sets from each river valley (Table 3). Even though the results are generally consistent between valleys, they show some regional differences. EIVs are closely associated with topography: sites with warmer aspects and higher heat index values are positively correlated with EIVs for light, temperature and continentality, and negatively correlated with EIVs for moisture and nutrients. The bottom of the Vltava valley is cold and shaded (in terms of EIV) and in both valleys the bottom is more wet, basic and nutrient-rich. Convex topography and slope are negatively correlated with moisture, soil reaction and nutrient availability. Soil variables also correlate with several EIVs: fluvisols are wet, basic and nutrient-rich; lithic leptosols are dry, acidic and nutrient-poor; hyperskeletic leptosols are wetter and richer in nutrients. Soil depth in both valleys is negatively correlated with EIVs for light and temperature, and positively with moisture, soil reaction and nutrients. In both valleys measured soil pH is strongly positively correlated with EIVs for soil reaction, moisture and nutrients; only in the Dyje valley is pH negatively correlated with EIVs for light and temperature.

Table 3. – Correlations between all explanatory variables and correlations between explanatory variables and Ellenberg indicator values (the latter calculated separately for the Vltava and Dyje valley). Spearman rank coefficients are used for all correlations except for soil type categories (fluvisol, skeletic, cambisol and lithic), for which the chi-square test is used. Positive correlation: +++ $P < 0.001$, ++ $P < 0.01$, + $P < 0.05$; negative correlation: – – – $P < 0.001$, – – $P < 0.01$, – $P < 0.05$. Meaning of P: for correlation of categorical soil variables – significance of Pearson's chi-squared test with Yates' continuity correction derived from a contingency table; for the others – significance of Spearman rank coefficient. For definitions of environmental variables, see Table 1.

Elevation	x											
Slope	n.s.	x										
Aspect	n.s.	n.s.	x									
Heat index	n.s.	n.s.	+++	x								
Surface SL	+++	+++	n.s.	n.s.	x							
Surface ISO	++	n.s.	n.s.	n.s.	+++	x						
Soil depth	– –	– – –	– – –	– – –	–	n.s.	x					
pH	– – –	– –	n.s.	n.s.	–	n.s.	+++	x				
Fluvisol	– – –	– – –	n.s.	n.s.	– – –	n.s.	+++	+++	x			
Skeletic	– – –	n.s.	n.s.	n.s.	– – –	---	n.s.	+	+	x		
Cambisol	+++	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	–	– –	– – –	x	
Lithic	+++	+++	+++	+++	+++	n.s.	– – –	– – –	– –	– – –	n.s.	x
	Elevation	Slope	Aspect	Heat index	Surface SL	Surface ISO	Soil depth	pH	Fluvisol	Skeletic	Cambisol	Lithic
Vltava												
Light	n.s.	n.s.	+++	+++	n.s.	+	– – –	n.s.	n.s.	– –	n.s.	+
Temperature	n.s.	n.s.	+++	+++	n.s.	n.s.	–	n.s.	n.s.	n.s.	n.s.	+
Continentality	n.s.	n.s.	+++	+++	n.s.	n.s.	– –	n.s.	n.s.	n.s.	n.s.	n.s.
Moisture	– – –	– – –	– – –	– – –	– – –	n.s.	+++	+++	+++	+++	–	– – –
Reaction	– –	– –	n.s.	n.s.	– – –	n.s.	+++	+++	+++	+	n.s.	– – –
Nutrients	–	– – –	– – –	– – –	– – –	n.s.	+++	+++	+++	+++	n.s.	– – –
Dyje												
Light	+++	n.s.	+++	+++	n.s.	n.s.	– – –	– – –	n.s.	n.s.	n.s.	+++
Temperature	+	n.s.	+++	+++	n.s.	n.s.	– – –	– –	n.s.	–	n.s.	++
Continentality	– – –	n.s.	+++	+++	n.s.	n.s.	n.s.	++	+	n.s.	n.s.	n.s.
Moisture	– – –	– – –	– –	– – –	– –	–	+++	+++	+++	++	– – –	– – –
Reaction	– – –	– – –	+	n.s.	–	n.s.	+++	+++	+++	n.s.	n.s.	– –
Nutrients	– – –	– – –	n.s.	– –	– –	n.s.	+++	+++	+++	++	– –	– – –

Effect of topographic and soil variables on vegetation

Table 4 shows the results of direct ordination analyses, processed separately for data from each river valley and each set of topographic and soil explanatory variables. The most parsimonious model (based on AIC), including only topographic variables, explains 10.3% of total inertia in the Vltava valley (*V.topo*) and 12.0% in the Dyje valley (*D.topo*), while models including only soil variables explain slightly more – 12.5% in the Vltava valley (*V.soil*) and 14.8% in the Dyje valley (*D.soil*). Partial CCA revealed conditional and shared effects of these models (Fig. 5). Full models, including all topographic and soil variables selected by previous topographic and soil models, explain 18.8% in the Vltava (*V.full*) and 21.6% in the Dyje valley (*D.full*). However, these models are not parsimonious, as measured by the AIC criterion. Parsimonious models including both topographic and soil variables (*V.parsim* and *D.parsim*, respectively) include only four out of the seven explanatory variables included in the full models and explain 13.8% in the Vltava valley (*V.parsim*) and 16.8% in the Dyje valley (*D.parsim*).

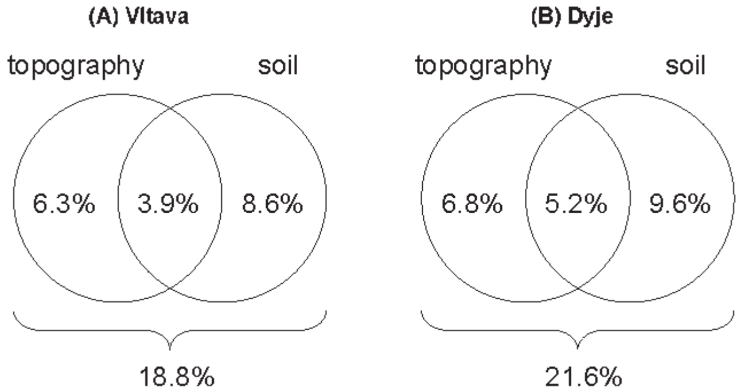

Fig. 5. – Venn diagrams showing conditional and shared effects of the groups of topographic and soil variables as fractions of the total inertia.

Relationship between vegetation, elevation and aspect: moving window CCA

Although elevation and aspect are not correlated, moving window CCA revealed that the explanatory power of aspect changes at different elevations above the valley bottom (Fig. 6). Explanatory power of aspect is lowest near the valley bottom, reaches the maximum half way up the side of the valley and decreases again near the top. Fractions of total inertia explained by aspect in particular steps range between 7–13% in the Vltava and 9.5–13.0% in the Dyje valley.

Discussion

Indirect ordination revealed that in both river valleys, the main gradients in vegetation composition are similar – the first NMDS axis represents a complex nutrient-moisture-soil reaction gradient and the second a light-temperature-continentality gradient. Distribution of vegetation types determined by cluster analysis along these gradients also displays similar patterns in both valleys, both in ordination space (Fig. 2) and the idealized spatial model of a deep valley (Fig. 3). This degree of similarity between the two river valleys accords with the results of previous phytosociological studies from deep river valleys (e.g. Blažková 1964, Türk 1994, Chytrý 1995, Chytrý & Vicherek 1995, 1996, Kolbek et al. 1997, Kolbek 1999–2003) and suggests that the patterns described in this study are general for river valleys of the Bohemian Massif, and not a result of local coincidences of vegetation and environment. Vegetation patterns in the Vltava and Dyje valleys are similar in spite of the fact that the former is situated in a cooler and wetter macroclimatic region than the latter (Fig. 4).

This analysis shows that soil and topographic variables are both good predictors of vegetation pattern in river valleys, but the former explains slightly more variation. While topographic variables can be derived from high resolution digital elevation maps, soil variables need detailed field inspection, which is more time and budget demanding. If money or time are limiting factors, topographic variables itself, such as elevation above the valley bottom, aspect and slope (or landform shape), can be still considered as good predictors of vegetation pattern (Tichý 1999a). These variables have no direct effect on plants, but exert a strong control on the distribution of resources and conditions necessary for plant growth, such as

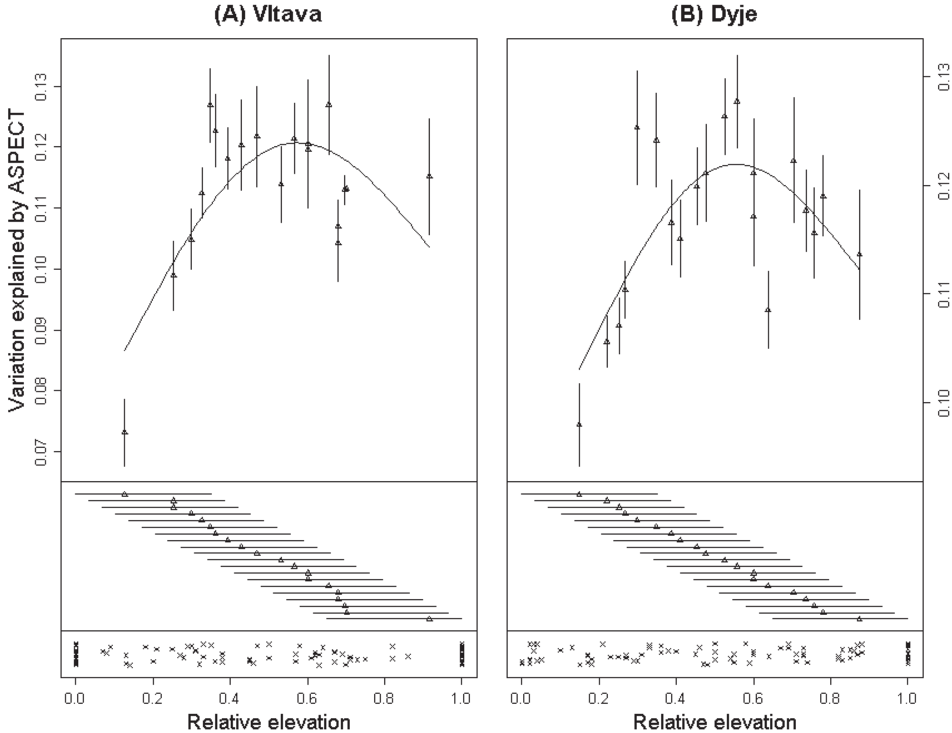

Fig. 6. – Joint effect of aspect and relative elevation above the valley bottom on species composition, analyzed using moving window CCA for the Vltava and Dyje river valleys. Horizontal axis is relative elevation above the valley bottom. The bottom parts of the diagrams show distribution of relative elevation (the points are slightly jittered along the vertical line to visualize overlapping values). The middle parts demonstrate the position of each moving window along the gradient of elevation (triangle shows the mean of all the values in a particular window, horizontal bar shows the range of relative elevation in a particular window). The upper part shows the explained variation (the fraction of total inertia explained by aspect), calculated by CCA for a given step; for each step of the moving window, mean (triangle) and confidence interval (vertical bar) of the explained variation, calculated using the random sub-samples, are shown; the positions of triangles along the horizontal axis correspond in the middle and upper part of the diagram.

moisture availability, nutrients or temperature (Pabst & Spies 1998). Aspect and elevation determine mesoclimatic conditions such as incoming solar radiation (Austin et al. 1984) or formation of temperature inversions in river valleys (Quitt 1996, Chytrý & Tichý 1998, Tichý 1999b). Slope is closely related to disturbance, caused by falling rocks, soil creep, surface erosion etc. (Rejmánek et al. 2004). The down slope increase in soil pH revealed in this study is probably also connected with down slope mass and nutrient migration, induced both by groundwater flow (Campbell 1973, Zinko et al. 2006) and superficial erosion (Cox et al. 2002), causing increased leaching of the upper slopes, followed by transport and accumulation of soluble base cations in the lower parts of the valley (Silver et al. 1994, Chen et al. 1997). Surface erosion is perhaps also responsible for the negative correlation between soil pH and slope, as steep slopes on acidic bedrock support the development of shallow soils with an acidic reaction. Apart from this, nutrient accumulation in the lower parts of the valleys is connected with flooding (in the case of fluvisols) or more intensive microbial activity in the highly skeletic soils of ravine forests on the lower slopes (Ellenberg 1996).

Table 4. – CCA models with various combinations of explanatory variables and covariables. Total inertia: Vltava = 7.144, Dyje = 7.898. See Table 1 for variable definitions. AIC = value of (generalized) Akaike information criterion; Σ eig. = sum of all canonical eigenvalues; % expl. = fraction of total inertia explained by the model. All models (excluding conditional effect models, which have not been tested) give significant results of Monte Carlo permutation test ($P < 0.001$, 1000 permutations). Model abbreviations: *V.topo, D.topo* – explanatory variables including topographic factors only for Vltava and Dyje valleys, respectively; *V.soil, D.soil* – explanatory variables including soil factors only; *V.topo.cond, D.topo.cond* – conditional effects of topographic variables with soil variables as covariables; *V.soil.cond, D.soil.cond* – conditional effects of soil variables with topographic variables as covariables; *V.full, D.full* – combines topographic and soil variables from *V.topo, D.topo* and *V.soil, D.soil*; *V.parsim, D.parsim* – the most parsimonious models including both topographic and soil variables.

	Explanatory variables	Covariables	AIC	Σ eig.	% expl.
Vltava					
V.topo	elevation + aspect + surface SL	–	447.00	0.733	10.3
V.soil	skeletic + fluvisol + soil depth + pH	–	446.59	0.896	12.5
V.topo.cond	elevation + aspect + surface SL	skeletic + fluvisol + soil depth + pH		0.452	6.3
V.soil.cond	skeletic + fluvisol + soil depth + pH	elevation + aspect + surface SL		0.615	8.6
V.full	elevation + aspect + surface SL + skeletic + fluvisol + soil depth + pH	–		1.347	18.8
V.parsim	aspect + fluvisol + soil depth + pH	–	445.21	0.987	13.8
Dyje					
D.topo	elevation + aspect + slope	–	384.42	0.945	12.0
D.soil	cambisol + fluvisol + soil depth + pH	–	383.78	1.166	14.8
D.topo.cond	elevation + aspect + slope	cambisol + fluvisol + soil depth + pH		0.537	6.8
D.soil.cond	cambisol + fluvisol + soil depth + pH	elevation + aspect + slope		0.758	9.6
D.full	elevation + aspect + slope + cambisol + fluvisol + soil depth + pH	–		1.703	21.6
D.parsim	aspect + cambisol + fluvisol + pH	–	381.83	1.324	16.8

Due to the complex topography of the valleys, the effects of some topographic variables on vegetation pattern are not easy to identify. In particular, the non-linear interaction between the elevation above the valley bottom and aspect can mask the effect of the latter when standard procedures of constrained ordination are used. The new method of moving window CCA, proposed here, proved successful in disentangling the complex effect of these two variables on vegetation (Fig. 6). It clearly showed that near the valley bottom, where the valley is rather narrow and shaded by the adjacent slopes in many places, aspect does not explain much of the variation in vegetation. Moving up the valley sides, the importance of aspect as a determinant of species composition increases, because of the more pronounced contrast between the dry and warm south-facing and more shaded, wetter and cooler north-facing slopes. At the upper edges of the valley, the importance of aspect decreases again, as the difference in insolation of south-facing and north-facing slopes diminishes due to the less steep topography.

Despite the strong correlations between several topographic and soil variables (Table 3), the shared fraction of variation in species composition explained by both topographic and soil variables is relatively low (Fig. 5). It means that soil variables explain a different part of the variability in vegetation than topography. Therefore, recording several simple soil variables, such as pH, soil depth and soil type, can significantly improve the explanatory power of vegetation-environment models, even in a landscape with strong topographic contrasts.

Conclusions

The similarity of the vegetation patterns between the two river valleys studied and their correspondence with the earlier phytosociological studies indicate that the patterns revealed in the present study are reasonably robust and can be generalized for most deep river valleys on non-calcareous soils at middle altitudes of the Bohemian Massif. Main topographic factors driving vegetation pattern are elevation above the valley bottom, aspect (being more important half way up the valley sides) and slope. Soil variables such as measured pH and soil type (mainly fluvisols vs the others) may significantly improve vegetation-environment models for these valleys. The vegetation pattern of the valleys can be briefly summarized as follows:

(1) Floodplain forests, mostly dominated by *Alnus glutinosa*, occur on the valley bottom on deep and moist fluvisols, which are rich in nutrients and have a relatively high pH.

(2) On lower valley slopes, there is usually a small difference in the vegetation on south-facing and north-facing slopes. Here the main factor is slope, which determines whether cambisols (on less steep slopes) or skeletic leptosols (on steeper slopes) develop, with the former supporting oak-hornbeam forests and the latter ravine forests of *Acer, Tilia* and *Carpinus betulus* (*Carpinus* being locally absent in the Vltava valley).

(3) Half way up the valley sides and to a lesser extent further up, there is a striking contrast between the vegetation on southern and northern slopes. The warmest south-facing slopes support thermophilous oak forests with *Quercus petraea*, which are better developed in the warmer and more continental Dyje valley. In contrast, north-facing slopes support forests dominated by fir (Vltava) or beech (Dyje) on relatively deep and nutrient-rich cambisols.

(4) Other habitats in deep river valleys are covered with acidophilous oak and/or pine forests on more or less shallow lithic leptosols of various aspects and pure pine stands restricted to extreme habitats on rocky outcrops.

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Souhrn

Cílem této studie je kvantitativní popis faktorů prostředí, které zásadním způsobem ovlivňují druhové složení a prostorové rozmístění vegetace v hlubokých říčních údolích Českého masivu s vyvinutými projevy tzv. „říčního fenoménu“. Problematika byla studována ve dvou klimaticky odlišných územích: údolí Vltavy v jižních Čechách a údolí Dyje na jižní Moravě. Data o vegetaci a proměnných prostředí byla sbírána na transektech vedených po

spádnici údolních svahů z horní hrany údolí k bázi svahu. Vegetační data byla analyzována kombinací shlukové analýzy a nepřímé ordinace (nemetrického mnohorozměrného škálování, NMDS). Vliv geomorfologických a půdních proměnných na vegetaci byl porovnáván sérií kanonických korespondenčních analýz (CCA) s metodou postupného výběru vysvětlujících proměnných založenou na Akaikeho informačním kritériu (AIC). Pro analýzu vlivu nelineárních interakcí mezi dvěmi proměnnými prostředí na vegetaci byla navržena nová metoda nazvaná „moving window CCA". V této studii metoda popsala, jak se mění vysvětlující síla jedné proměnné (orientace svahu) se změnou druhé proměnné (výšky nad řekou). Hlavní směry variability ve vegetaci jsou v hlubokých říčních údolích korelovány s dvěma komplexními gradienty proměnných prostředí: vlhkost-živiny-půdní reakce a světlo-teplota-kontinentalita. Přímá ordinační analýza ukázala, že půdní faktory lépe korelují s druhovým složením vegetace než geomorfologie terénu, přičemž dohromady obě tyto skupiny proměnných vysvětlily 18.8–21.6 % celkové variability v druhovém složení vegetace. Ačkoliv některé půdní a geomorfologické proměnné těsně korelují, množství variability vysvětlené sdíleným vlivem obou skupin není příliš vysoké (3.9–5.2 %), což znamená, že každá skupina proměnných ovlivňuje vegetaci poněkud jiným způsobem. Nejvíce parsimonní model CCA pro údolí Vltavy vysvětluje druhové složení vegetace pomocí následujících faktorů: orientace svahu, půdní pH, přítomnost fluvizemě a hloubka půdy; pro údolí Dyje vypadá model podobně, jen faktor hloubka půdy je nahrazen přítomností kambizemě. „Moving windows CCA" ukázala, že orientace svahu má na vegetaci vliv nejvíce ve střední části údolního svahu a nejméně při bázi svahu. Výsledky všech analýz ukazují výraznou shodu ve vztazích mezi vegetací a prostředím v obou říčních údolích, což naznačuje možnosti zobecnění popsaných vztahů i na další hluboká říční údolí Českého masivu.

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