

## Are species with similar ranges confined to similar habitats in a landscape?

Jsou druhy s podobnými areály vázány v krajině na podobná stanoviště?

Milan Chytrý

*Department of Systematic Botany and Geobotany, Masaryk University, Kotlářská 2, CZ–611 37 Brno, Czech Republic*

Chytrý M. (1995): Are species with similar ranges confined to similar habitats in a landscape? – *Preslia, Praha, 67:25–40.*

Correlations between the environment (topography, soil factors, canopy cover) and the proportion of plant species with different geographical distributions were studied in the deep crystalline valley of the Dyje/Thaya river on the Czech-Austrian border. Modified classification of species ranges into range types (Arealtypen) of Meusel et Jäger (1992) was used. It is suggested that there is a correlation between the performance of particular range types and certain types of environments. The main trends in the data are summarized in a model based on the canonical correspondence analysis.

**Key words:** Plant-environment relationships, phytogeography, canonical correspondence analysis, Dyje/Thaya river valley, Podyjí/Thayatal National Park, Czech Republic

### Introduction

The classification of species geographical patterns is a challenging problem in phytogeography. Species ranges with similar shape, size, and geographical confinement to some part of the Earth are grouped into range types (Arealtypen, see Wangerin 1932, Meusel 1943, Holub et Jirásek 1967). It is supposed that species belonging to particular range types are characterized by specific environmental requirements and the classification of a species' range into a range type suggests that the species is confined to a specified environment (Meusel et Jäger 1992). Causally oriented ecological approaches to phytogeography also pursue the ecological interpretation of species ranges (Walter et Straka 1970).

This presumed correlation between the plant range types and environmental factors on the landscape level is commonly used for phytogeographical characterization of plant community types (e.g. Jakucs 1961, Meusel 1969, Jäger 1971, Hundt 1985 etc.). Ellenberg (1974) suggested a calibration method for evaluating plant communities in which the continentality of a species, as a simplified ordinal variable expressing the distribution pattern, is taken into account. Quantitative analyses of the relationships between the distribution and ecology of plant species were carried out by Lausi et Nimis (1991) for southern Yukon region and a correlation between species ecology and geographical distribution was also reported by Nimis et Bolognini (1993) for Italian beech forest flora, and by Nimis, Malyshev et Bolognini (1994) for south-western Siberian birch woodlands. There are also attempts at finding the relationships between species ranges and distribution

patterns in certain territories, and thus finding phytogeographical boundaries in the territory under study (Timoney et al. 1993). In some species, an effort has been made at causal explanation of distribution patterns on the basis of studies of their ecophysiological traits (Rychnovská et Úlehlová 1975).

The present study focuses on the relationships between species range types and environmental factors on landscape scale. The objective is to analyse which environmental factors support species of particular range types and what are the interrelations among the range types, with respect to their relationships to environmental factors.

## Study site

The study site is a part of the Dyje/Thaya river valley on the border between the Czech Republic and Austria. It is situated in the Podyjí/Thayatal National Park between the towns of Vranov n. D. (48°54 N, 15°49 E) and Znojmo (48°51 N, 16°03 E). The river forms a valley 60–200 m deep, dissecting crystalline plateaus and flat hilly landscapes. Due to numerous meanders, the slopes of various aspects change with comparatively small distances. The bottom of the valley is narrow, reaching a width of only 40 m in some sections, with fragmentarily developed floodplain. Altitude ranges between 536 m (Býčí hora hill) and cca 220 m a. s. l. (water level of the Znojmo reservoir).

Predominant rocks are the nutrient-poor gneisses and granites. In the surroundings of the town of Hardegg, crystalline limestones occur (Batík 1992). On convex landforms on the upper part of the valley slopes, rock outcrops and cliffs are common, whereas the occurrence of block fields is typical for the lower part of the slopes. The soils on convex landforms of siliceous rocks are Dystric (to Eutric) Lithosols and Rankers, alternating with Rendzinas on limestones. Cambisols predominate on the flat or concave slopes of the valley, and are accompanied by Rankers on the sites with accumulations of stony blocks. Eutric Fluvisols are confined to the floodplain (Hynek et Trnka 1981, Chytrý et Vicherek 1995).

There is a climatic gradient in this area running parallel to the direction of the river valley, from the NW upstream part being mildly warm to the eastern downstream part with warm climate. Mean annual temperature is 8.8 °C and mean annual rainfall 564 mm (Vesecký 1961, Znojmo-Kuchařovice meteorological station). However, in the river valleys of south-western Moravia, temperature differences due to inversions may reach 1–3°C (Quitt 1984).

The vegetation of the river valley is very well conserved, dominated by natural forests with scattered patches of natural non-forest vegetation on rocks and block fields (Grulich et Chytrý 1993, Chytrý 1993, Chytrý et Vicherek 1995). Oak-hornbeam forests of the association *Melampyro nemorosi-Carpinetum* predominate. On sunny sites of the upper part of the slopes, thermophilous oak forests (*Sorbo torminalis-Quercetum*, *Genisto pilosae-Quercetum petraeae*) occur, whereas on the opposite north-facing slopes, acidophilous oak forests (*Luzulo albidae-Quercetum petraeae*) are common. Pine forests (*Cardaminopsio petraeae-Pinetum*) are confined to the tops of siliceous rocks, especially in the western part of the study area. Occurrence of ravine forests (*Aceri-Carpinetum*) is typical of the lower part of slopes that have accumulated stony blocks. On the north-facing slopes in the western part of the study area, oak-hornbeam forests are replaced by beech forests (*Tilio cordatae-Fagetum*), and acidophilous oak forests by acidophilous beech

forests (*Luzulo nemorosae-Fagetum sylvaticae*). On west- and north-facing slopes of crystalline limestones, specific types of lime and pine forests have developed (*Sesleria varia-Tilia cordata-Pinus sylvestris* community). River banks are bordered by alder floodplain forests (*Stellario-Alnetum glutinosae*). Non-forest vegetation is represented by various types of thermophilous shrublands, grasslands and rock communities on southern aspects, and species poor vegetation dominated by grasses, ferns and mosses on rocks and block fields of northern aspects.

## Methods

Field sampling was carried out in July–August 1992 (data on occurrence of vernal geophytes and therophytes were added in April 1993) using 18 transects running in the Dyje river valley from the river bank up to the margin of the plateau. The transects were located on both sides of the valley in order to cover all the main vegetation types, avoiding sites with disturbed or man-influenced vegetation. Along these transects, a total of 104 10 × 15 m sample plots were regularly placed in 40 m distances, with the first plot of each transect beginning 1 m from the river bank.

All vascular plant species and some variables describing topography, soils and vegetation were recorded in each plot. Soil depth was measured in four regularly spaced points within each plot and the mean value was calculated. The soils deeper than 100 cm were treated as equal to 100 cm. From the same points, soil samples were taken from the depth of 3–10 cm, mixed up, and the mixed sample was used for chemical analyses. Soil reaction (pH/H<sub>2</sub>O) was determined potentiometrically, calcium carbonate in Janko lime gauge, total nitrogen using the Kjehldahl method, total organic carbon (C<sub>ox</sub>) using the Alten-Rautenberg-Kremkus method, base saturation (V) using the Mehlich method. The analytical methods are described in Hraško et al. (1962). Most of the variables were used directly and slope and aspect were combined into environmental scalar: “xericity index” (see Parker 1988). Two variables with skewed distribution were log transformed.

The following variables were used (figures in parentheses indicate mean ± standard deviation, in variables 6–9 and 20 median ± quartile deviation, and in categorial variables 11–17 number of occurrences of the particular category):

- |                     |   |
|---------------------|---|
| 1 INCLINATION       | – slope inclination [°] (34±15)   |
| 2 ASPECT (SSW)      | – difference of the slope aspect from 22.5° [°] (99±61)   |
| 3 XERICITY (SSW)    | – xericity index [ $\cos(\text{slope aspect} - 202.5^\circ) * \text{tg INCL}$ ] (0.19±0.73)   |
| 4 RELAT. ALTITUDE   | – relative altitude above the river [m] (62±43)   |
| 5 ALTITUDE          | – altitude [m a. s. l.] (336±51)  |
| 6 SURFACE (SLOPE)   | – landform shape downslope: 1 – concave, 2 – flat, 3 – convex (2±0)   |
| 7 SURFACE (ISOLINE) | – landform shape along the isoline: 1 – concave, 2 – flat, 3 – convex (2±0)   |
| 8 RELAT. LOCATION   | – relative location: 1 – below the opposite plateau, 2 – at the level of the opposite plateau, 3 – above the opposite plateau (1±0.5) |

- 9 TOPOGR. LOCATION – topographic location: 1 – bottom of the valley, 2 – valley slope, 3 – margin of the plateau (2±0)
- 10 SOIL DEPTH – log [soil depth (cm) + 1] (1.39±0.32)
- 11–17 – soil type (categorical variables)
- LITHOSOL – Lithosol (8)
- RANKER – Ranker (16)
- RANKER (TALUS) – Ranker on talus slopes (31)
- FLUVISOL – Fluvisol (10)
- CAMBISOL – Cambisol (55)
- RENDZINA – Rendzina (9)
- LUVISOL – Luvisol (1)
- 18 LITTER COVER – litter cover [%] (70±24)
- 19 LITTER DEPTH – litter depth [cm] (4±2)
- 20 PARENT MATERIAL – structure of parent material: 1 – clayey, 2 – loamy, 3 – sandy, 4 – gravelly, 5 – stony, 6 – boulders, 7 – rock (5±2)
- 21 pH – pH/H<sub>2</sub>O (5.2±1.1)
- 22 CaCO<sub>3</sub> – log [CaCO<sub>3</sub>-content (%) + 1] (0.10±0.32)
- 23 NITROGEN – total nitrogen content [%] (0.30±0.14)
- 24 ORGANIC MATTER – organic carbon content [%] (0.62±0.25)
- 25 BASE SATURATION – base saturation (V) [%] (0.99±0.75)
- 26 COVER E<sub>3</sub> – tree layer cover [%] (73±23)
- 27 COVER E<sub>2</sub> – shrub layer cover [%] (18±18)

Categorical variable 17 (LUVISOL) was recorded only in one sample plot and thus omitted from further analyses.

Species were classified into range type groups according to Meusel et Jäger (1992), using the maps and range diagnoses in Meusel, Jäger et Weinert (1965), Meusel et al. (1978) and Meusel et Jäger (1992). The groups of range types were recognized as follows (numbered according to Meusel et Jäger l. c.):

- 1 – Macaronesian–Mediterranean range types
- 2 – Oriental–Turcestanian–Mediterranean range types
- 4 – Euroasian and European meridional–submeridional–(temperate).continental range types
- 5 – (Mediterranean/montane)–Submediterranean–(Pontic) range types
- 6 – (Mediterranean)–Submediterranean oreophytic range types
- 7 – Euroasian (tropical)–meridional–submeridional–oceanic range types
- 8 – (Submediterranean/montane)–Central European range types
- 9 – (Submediterranean)–Central European oreophytic range types
- 10 – Euroasian (submeridional/montane)–temperate range types
- 11 – Euroasian (+ circumpolar) boreal range types

As the largest group 8 contained 40.5 % of the species, and was rather heterogeneous, it was divided into the following four groups:

- 8CE – Central European: range types with center in Central Europe (Meusel and Jäger's range types 8.0, 8.7, 8.8, 8.10, 8.12 and 8.15)
- 8pa – perialpine (Meusel and Jäger's range type 8.9)
- 8sa – subatlantic: range types with center in Western Europe (Meusel and Jäger's range types 8.1, 8.2, 8.3, 8.4, 8.5 and 8.6, the former two absent in the sample plots)
- 8sc – subcontinental: range types with center in East-Central Europe (Meusel and Jäger's range types 8.11, 8.13, 8.14 and 8.15)

Group 6, containing only one species was united with group 8pa for the purpose of analysis. As the classification of species into range type groups is subjective, the classification used is presented in Appendix.

In all the plots, the number of species belonging to each range type group was counted. As the results may be less reliable in the range type groups with lower number of species and lower evenness, being based on small non-representative sample and affected mainly by the dominant species, respectively, diversity indices  $N_2$  of Hill (1973, see also Ludwig et Reynolds 1988) were calculated as a measure of reliability of the results for particular range type groups.

Species composition and dominants within the particular range type groups are listed in Appendix. The resulting matrix of range types  $\times$  sample plots was standardized by sample plot totals in order to remove the effects of different numbers of species in particular plots, and subjected to canonical correspondence analysis, using program CANOCO 3.1 (ter Braak 1987, 1990). To eliminate the effects of blocks (each transect is considered as a block), partial CCA was used with 18 transects defined as covariables. The effect of environmental variables on the range type pattern was analysed using Monte Carlo permutation test from CANOCO 3.1, with 500 permutations within the blocks. Additional effect of each of the environmental variables to the effect of covariables (blocks) was tested separately using this test. In order to build an ordination model with minimum set of environmental variables, forward selection of variables was applied prior to the analysis and selected variables were tested for their additional contribution to direct ordination. Monte Carlo test with the same options was used.

In order to ascertain correlations between range type groups and the environmental variables not included in the ordination model, Spearman rank correlation coefficients were calculated between numbers of species belonging to particular range type groups and environmental variables.

Plant nomenclature follows Ehrendorfer (1973).

## Results

In 104 sample plots, a total of 324 species were recorded. After removing the alien species *Impatiens parviflora*, numbers of species, percentage proportions, and  $N_2$  diversity indices for particular range type groups were summarized (Table 1). The weakest reliability of results is to be expected in group 9, with low number of species and strong dominance of the species *Cyclamen purpurascens* (see Appendix 1). On the contrary, fairly good results may be reached in groups 8CE, 10, 5, and 8sc.

Table 1. – Numbers of species, percentage proportions and N2 diversity indices for particular range type groups. Labels of particular range type groups are explained in the Methods section.

Range type group	Number of species	Percentage proportion	N2 diversity
1	5	1.5 %	2.33
2	9	2.7 %	3.33
4	18	5.6 %	7.73
5	58	18.0 %	23.42
7	6	1.9 %	2.76
8CE	80	24.8 %	36.10
8pa+6	12	3.7 %	6.67
8sa	9	2.7 %	3.92
8sc	31	9.6 %	14.33
9	6	1.9 %	1.61
10	81	25.1 %	29.36
11	8	2.5 %	2.92

Table 2. — Spearman rank correlation coefficients between numbers of species belonging to particular range type groups in sample plots and environmental variables. Numbers of particular range type groups are explained in the Methods section. In the first column, significance levels are indicated of the effects of particular environmental variables on the range type pattern (Monte Carlo permutation test). \*\*\* —  $P < 0.001$ , \*\* —  $P < 0.01$ , \* —  $P < 0.05$ , NS — not significant (significances at  $P < 0.001$  were not calculated in the Monte Carlo test).

Range type group	1	2	4	5	7	8CE	8pa+6	8sa	8sc	9	10	11
** INCLINATION	0.255**	NS	0.210*	NS	NS	-0.334***	NS	NS	-0.297**	NS	NS	NS
NS ASPECT (SSW)	0.446***	0.527***	0.460***	0.528***	NS	NS	-0.226*	NS	NS	-0.221*	NS	NS
* XERICITY (SSW)	0.523***	0.563***	0.528***	0.558***	NS	NS	-0.216*	NS	NS	-0.325**	NS	NS
** RELAT. ALTITUDE	NS	NS	NS	-0.289**	NS	-0.500***	NS	0.225**	-0.546***	NS	-0.447***	NS
** ALTITUDE	NS	NS	NS	-0.276**	NS	-0.315**	NS	NS	-0.449***	0.262**	-0.399***	NS
** SURFACE (SLOPE)	0.306**	NS	0.310**	NS	NS	-0.244**	NS	NS	-0.264**	NS	NS	NS
NS SURFACE (ISOLINE)	0.219*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
** RELAT. LOCATION	NS	NS	NS	-0.262**	NS	-0.205*	NS	NS	-0.443***	NS	-0.206*	NS
** TOPOGR. LOCATION	NS	NS	NS	NS	NS	-0.411***	-0.326**	NS	-0.230*	NS	-0.527***	NS
** SOIL DEPTH	-0.347***	-0.195*	-0.434***	-0.283**	NS	0.323**	0.214*	NS	NS	0.337**	NS	NS
** LITHOSOL	0.264**	NS	NS	NS	NS	-0.412***	-0.225*	NS	-0.312**	-0.233*	NS	NS
NS RANKER	0.256**	0.210*	0.317**	0.210*	NS	NS	NS	NS	NS	NS	NS	NS
** RANKER (TALUS)	NS	NS	-0.297**	-0.278**	NS	NS	NS	NS	NS	NS	NS	NS
** FLUVISOL	NS	NS	NS	NS	NS	0.414***	NS	NS	0.241*	-0.196*	0.494***	NS
* CAMBISOL	NS	NS	NS	NS	NS	NS	NS	0.220*	NS	NS	NS	NS
** RENDZINA	NS	NS	0.363***	0.452***	NS	0.257**	NS	-0.272**	0.272**	0.312**	NS	-0.229*
** LITTER COVER	-0.251*	NS	-0.211*	NS	NS	0.301**	NS	-0.327***	0.201*	0.440***	NS	-0.237*
** LITTER DEPTH	-0.218*	NS	-0.365***	-0.266**	NS	NS	NS	-0.269**	NS	0.201*	NS	-0.202*
* PARENT MATERIAL	0.204*	NS	NS	NS	NS	NS	NS	NS	-0.214*	NS	NS	NS
* pH	0.272**	0.213*	0.288**	0.436***	0.383***	0.440***	NS	-0.634***	0.366***	0.265**	0.267**	-0.516***
** CACO3	0.264**	NS	0.355***	0.451***	NS	0.239*	NS	-0.389***	0.242*	NS	NS	NS
NS NITROGEN	NS	NS	NS	NS	NS	NS	NS	NS	-0.257**	NS	NS	NS
* ORGANIC MATTER	NS	NS	NS	NS	-0.206*	-0.250*	NS	0.209*	NS	-0.195*	-0.216*	0.226*
** BASE SATURATION	NS	NS	NS	NS	0.387***	0.253*	NS	-0.316**	0.207*	NS	0.308**	-0.259**
** COVER E3	-0.487***	-0.419***	-0.438***	NS	0.229*	0.456**	NS	-0.261**	0.257**	0.372**	NS	-0.274**
** COVER E2	NS	0.275**	0.235*	0.340***	NS	0.288**	0.205*	-0.373***	0.199*	NS	0.352***	NS

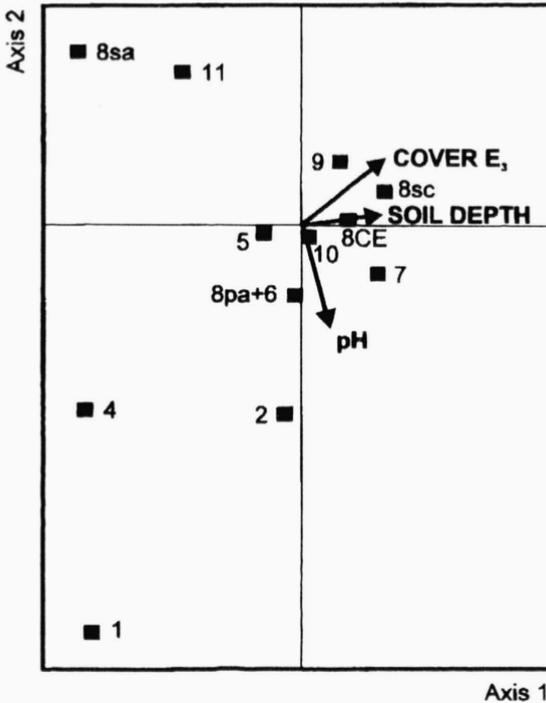


Fig. 1. – CCA ordination biplot of the range type groups. See Methods for the labels of particular groups and environmental variables.

Significance levels of the effects of particular environmental variables on the range type pattern are indicated in Table 2. This pattern is significantly influenced by most of the variables, except of ASPECT (SSW), SURFACE (ISOLINE), RANKER, and NITROGEN.

The following variables were selected in the forward selection (F value and significance level of Monte Carlo test is indicated in parentheses): COVER E<sub>3</sub> (F=9.43, P<0.01), pH (F=5.70, P<0.01), SOIL DEPTH (F=2.77, P<0.05).

A canonical correspondence analysis biplot of the groups of range types and environmental variables is presented in Fig. 1. Groups 1, 2, and 4 (i. e. mainly meridional and submeridional range types), are situated in the bottom left corner of the biplot where low cover of the tree layer, shallow soils, and high pH-values are predicted. In the upper left part with low tree layer cover, shallow soils, and low pH, subatlantic group 8sa and boreal group 11 are located. The other groups are found around the center of the biplot. Temperate groups 8CE, 8sc, and 9 respond to higher tree layer cover and deep soils. Group 10 is situated in the center of the biplot with average values of the environmental variables used in the model. Group 7 shows the response to higher values of all the environmental variables used. The groups 5 and 8pa+6 are confined to habitats with low tree layer cover, representing transition to the groups 1, 2, and 4.

Spearman rank correlation coefficients between the numbers of species belonging to particular range type groups in a sample plot and environmental variables are given in Table 2. Correlations with categorial variables and three-level ordinal variables have to be interpreted with a caution because the number of ties may become high. It is evident that whereas the range type groups 1 and 4 show positive correlation with steeper slopes and convex landforms, range type 8CE and 8sc are negatively correlated with these habitats. The species of the latter two groups and group 10 occur more frequently in lower altitudes or on the valley bottom, usually on Fluvisols. The reverse pattern is encountered in group 5. Groups 1, 2, 4, and 5 are positively correlated with sunny aspects, xeric sites and shallow soils, usually of a ranker type, whereas the groups 8p+6 and 9 are predicted to be confined to shady north-facing slopes and deeper soils. A positive correlation with deeper soils is also found in group 8CE. Groups 4, 5, 8CE, 8sc, and 9 appear to be confined to Renzinas, whereas groups 8sa and 11 seem to avoid this soil type. Habitats with lower litter cover/depth are preferred by groups 1, 4, 8sa, 11, and partially also 5. On the contrary, higher performance of group 9, partially also 8CE and 8sc, is typical of habitats with more developed litter layer. Among the chemical properties of soils, pH is most conspicuously related to range types, being positively correlated with groups 1, 2, 4, 5, 7, 8CE, 8sc, 9, and 10, and negatively with groups 8sa and 11. An analogous pattern is detected in  $\text{CaCO}_3$  for groups 1, 4, 5, 8CE, and 8sc, and 8sa, respectively. Nitrogen does not appear to influence the distribution of range type groups except for the negative correlation with group 8sc. A higher organic matter is predicted for the soils of range type groups 8sa and 11 that also have lower base saturation. Lower organic matter is typical of the soils with the occurrence of groups 7, 8CE, 9, and 10, and higher base saturation of that with groups 7, 8CE, 8sc, and 10. The range type groups 1, 2, 4, 8sa, and 11 are rather confined to open woodlands whereas the groups 7, 8CE, 8sc, and 9 prefer more or less closed forests. A well developed shrub layer is encountered on the habitats of groups 2, 4, 5, 8CE, 8p+6, 8sc, and 10. On the contrary, group 8sa is particularly confined to habitats with scarce or no shrub layer.

## Discussion and conclusions

The analyses support the hypothesis that there are relationships between the species range types and environmental factors on a landscape scale: each range type group may be characterized by its particular environmental requirements. There is also an evidence for co-occurrence patterns among the species belonging to the same range types.

The distribution pattern of the range type groups may be explained by the model using the combination of variables COVER  $E_3$ , pH and SOIL DEPTH. Apparently high importance of the tree layer cover as explanatory variable for the range type groups suggests that range type distribution patterns are, besides physiographic and soil factors, strongly influenced by community structure, at least by the position on the gradient from an open grassland or shrubland to a closed forest. Thus the species of particular range type groups occur particularly in vegetation types which reflect predominant vegetation in the centre of their range.

The environmental requirements of the particular groups in the study area may be summarized as follows:

Macaronesian-Mediterranean range types (group 1) are predominantly chamaephytes *Teucrium chamaedrys* and *Sedum album* and therophytes such as *Saxifraga tridactylites*. These species are confined to open xeric sites on steep slopes with sunny aspects, usually on convex landforms. The soils are shallow, usually Lithosols or Rankers neighbouring rock outcrops, with scarcely developed or absent litter layer and higher pH and moderate  $\text{CaCO}_3$ -content. The principal vegetation types in which these species occur in the study area belong to *Festucetalia valesiacae*, *Geranion sanguinei* and *Quercetalia pubescenti-petraeae*. This vegetation is different from the predominant vegetation types in the Mediterranean region which include evergreen forests of *Quercetia ilicis* and derived shrublands and heathlands with prevailing chamaephytes and conspicuous therophyte facies (Walter 1968, Peinado Lorca et Rivas-Martínez 1987, Horvat, Glavač et Ellenberg 1974). Central Europe lies outside the range of these vegetation types. That is why, Macaronesian-Mediterranean species are rare and occur in other vegetation types in environments most resembling the Mediterranean ones (Ellenberg 1986).

Oriental-Turcestani-Mediterranean range types (group 2) are dominated by the shrub *Rosa canina*. However, predominant life history form are therophytes (e. g. *Thlaspi perfoliatum*, *Galium aparine*, *Bromus squarrosus*), and some hemicryptophytes (*Hypericum perforatum*) are also encountered. These species inhabit open xeric habitats on sunny aspects with shallow soil, similarly to the preceding group. Communities in which these species occur are usually open woodlands or shrublands in canopy gaps. They are derived from various types of thermophilous vegetation which have been altered by some disturbance events. Often they may be classified as syntaxa of *Rhamno-Prunetea* or *Sedo-Scleranthetea*. In Mediterranean regions, they may be confined to similar vegetation types as group 1. However, their ranges extend into the Turcestani region where semi-deserts prevail, i. e. environments preferred by therophytes (Walter 1974).

Euroasian and European meridional-submeridional-(temperate).continental range types (group 4) comprise mainly perennial hemicryptophytes (e. g. *Bupleurum falcatum*, *Linaria genistifolia*), sedge *Carex humilis* and perennial grasses (e. g. *Stipa* sp. div.). Despite the fact that they possess different life history forms, they are very similar to group 1 in environmental requirements. They occur on open xeric sites of steep slopes, oriented to S-SW, on shallow soils, especially Rankers and Rendzinas with high pH and  $\text{CaCO}_3$ -content. A significant positive correlation with cover of the shrub layer is due to co-occurrence of the species of these range types and shrubs on open sites of forest canopy gaps. In the study area, these species occur particularly in the communities of *Festucetalia valesiacae*, and also in *Geranion sanguinei* and *Quercetalia pubescenti-petraeae*. Similar vegetation types predominate in the steppe and forest-steppe zones of Eastern Europe where the geographical center of this range type group is situated: steppe grasslands of *Festucetalia valesiacae* and steppe oak woodlands of the forest steppe zone, classified as *Aceri tatarici-Quercion* (Walter 1974, Gribova, Isačenko et Lavrenko 1980, Royer 1991, Zólyomi 1957, Jakucs 1960, 1961). Although the range type groups 1, 2, and 4 are clearly separated from the phytogeographical point of view, being components of the Mediterranean type vegetation, semi-deserts and steppes, respectively, in Central Europe they commonly co-occur in deforested or primary non-forest and xeric habitats, forming grassland communities of the class *Festuco-Brometea* and the order *Festucetalia valesiacae*, and in thermophilous oak forests of the order *Quercetalia pubescenti-petraeae* (Ellenberg 1986, Royer 1991, Jakucs 1961).

(Mediterranean/montane)-Submediterranean-(Pontic) range types (group 5) are common in the study area. They include mainly hemicryptophytes, particularly perennial herbs among them (e. g. *Hieracium sabaudum*, *Vincetoxicum hirsutinaria*, *Tanacetum corymbosum*), trees and shrubs (*Carpinus betulus*, *Acer campestre*, *Cornus mas*, etc.), and geophytes (*Anthericum ramosum*, *Galium sylvaticum*, *Allium flavum*, etc.). Typical habitats are on xeric and sunny slopes in higher altitudes within the valley, with shallow soils, particularly Rankers and Rendzinas. These soils are usually basic with increased  $\text{CaCO}_3$ -content. Vegetation of these habitats belongs to various associations of *Quercetalia pubescenti-petraeae*, *Sesleria varia-Tilia cordata-Pinus sylvestris* community, forest edges of *Geranium sanguinei* and rocky steppes of *Festucetalia valesiacae*. Some species also occur in mesophilous forests of *Fagetalia sylvaticae*. These vegetation types correspond with those in the geographical centre of this range type group, in the submediterranean part of the Balkans: thermophilous forests of *Quercetalia pubescenti-petraeae* and derived secondary vegetation (Horvat, Glavač et Ellenberg 1974, Jakucs 1961, Mayer 1984).

Euroasian (tropical)-meridional-submeridional.oceanic range types (group 7) form a rather heterogeneous group, dominated by the tree *Acer platanoides* and including ferns, therophytes and hemicryptophytes. They hardly show any relationships to environmental factors, except their affinity for basic soils with higher base saturation and lower organic matter content, and to the habitats with more or less closed forest canopy. Due to the strong influence of *Acer platanoides* on the analysis of this group, combined with its apparent heterogeneity, hardly any conclusions may be inferred concerning the environmental requirements of this group.

(Submediterranean/montane)-Central European range types: Central European (group 8CE) represent, besides the group 10, the largest group in the study area with predominant hemicryptophytes, both perennial herbs (e. g. *Sedum maximum*, *Galium odoratum*) and perennial grasses (*Dactylis polygama*, *Brachypodium sylvaticum* etc.), and also trees and shrubs (*Quercus petraea* agg., *Tilia cordata*, *Corylus avellana* etc.). They avoid steeper slopes and prefer lower altitudes in the valley and its bottom. The soils are deep, usually Fluvisols but these species also show positive correlation with Rendzinas. They usually have higher pH, with higher base saturation, and contain  $\text{CaCO}_3$ . The species of this group usually occur in closed forests with vigorous shrub understorey; they are predominantly species of broad-leaved deciduous forests of the order *Fagetalia sylvaticae*, in the study area mainly of the associations *Melampyro nemorosi-Carpinetum*, *Tilio cordatae-Fagetum*, *Aceri-Carpinetum*, and *Stellario-Alnetum glutinosae*. This group has its distribution center in Central Europe. In the study area, this is reflected in the occurrence of the species of this group in the most productive habitats from which most of the species belonging to the other range types were outcompeted and pushed out to more extreme habitats. These most productive habitats are in the whole of Central Europe, such as the study area, covered with *Fagetalia sylvaticae* forests (Ellenberg 1986, Mayer 1984).

(Submediterranean/montane)-Central European range types: perialpine + (Mediterranean)-Submediterranean oreophytic range types (group 8pa + group 6) comprise hemicryptophytes such as *Senecio germanicus*, chamaephytes (*Lamiastrum montanum*) and other life history forms. These species are encountered in shady aspects, usually on deeper soils near the bottom of the valley. Their habitats possess a well developed shrub layer. Phytosociologically, this range type group is composed firstly of the species which are, in the study area, typical of ravine forests of the association *Aceri-Carpinetum* and

beech forests of *Tilio cordatae-Fagetum* (*Lamiastrum montanum*, *Senecio germanicus*, *Dentaria enneaphyllos*, etc.), and secondly of species of the *Sesleria varia-Tilia cordata-Pinus sylvestris* community (*Sorbus aria* agg., *Thymus praecox*, *Sesleria varia*, etc.). Similar vegetation types are typical of landscapes with complicated topography, such as in marginal areas of the Alps and Carpathians where the range centers of perialpine species are situated.

(Submediterranean/montane)-Central European range types: subatlantic (group 8sa) include comparatively few species with different life histories (e. g. perennial grass *Avenella flexuosa*, perennial herb *Jasione montana*, ericoid low shrub *Calluna vulgaris*, succulent *Sedum reflexum* and evergreen climber *Hedera helix*). These species prefer habitats in higher altitudes within the river valley, usually on Cambisols with scarcely developed or absent litter layers. The soils are usually acidic, without CaCO<sub>3</sub>, with low base saturation and high organic matter content. On these habitats, woody plants have a poorly developed canopy. In the study area, these species are predominantly confined to low-growing acidophilous oak and beech forests that often form a fairly open canopy. Phytosociologically, these forests are classified into the *Genisto germanicae-Quercion* (*Luzulo albidiae-Quercetum petraeae*, *Calluno-Quercetum*), *Luzulo-Fagion* (*Luzulo nemorosae-Fagetum sylvaticae*), and partly also into the alliance *Quercion petraeae*, comprising Central European thermophilous oak forests on oligotrophic parent materials (e. g. the *Sorbo torminalis-Quercetum* and the *Genisto pilosae-Quercetum petraeae*). Similar acidophilous oak forests of *Quercetalia roboris* have a wide distribution in the western part of Central Europe and in Western Europe (Mayer 1974, Ellenberg 1986, Rodwell 1991). This indicates that species of this range type group occur in the study area with similar vegetation types as in their homeland.

(Submediterranean/montane)-Central European range types: subcontinental (group 8sc) comprise particularly hemicryptophytic herbs such as *Hieracium sylvaticum*, *Lychnis viscaria*, *Pulmonaria officinalis* agg., *Hepatica nobilis* etc. Their environmental relationships are similar to that of group 8CE except that there is no correlation with soil depth and soil organic matter, whereas they are negatively correlated with the soil nitrogen content. Phytosociologically, this group is also similar to the group 8CE, which has its optimum in *Fagetalia sylvaticae* forests. As may be inferred from the lack of correlation with soil depth and the less significant correlation with Fluvisols compared to the group 8CE, the group 8sc may appear slightly more xerophilous. This is in accordance with the fact that in this group more *Carpinion*-species are represented. *Carpinion*-forests replace *Fagion*-forests in the eastern part of Central Europe, with more continental and drier climate (Ellenberg 1986).

(Submediterranean)-Central European oreophytic range types (group 9) form a small group strongly dominated by the geophyte *Cyclamen purpurascens*. Thus the results obtained reflect the environmental relationships of this species rather than the whole group. Negative correlations with sunny aspects and xeric sites were revealed. Positive correlations exist with higher altitudes within the study area, and deeper soils with well-developed litter layer, higher pH and lower organic matter in the topsoil – among them particularly Rendzinas. A higher probability of occurrence is predicted for closed forest stands.

Euroasian (submeridional/montane)-temperate range types (group 10) represent the largest group in the study area, if the group 8 is divided into subgroups. It comprises

mostly perennial herbs (e. g. *Stellaria holostea*, *Fallopia convolvulus*, *Polygonatum odoratum*), grasses (*Poa nemoralis*, *Calamagrostis arundinacea* etc.), ferns (*Dryopteris filix-mas*, *Polypodium vulgare*, etc.), and also some woody plants (*Betula pendula*, *Pinus sylvestris*, etc.). They are forest species with clear preferences for Fluvisols on the bottom of the valley. Among the chemical properties of soils, they prefer higher pH, higher base saturation, and lower organic matter content. Their habitats have usually well developed shrub layers. Environmental correlates of this group are similar to that of groups 8CE and 8sc. Nevertheless, group 10 does not seem to avoid steep slopes and Lithosols. In the study area, *Stellario-Alnetum glutinosae* floodplain forests are confined to Fluvisols on the valley bottom, and in these forests the larger part of group 10 species occurs. However, this group varies in the phytosociological relations of the species that may occur (in the study area) both in various mesophilous broad-leaved forests of the order *Fagetalia sylvaticae*, and in the relict pine forests of the association *Cardaminopsio petraeae-Pinetum*. This corresponds with the principal communities within the range of this group, the temperate zone of Europe and Siberia, which are mesophilous deciduous forests of *Fagetalia sylvaticae*, coniferous forests of *Vaccinio-Piceetea* and partly also Siberian small-leaved deciduous forests of *Brachypodio pinnati-Betuletea* (Walter 1974, Gribova, Isačenko et Lavrenko 1980, Braun-Blanquet, Sissingh et Vlieger 1939, Ermakov, Koroljuk et Laščinskij 1991).

Euroasian (+ circumpolar) boreal range types (group 11) are represented by a few species in the study area. Perennial tussocky grass *Festuca ovina* (incl. "*F. firmula*") prevails among them, accompanied by the dwarf shrub *Vaccinium myrtillus* and some hemicryptophytic herbs (e. g. *Stellaria nemorum*). These species prefer acid soils with low base saturation, high organic matter content, and poorly developed litter layer. The tree canopy is scarce. In the study area, these conditions are found especially in relict pine forests on gneiss outcrops, belonging to the association *Cardaminopsio petraeae-Pinetum*. This reflects the predominant vegetation type of the boreal zone – coniferous forests (Walter 1974, Gribova, Isačenko et Lavrenko 1980, Braun-Blanquet, Sissingh et Vlieger 1939). An apparent similarity between this group and the (Submediterranean/montane)-Central European (subatlantic) species may be explained by the fact that in both boreal and subatlantic-atlantic regions, oligotrophic soils prevail which usually do not allow closed canopy succession (Walter 1974, Mayer 1984, Rodwell 1991).

## Acknowledgments

My thanks are due to Prof. Dr. Jiří Vicherek for his continuous support during this research and Dr. Vít Grulich for his help in classifying plants into range type groups. Soil samples were analysed by the team of Dr. Vlastimil Zezula at the Czech Institute for Nature Conservation, Brno. The English text was kindly improved by Kara Weller. This study is a part of a project from Grant no. 204/93/2052, supported by the Grant Agency of the Czech Republic (project leader: J. Vicherek).

## Souhrn

V hlubokém krystalinickém údolí řeky Dyje na česko-rakouské hranici byly studovány korelace mezi prostředím (geomorfologie, půdní faktory, zápoj dřevinných pater) a poměrným zastoupením druhů s různým zeměpisným rozšířením. Byla použita modifikovaná klasifikace areálů druhů do skupin areáltypů podle díla Meusel et Jäger (1992). Výsledky ukazují, že existuje korelace mezi zastoupením jednotlivých skupin

areálpů a určitými typy stanovišť. Mezi 12 skupinami areálpů vyskytujícími se ve studovaném území převažují euroasijské (submeridionálně/montánní)-temperátní areály, následované (submediteránně/montánní)--středoevropskými *sensu stricto* a (mediteránně/montánní)-submediteránně-pontickými. První dvě skupiny a (submediteránně/montánní)-středoevropské (subkontinentální) areály jsou si podobné ve svých ekologických nárocích především preferencí stanovišť na dně a v nižších polohách údolí s bázemi bohatými půdami a zapojeným stromovým a keřovým patrem. Na druhé straně makaronésko-mediteránní, orientálně-turkeštánsko-mediteránní a euroasijské a evropské meridionálně-submeridionálně-(temperátně) kontinentální druhy jsou vázány na xerická stanoviště s rozvolněným zápojem dřevin a na mělké a bazické půdy. (Mediteránně/montánní)-submediteránně-pontické a (submediteránně/montánní)-středoevropské (peri-alpinské) skupiny areálpů mají vesměs intermediární nároky mezi těmito extrémly. Odlišné vazby vykazují euroasijské (+ cirkumpolární) boreální a (submediteránně/montánní)-středoevropské (subatlantské) druhy, které jsou si podobné ve svých ekologických nárocích a vyskytují se především na otevřených stanovištích kyselých půd. Hlavní trendy v datech jsou shrnuty v modelu založeném na kanonické korespondenční analýze.

## References

- Batík P. (1992): Geologická mapa Národního parku Podyjí. – Český geologický ústav, Praha.
- Braun-Blanquet J., Sissingh G. et Vlieger J. (1939): Prodrum der Pflanzengesellschaften. 6. Klasse der *Vaccinio-Piceetea*. – Montpellier, 123 p.
- Chytrý M. (1993): Bemerkungen zur Vegetation der primär waldfreien Flächen auf nichtxerothermen Standorten in Flusstälern des Südostrandes des Böhmisches Massivs. – Acta Mus. Morav. – Sci. Nat., Brno, 77(1992):123–137.
- Chytrý M. et Vicherek J. (1995): Lesní vegetace Národního parku Podyjí/Thayatal. Die Waldvegetation des Nationalparks Podyjí/Thayatal. – Academia, Praha, 166 p.
- Ehrendorfer F. [red.] (1973): Liste der Gefäßpflanzen Mitteleuropas. – G. Fischer, Stuttgart, 318 p.
- Ellenberg H. (1974): Zeigerwerte der Gefäßpflanzen Mitteleuropas. – Scr. Geobot., Göttingen, 9:1–97.
- Ellenberg H. (1986): Vegetation Mitteleuropas mit den Alpen. Ed. 4. – E. Ulmer, Stuttgart, 989 p.
- Ermakov N. B., Koroljuk A. Ju. et Laščinskij N. N. (1991): Florističeskaja klassifikacija mezofilnych travjanych lesov Južnoj Sibiri [Floristic classification of the mesophilous herb-rich forests of South Siberia]. – Sibir. Otd. AN SSSR, Novosibirsk, 96 p.
- Gribova S. A., Isačenko T. I. et Lavrenko E. M. [red.] (1980): Rastitelnost evropejskoj časti SSSR. – Nauka, Leningrad, 429 p.
- Grulich V. et Chytrý M. (1993): Botanische Untersuchungen im Nationalpark Podyjí (Thayatal) und im grenznahen Österreich. – Verh. Zool.-Bot. Ges. Österr., Wien, 130:1–31.
- Hill M. O. (1973): Diversity and evenness: A unifying notation and its consequences. – Ecology, Durham, 54:427–432.
- Holub J. et Jirásek V. (1967): Zur Vereinheitlichung der Terminologie in der Phytogeographie. – Folia Geobot. Phytotax., Praha, 2:69–113.
- Horvat I., Glavač V. et Ellenberg H. (1974): Vegetation Südosteuropas. – G. Fischer, Jena, 768 p.
- Hraško J. et al. (1962): Rozbory pôd. – SVPL, Bratislava, 342 p.
- Hundt R. (1985): Zur Nutzung der Arealdiagnosen nach Meusel, Jäger und Weinert zur pflanzengeographischen Charakterisierung von Phytozönosen. – Flora, Jena, 176:325–340.
- Hynek A. et Trnka P. (1981): Topochory dyjské části Znojemska. – Folia Fac. Sci. Natur. Univ. Purkyn. Brun.-Geogr., Brno, 22/4:1–99.
- Jäger E. J. (1971): Die pflanzengeographische Stellung der "Steppen" der Iberischen Halbinsel. – Flora, Jena, 160:217–256.
- Jakucs P. (1961): Die phytozoologischen Verhältnisse der Flaumeichen Buschwälder Südostmitteleuropas. – Akadémiai Kiadó, Budapest, 314 p.
- Lausi D. et Nimis P. L. (1991): Ecological phytogeography of the southern Yukon Territory (Canada). – In: Nimis P. L. et Crovello T. J. [red.], Quantitative approaches to phytogeography, p. 35–122, Kluwer, Dordrecht.
- Ludwig J. A. et Reynolds J. F. (1988): Statistical ecology. A primer on methods and computing. – J. Wiley, New York etc., 337 p.
- Mayer H. (1984): Wälder Europas. – G. Fischer, Stuttgart et New York, 691 p.
- Meusel H. (1943): Vergleichende Arealkunde. – Berlin-Zehlendorf, 466 + 92 p.
- Meusel H. (1969): Chorologische Artengruppen der mitteleuropäischen Eichen-Hainbuchenwälder. – Feddes Report., Berlin, 80:113–132.

- Meusel H. et Jäger E. J. [red.] (1992): Vergleichende Chorologie der zentraleuropäischen Flora. Band III. – G. Fischer, Jena etc., 333 + 688 p.
- Meusel H., Jäger E. et Weinert E. (1965): Vergleichende Chorologie der zentraleuropäischen Flora. – G. Fischer, Jena, 583 + 258 p.
- Meusel H. et al. [red.] (1978): Vergleichende Chorologie der zentraleuropäischen Flora. Band II. – G. Fischer, Jena, 418 + 421 p.
- Nimis P. L. et Bolognini G. (1993): Quantitative phytogeography of the Italian beech forests. – *Vegetatio*, Dordrecht, 109:125–143.
- Nimis P. L., Malyshev L. I. et Bolognini G. (1994): A phytogeographic analysis of birch woodlands in the southern part of West Siberia. – *Vegetatio*, Dordrecht, 113:25–39.
- Parker K. C. (1988): Environmental relationships and vegetation associates of columnar cacti in the northern Sonoran Desert. – *Vegetatio*, Dordrecht, 78:125–140.
- Peinado Lorca M. et Rivas-Martínez S. [red.] (1987): La vegetación de España. – Universidad de Alcalá de Henares, Alcalá de Henares, 544 p.
- Quitt E. (1984): Klima jihomoravského kraje. – Krajský pedagogický ústav, Brno, 164 p.
- Rodwell J. S. [red.] (1991): British plant communities. Vol. 1. Woodlands and scrub. – Cambridge University Press, Cambridge, 395 p.
- Royer J. M. (1991): Synthèse eurosibérienne, phytosociologique et phytogéographique de la classe des *Festuco-Brometea*. – *Diss. Bot.*, Berlin et Stuttgart, 178:1–296.
- Rychnovská M. et Úlehlová B. (1975): Autökologische Studie der tschechoslowakischen *Stipa*-Arten. – Academia, Praha, 170 p.
- ter Braak C. J. F. (1987): CANOCO – a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal component analysis and redundancy analysis (version 2.1). – Agricultural Mathematics Group, Wageningen, 95 p.
- ter Braak C. J. F. (1990): Update notes: CANOCO version 3.10. – Agricultural Mathematics Group, Wageningen, 34 p.
- Timoney K. P. et al. (1993): Vegetation communities and plant distributions and their relationships with parent materials in the forest-tundra of northwestern Canada. – *Ecography*, Copenhagen, 16:174–188.
- Vesecký A. [red.] (1961): Podněbí Československé socialistické republiky. Tabulky. – Hydrometeorologický ústav, Praha, 380 p.
- Walter H. (1968): Die Vegetation der Erde in öko-physiologischer Betrachtung. Band II. Die gemäßigten und arktischen Zonen. – G. Fischer, Jena, 1001 p.
- Walter H. (1974): Die Vegetation Osteuropas, Nord- und Zentralasiens. – G. Fischer, Stuttgart, 452 p.
- Walter H. et Straka H. (1970): Arealkunde, floristisch-historische Geobotanik. Ed. 2. – E. Ulmer, Stuttgart 478 p.
- Wangerin W. (1932): Florenelemente und Arealtypen. – *Beih. Bot. Centralbl.*, Dresden, 49: 515–566.

Received 23 August 1994

Accepted 4 March 1995

## Appendix

The classification of river valley species into range type groups with the numbers of occurrences of particular species within the set of 104 samples.

**1 – Macaronesian-Mediterranean:** *Teucrium chamaedrys* 17, *Sedum album* 6, *Ballota nigra* 3, *Saxifraga tridactylites* 1, *Veronica hederifolia* agg. 1;

**2 – Oriental-Turcestani-Mediterranean:** *Rosa canina* 33, *Hypericum perforatum* 8, *Thlaspi perfoliatum* 7, *Galium aparine* 6, *Bromus squarrosus* 3, *Erophila verna* 3, *Poa trivialis* 3, *Bromus tectorum* 1, *Poa bulbosa* 1;

**4 – Euroasian and European meridional-submeridional-(temperate) continental:** *Bupleurum falcatum* 24, *Linaria genistifolia* 9, *Carex humilis* 7, *Artemisia campestris* 5, *Phleum phleoides* 5, *Potentilla arenaria* 5, *Allium montanum* 4, *Achillea nobilis* 3, *Dictamnus albus* 3, *Scabiosa ochroleuca* 3, *Stipa joannis* 3, *Asparagus officinalis* 2, *Stipa capillata* 2, *Veratrum nigrum* 2, *Bothriochloa ischaemum* 1, *Inula oculus-christi* 1, *Iris pumila* 1, *Melica transsilvanica* 1;

**5 – (Mediterranean/montane)-Submediterranean-(Pontic):** *Carpinus betulus* 62, *Acer campestre* 31, *Anthericum ramosum* 22, *Hieracium sabaudum* 22, *Galium sylvaticum* 19, *Vincetoxicum hirundinaria* 19, *Cornus mas* 17, *Tanacetum corymbosum* 15, *Allium flavum* 14, *Galium glaucum* 13, *Ligustrum vulgare* 13,

*Aurinia saxatilis* 12, *Verbascum austriacum* 12, *Geranium sanguineum* 10, *Arabis turrata* 8, *Carex pilosa* 8, *Prunus mahaleb* 8, *Viburnum lantana* 8, *Fragaria moschata* 7, *Stachys recta* 7, *Staphylea pinnata* 7, *Campanula moravica* 6, *Carex buekii* 6, *Centaurea stoebe* 6, *Festuca pallens* 6, *Melica ciliata* 6, *Sorbus terminalis* 6, *Berberis vulgaris* 5, *Iris variegata* 5, *Melittis melissophyllum* 5, *Sedum sexangulare* 5, *Anthemis tinctoria* 4, *Aster amellus* 4, *Buglossoides purpurocerulea* 4, *Inula conyza* 4, *Salvia pratensis* 4, *Veronica vindobonensis* 4, *Carex michelii* 3, *Dianthus carthusianorum* agg. 3, *Galanthus nivalis* 3, *Inula ensifolia* 3, *Lembotropsis nigricans* 3, *Salvia glutinosa* 3, *Seseli osseum* 3, *Alyssum alyssoides* 2, *Coronilla varia* 2, *Pyrus communis* agg. 2, *Sisymbrium strictissimum* 2, *Thesium linophyllum* 2, *Trifolium alpestre* 2, *Aristolochia clematitis* 1, *Aruncus sylvestris* 1, *Centaurea triumfettii* 1, *Epilobium roseum* 1, *Gagea bohémica* 1, *Hieracium bahuinii* 1, *Lactuca quercina* 1, *Viola odorata* 1;

**6 – (Mediterranean)-Submediterranean oreophytic:** *Sorbus aria* agg. 18;

**7 – Euroasian (tropical)-meridional-submeridional-oceanic:** *Acer platanoides* 31, *Arabidopsis thaliana* 10, *Asplenium trichomanes* 6, *Torilis japonica* 6, *Mentha longifolia* 2, *Polystichum aculeatum* 1;

**8CE – (Submediterranean/montane)-Central European (Central European s. s.):** *Quercus petraea* agg. 56, *Tilia cordata* 56, *Dactylis polygama* 34, *Luzula luzuloides* 33, *Sedum maximum* 31, *Galium odoratum* 25, *Geranium robertianum* 24, *Alliaria petiolata* 23, *Corylus avellana* 21, *Melica uniflora* 21, *Fagus sylvatica* 20, *Ulmus glabra* 19, *Acer pseudoplatanus* 18, *Genista tinctoria* 18, *Brachypodium sylvaticum* 17, *Lapsana communis* 17, *Sorbus aucuparia* 17, *Tilia platyphyllos* 17, *Mycelis muralis* 16, *Campanula persicifolia* 15, *Euphorbia cyparissias* 15, *Carex digitata* 14, *Genista pilosa* 14, *Arrhenatherum elatius* 13, *Convallaria majalis* 13, *Alnus glutinosa* 11, *Sambucus nigra* 11, *Crataegus monogyna* 10, *Festuca gigantea* 10, *Chaerophyllum temulum* 9, *Quercus robur* 9, *Festuca altissima* 8, *Fraxinus excelsior* 8, *Stachys sylvatica* 8, *Asperula cynanchica* 7, *Bromus benekenii* 7, *Polygonatum multiflorum* 7, *Ranunculus ficaria* subsp. *bulbifer* 7, *Clinopodium vulgare* 6, *Lonicera xylosteum* 6, *Luzula divulgata* Kirschner 6, *Pimpinella saxifraga* 6, *Ribes uva-crispa* 6, *Symphytum officinale* 6, *Epilobium montanum* 5, *Euonymus europaea* 5, *Sambucus racemosa* 5, *Silene dioica* 5, *Campanula trachelium* 4, *Mercurialis perennis* 4, *Phyteuma spicatum* 4, *Prenanthes purpurea* 4, *Astragalus glycyphyllos* 3, *Prunus spinosa* 3, *Ribes alpinum* 3, *Scleranthus perennis* 3, *Veronica officinalis* 3, *Acinos arvensis* 2, *Aconitum lycoctonum* 2, *Aethusa cynapium* 2, *Euphorbia dulcis* 2, *Primula elatior* 2, *Rumex obtusifolius* 2, *Sanicula europaea* 2, *Abies alba* 1, *Anemone nemorosa* 1, *Astrantia major* 1, *Betonica officinalis* 1, *Circaea lutetiana* 1, *Epipactis helleborine* 1, *Eupatorium cannabinum* 1, *Helianthemum nummularium* 1, *Hypericum montanum* 1, *Linum catharticum* 1, *Moehringia trinervia* 1, *Pimpinella major* 1, *Rubus fruticosus* agg. 1, *Thymus pulegioides* 1, *Valeriana wallrothii* 1, *Viola reichenbachiana* 1;

**8pa – (Submediterranean/montane)-Central European (perialpine):** *Lamiastrum montanum* 27, *Senecio germanicus* Wallr. 12, *Thymus praecox* 9, *Dentaria enneaphyllos* 7, *Arabis pauciflora* 6, *Cotoneaster integerrimus* 6, *Achillea* cf. *distans* 4, *Sesleria varia* 4, *Aconitum variegatum* 2, *Galium valdepiilosum* 2, *Geranium phaeum* 1;

**8sa – (Submediterranean/montane)-Central European (subatlantic):** *Avenella flexuosa* 33, *Jasione montana* 10, *Calluna vulgaris* 9, *Sedum reflexum* 6, *Hedera helix* 5, *Taxus baccata* 4, *Senecio sylvaticus* 3, *Senecio viscosus* 2, *Valeriana sambucifolia* 1;

**8sc – (Submediterranean/montane)-Central European (subcontinental):** *Hieracium sylvaticum* 31, *Euonymus verrucosa* 28, *Corydalis solida* 25, *Lychnis viscaria* 25, *Pulmonaria officinalis* agg. 25, *Hepatica nobilis* 23, *Asarum europaeum* 20, *Galium album* 17, *Dentaria bulbifera* 15, *Hieracium pilosella* 12, *Actaea spicata* 7, *Veronica dillenii* 7, *Consolida regalis* 5, *Campanula rotundifolia* 4, *Cardaminopsis arenosa* 4, *Anemone ranunculoides* 3, *Chaerophyllum aromaticum* 3, *Cirsium oleraceum* 3, *Lamium maculatum* 3, *Verbascum lychnitis* 3, *Chamaecytisus ratisbonensis* 2, *Inula hirta* 2, *Isopyrum thalictroides* 2, *Lathyrus niger* 2, *Melampyrum nemorosum* 2, *Asperula tinctoria* 1, *Corydalis cava* 1, *Digitalis grandiflora* 1, *Gagea minima* 1, *Myosotis stricta* 1, *Viola collina* 1;

**9 – (Submediterranean)-Central European oreophytic:** *Cyclamen purpurascens* 32, *Aconitum anthora* 3, *Bupthalmum salicifolium* 2, *Rosa pendulina* 2, *Biscutella laevigata* 1, *Thlaspi caerulescens* 1;

**10 – Euroasian (submeridional/montane)-temperate:** *Poa nemoralis* 57, *Stellaria holostea* 46, *Dryopteris filix-mas* 31, *Fallopia convolvulus* 24, *Polygonatum odoratum* 23, *Urtica dioica* 23, *Campanula rapunculoides* 22, *Polypodium vulgare* 19, *Hieracium lachenalii* 17, *Rumex acetosella* agg. 16, *Calamagrostis arundinacea* 12, *Origanum vulgare* 13, *Lathyrus vernus* 12, *Aegopodium podagraria* 11, *Betula pendula* 11, *Glechoma hederacea* 11, *Impatiens noli-tangere* 11, *Oxalis acetosella* 11, *Geum urbanum* 10, *Pinus sylvestris* 9, *Artemisia absinthium* 8, *Asplenium septentrionale* 8, *Primula veris* 8, *Scrophularia nodosa* 8, *Agropyron caninum* 7, *Agropyron repens* 7, *Carduus crispus* 7, *Hieracium umbellatum* 7, *Rubus idaeus* 7, *Silene nutans* 7, *Phalaris arundinacea* 6, *Cardamine impatiens* 5, *Lilium martagon* 5, *Rhamnus catharticus* 5, *Agrostis stricta* 4, *Angelica sylvestris* 4, *Arctium tomentosum* 4, *Echium vulgare* 4, *Gagea lutea* 4, *Juniperus*

*communis* 4, *Poa angustifolia* 4, *Asplenium ruta-muraria* 3, *Chelidonium majus* 3, *Daphne mezereum* 3, *Filipendula ulmaria* 3, *Fragaria vesca* 3, *Galeopsis ladanum* 3, *Seseli libanotis* 3, *Solidago virgaurea* 3, *Viola mirabilis* 3, *Brachypodium pinnatum* 2, *Chenopodium hybridum* 2, *Cuscuta europaea* 2, *Dryopteris dilatata* 2, *Festuca rubra* 2, *Lysimachia vulgaris* 2, *Maianthemum bifolium* 2, *Melica nutans* 2, *Poa palustris* 2, *Rubus caesius* 2, *Silene vulgaris* 2, *Arabis hirsuta* 1, *Arctium lappa* 1, *Arenaria serpyllifolia* 1, *Artemisia vulgaris* 1, *Athyrium filix-femina* 1, *Campanula glomerata* 1, *Carex caryophyllea* 1, *Dryopteris carthusiana* 1, *Equisetum pratense* 1, *Filago arvensis* 1, *Frangula alnus* 1, *Galeopsis bifida* 1, *Gymnocarpium dryopteris* 1, *Humulus lupulus* 1, *Koeleria macrantha* 1, *Lycopus europaeus* 1, *Melampyrum cristatum* 1, *Myosotis scorpioides* 1, *Paris quadrifolia* 1, *Senecio jacobaea* 1;

**11 – Euroasian (+ circumpolar) boreal:** *Festuca ovina* (Incl. “*F. firmula*”) 39, *Vaccinium myrtillus* 15, *Stellaria nemorum* 10, *Melampyrum pratense* 5, *Silene alba* 2, *Cystopteris fragilis* 1, *Epilobium angustifolium* 1, *Galeopsis speciosa* 1.

de Waal L. C., Child L. E., Wade P. M. et Brock J. H. [red.]

### Ecology and management of invasive riverside plants

John Wiley & Sons, Chichester 1994, 217 str. Cena váz. 45.00 GBP.

Recenzovaná kniha je prvním svazkem plánované řady *Landscape Ecology Series* vydávané „u Wileyho“ Centrem pro krajinnou ekologii při Universitě v Loughborough v Anglii. V knize je shrnuto dvacet příspěvků přednesených na semináři, který se uskutečnil na dané téma v dubnu roku 1992 právě v Loughborough. Tento seminář položil základ, zdá se, sérii dalších konferencí o invazních rostlinách: druhý se uskutečnil na podzim 1993 u nás a třetí je plánován na podzim 1995 do Arizony. Tradicí by se mohlo stát i publikování výsledků semináře formou slušné knižní publikace (viz Pyšek et al. 1995). Nyní však k vlastní knize.

Zařazené příspěvky se většinou týkají druhů *Heracleum mantegazzianum* (7) a *Reynoutria japonica* (5), nebo obou (3). V posledním případě společně s třetím druhem cizího původu, intenzivně se šířícím podél řek i u nás, a sice *Impatiens glandulifera* (té je samostatně věnován jeden příspěvek). Dva články se zabývají druhem *Crassula helmsii*, který zatím u nás zjištěn nebyl, avšak na Britských ostrovech se stává velmi invazním. Druh se ale nešíří podél řek, tudíž jeho zařazení do knihy o invazních poříčních druzích se mi zdá problematické. Je to druh stojatých vod původem z Austrálie. Jinými, pro nás exotickými druhy (*Tamarix spec. div.*, *Salvinia molesta* aj.) se zabývají zbylé dva příspěvky. Bohužel, kniha je souborem jednotlivých článků, sice převážně kvalitních, avšak chybí jakákoliv syntéza nebo pokus o ni. Měla být zahrnuta obecnější úvodní, případně shrnující závěrečná kapitola. Takto kniha nepřekračuje rámeček sborníku. Přesto však je cenným pohledem na problematiku invazí rostlin podél řek. Důležité je shrnutí mnoha výsledků z experimentů s omezováním druhů a další postřehy o možnostech jejich kontroly. Tím je kniha aktuální i pro nás, protože všechny tři druhy, kterým je především věnována, jsou nepříjemnými invazními druhy i podél našich řek. U nás se zdá v tomto ohledu asi nejnebezpečnější *Reynoutria japonica*, která se masově šíří hlavně podle některých severočeských řek, totálně degraduje invadovaná stanoviště a její eliminace je nejproblematictější, jak vyplynulo i z recenzované knihy. Situace u nás zatím nedospěla tak daleko, jako na Britských ostrovech, kde v nivách některých řek najdete pozoruhodné společenstvo tvořené *Reynoutria japonica*, *Heracleum mantegazzianum* a *Impatiens glandulifera* a jako vzácnost mezi nimi tak leda kopřivu. K tomu, aby v budoucnu takto nevypadaly i naše nivy, by mohly přispět mnohé informace obsažené v této recenzované knize.

### Literatura

Pyšek P., Prach K., Wade P. et Rejmánek M. (1995): Plant invasions: general aspects and special problems. - SPB Academic Publishing, Amsterdam, 263 p.