JOURNAL OF FOREST SCIENCE, *54*, 2008 (8): 340–354

The evolution of natural floodplain forests in South Moravia between 1973 and 2005

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ABSTRACT: Since the mid-1970's, the landscape around the confluence of the Morava and Dyje rivers has undergone substantial changes related to the drop of water table caused by water management measures undertaken on both rivers. Periodical spring floods are among the phenomena lost due to ameliorations. In this study, the reaction of forest ecosystems to the decrease in soil moisture is assessed on the basis of changes in species composition of the herb layer as well as of the known requirements of individual recorded taxa and the entire herb synusiae for the water content of soils. The results confirm that the species with the greatest demand for water disappear over time. The tendency of decreasing Ellenberg indicator values of the herb layers within the phytocoenological relevés is obvious also with the consideration of the influence of different numbers of species recorded on the same plots in different years of the survey. The changes are most visible in the dampest habitats, while elevated sites, so-called "hrudy", tend to be most stable. The intensity of vegetation changes increases in direct proportion to the altitude of the sites. The process of changes in some habitats caused by the alteration of the water regime has to be separated from the changes in the vegetation structure, which are easier to observe optically. The limiting factor of their development in the given conditions is the forest wildlife. After the elimination of wildlife's influence, the woody species synusia differentiates in height. A qualitative shift is represented by the recession of the formerly dominant *Quercus robur* on the main level, and its gradual replacement by other species. The impact of changes going on in the woody synusia on selected characteristics of the herb layer are included in the analyses.

Keywords: floodplain forest; phytocoenosis; woody synusia; herb synusia

Forest communities bound to broad shallow river valleys are ecosystems under a long-term intensive anthropic influence. The way they look today is the result of centuries of cultivation and selection of a combination of tree species, forest type, and form of its regeneration in order to achieve the best functional and economic yield. These criteria were continuously adjusted according to changing human needs.

The history of Ranšpurk and Cahnov-Soutok National Nature Reserves (hereinafter Ranšpurk and Cahnov-Soutok) has been described in many texts (e.g. Vrška 1997, 1998; Vrška et al. 2006). Historic surveys have shown that in these cases the forests were altered by people in the past. Intensive grazing of domestic cattle in the forests was practised until approximately the second half of the 19th century. Once it ceased, the forests suffered from a strong pressure from deer and other game kept in enclosures. This game reserve was established between the 1960's and 1970's. Although the forest stands on both sites underwent logging in the past, it can be assumed that the gene pool of woody species was not substantially disrupted there. In 1949, the

Supported by the Ministry of Education, Youth and Sports of the Czech Republic, Projects No. VaV-SM/6/153/05 and MSM 6293359101.

Ranšpurk and Cahnov-Soutok sites were declared State Nature Reserves, which meant the forests were left to develop without intervention. At the end of the millennium, the protected areas were fenced off to prevent further damage by game.

Many authors focused on the study of forest ecosystems of the South-Moravian floodplains (Mezera 1956, 1958; Vyskot 1959; Horák 1969; Staněk, Barták 1989; Maděra 2001; Viewegh 2002, and others). The published texts often issue from repeated surveys carried out in one or both these reserves. The authors usually concentrate on a particular segment of the plant society. Dendrometric surveys are accompanied by phytocoenological relevés used to illustrate the complex conditions of the sites. Assessment of phytocoenoses, on the other hand, is based on the monitoring of the herb layer with information about the species composition of the shrub and tree layers. Certain separation of the individual parts of the phytocoenose is necessary for specialized studies, and from this point of view, this text is no exception. However, by analyzing the development of woody and herbaceous synusia including the definition of their mutual interactions, more complex information can be found about what is going on within the present forest communities. The aim of the work is to describe changes in the composition and structure of the studied communities with reference to their likely causes, and also to suggest the relations between the recorded phytocoenological features.

MATERIALS AND METHODS

Study area

Ranšpurk and Cahnov-Soutok forest reserves are situated in the south-eastern corner of the Czech Republic close to the border with Slovakia and Austria, on the confluence of the Morava and Dyje rivers. In geographic terms, the area belongs to the Lower Moravian Lowland geomorphological unit (Dolnomoravský úval) and sub-unit of the Dyje-Morava floodplain (Dyjsko-moravská niva) (Demek et al. 1987). The altitude of the studied sites ranges between 151.4 and 152.2 m (Cahnov-Soutok) and 152.7–154.5 m (Ranšpurk). The soils are mostly classified (Anonymous 1998; Driessen et al. 2001; Michéli et al. 2006) as Gley-Eutric Fluvisols or Eutric Fluvisols, less frequently as Eutric Gleysols (lower parts) or Arenosols (elevated parts). From the aspect of the phytocoenological zoning of the Czech Republic (Skalický in Hejný, Slavík 1997), the area belongs to the Pannonian thermophytic district.

Table 1. Scores of relevés from the DCA of woody synusia were studied in relation to the cover of selected species, diversity index, cover of woody synusia level, average *EIV* of woody synusia, diversity index of the herb layer and its mean *EIV* values

Veg layer		Trees and shrubs												Herb layer			
Factor		diversity and species					structure				abiotic factors			diversity and abiotic factors			
Score of samples	Shannon index	Acecam	Querob	Jugnig	Cratmon	Sambnig	layer 1	layer 2	layer 3	layer 4 + 5	M	L	A	N	Shannon index	M	L	A
Axis 1	–	–	–	–0.44***	0.34***	–0.28**	–	–	–	–	–	–	–	–0.22*	–	0.68***	0.64***	0.24*
Axis 2	0.29**	–	–	0.22*	0.22*	0.31**	–0.41***	0.28**	0.45***	0.23*	–	–	–	–	0.46***	–0.42***	–0.37***	0.24*
Axis 3	0.27**	–	0.32**	–	–	–	–	–	0.33**	–	0.38***	0.35***	–	0.28**	–	–	–	–
Axis 4	–	0.34***	–0.59***	–	0.25*		–	–	0.25*	–	–	–0.28**	0.21*	–	–	0.26*	0.27**	–

Acecam – *Acer campestre*, Querob – *Quercus robur*, Jugnig – *Juglans nigra*, Cratmon – *Crataegus monogyna*, Sambnig – *Sambucus nigra*, M – moisture, L – light, A – acidity, N – nutrients. The studied relationship is expressed by the value of the correlation coefficient and the level of statistical significance (* $0.049 > P > 0.01$, ** $0.009 > P > 0.001$, *** $P < 0.001$). Axes 1 and 4 explain the variability of woody plants according to the presence of individual species, while axis 3 classifies the relevés according to their habitats. Changes in the species composition and vertical structure of woody synusia, including their projection onto the herb layer, are explained by axis 2

Table 2. Synoptic table with percentage constancy and modified fidelity index phi coefficient (exponent). Vegetation layers are described in the text (data capture)

Year (No. of relevés)	1973–74 (24)	1994 (24)	2000 (24)	2005 (24)
Synusia of woody species				
Layer 1				
Acer campestre	38 $^{12.0}$	29 $^{1.3}$	29 $^{1.3}$	17^{---}
Carpinus betulus	62 $^{27.1}$	38 $^{---}$	46 $^{7.4}$	12^{---}
Fraxinus angustifolia subsp. *danubialis*	58^{---}	54^{---}	71 $^{13.5}$	54^{---}
Juglans nigra	.$^{---}$	4$^{3.5}$	4 $^{3.5}$	4 $^{3.5}$
Quercus robur	42^{---}	50 $^{7.3}$	54 $^{12.1}$	29^{---}
Tilia cordata	17^{---}	21^{---}	38 $^{20.0}$	17^{---}
Ulmus laevis	25 $^{17.0}$	8^{---}	12^{---}	12^{---}
Layer 2				
Acer campestre	4 $^{---}$	46 $^{8.6}$	54 $^{18.5}$	50 $^{13.6}$
Carpinus betulus	4^{---}	38 $^{2.5}$	50 $^{17.6}$	50 $^{17.6}$
Fraxinus angustifolia subsp. *danubialis*	.$^{---}$	17 $^{---}$	29 $^{17.3}$	25 $^{11.0}$
Juglans nigra	4$^{8.4}$	.$^{---}$	4$^{8.4}$	.$^{---}$
Pyrus pyraster	.$^{---}$	.$^{---}$	4 $^{17.8}$	.$^{---}$
Quercus robur	.$^{---}$	8^{---}	12$^{6.2}$	17 $^{14.4}$
Tilia cordata	.$^{---}$	12$^{1.9}$	17$^{9.4}$	17$^{9.4}$
Ulmus laevis	4^{---}	12$^{3.9}$	12$^{3.9}$	12$^{3.9}$
Layer 3				
Acer campestre	8^{---}	29^{---}	71 $^{29.0}$	75 $^{33.8}$
Carpinus betulus	12^{---}	17^{---}	67 $^{29.3}$	71 $^{34.2}$
Cornus sanguinea	.$^{---}$	.$^{---}$	.$^{---}$	4 $^{17.8}$
Crataegus laevigata	.$^{---}$	8^{---}	.$^{---}$	29 $^{39.2}$
Crataegus monogyna	12^{---}	46$^{8.6}$	58 $^{23.5}$	38^{---}
Euonymus europaea	.$^{---}$	.$^{---}$	8$^{2.3}$	21 $^{30.1}$
Fraxinus angustifolia subsp. *danubialis*	4^{---}	4^{---}	54 $^{33.4}$	50 $^{28.1}$
Juglans nigra	.$^{---}$	4^{---}	8$^{8.1}$	8$^{8.1}$
Malus sylvestris	.$^{---}$	.$^{---}$	.$^{---}$	4 $^{17.8}$
Prunus spinosa	.$^{---}$	.$^{---}$	.$^{---}$	4 $^{17.8}$
Pyrus pyraster	.$^{---}$	4^{---}	8$^{2.3}$	17 $^{20.8}$
Quercus robur	.$^{---}$	.$^{---}$	4$^{3.5}$	8 $^{17.3}$
Rhamnus cathartica	.$^{---}$	.$^{---}$	4 $^{17.8}$	.$^{---}$
Rosa canina	.$^{---}$	8$^{8.1}$	8$^{8.1}$	4^{---}
Sambucus nigra	.$^{---}$	.$^{---}$	17 $^{20.8}$	12 $^{11.6}$
Tilia cordata	4^{---}	12^{---}	54 $^{28.5}$	54 $^{28.5}$
Ulmus laevis	8^{---}	8^{---}	54 $^{30.1}$	50 $^{24.9}$
Layer 4				
Acer campestre	29^{---}	79 $^{11.8}$	79 $^{11.8}$	92 $^{27.5}$
Aesculus hippocastanum	.$^{---}$	.$^{---}$	.$^{---}$	8 $^{25.3}$
Alnus glutinosa	.$^{---}$	4 $^{17.8}$	.$^{---}$	.$^{---}$
Carpinus betulus	17^{---}	58$^{3.6}$	71 $^{18.1}$	75 $^{23.0}$
Cornus sanguinea	.$^{---}$	.$^{---}$	.$^{---}$	4 $^{17.8}$
Crataegus laevigata	4^{---}	17 $^{17.4}$	.$^{---}$	12$^{8.7}$
Crataegus monogyna	12^{---}	50^{---}	58$^{8.4}$	83 $^{37.3}$

Table 2 to be continued

Year (No. of relevés)	1973–74 (24)	1994 (24)	2000 (24)	2005 (24)
Euonymus europaea	.---	8---	21 1.5	50 43.8
Fraxinus angustifolia subsp. *danubialis*	50---	88 13.1	83 7.3	92 18.9
Juglans nigra	.---	12 3.9	8---	21 19.7
Parthenocissus quinquefolia	.---	.---	.---	4 17.8
Prunus spinosa	.---	.---	8 8.1	12 18.9
Pyrus pyraster	.---	4---	29 26.4	21 12.3
Quercus robur	.---	8---	25 21.8	17 7.3
Rhamnus cathartica	.---	.---	8 12.0	8 12.0
Rosa canina	.---	17---	42 29.6	25 5.9
Sambucus nigra	.---	25 27.6	8---	8---
Tilia cordata	38---	46 2.4	46 2.4	46 2.4
Ulmus laevis	8---	12---	58 33.7	46 18.2
Ulmus minor	12 1.9	25 24.5	.---	8---
Viburnum opulus	.---	.---	4 8.4	4 8.4
Layer 5				
Acer campestre	.---	92 32.7	92 32.7	75 12.6
Aesculus hippocastanum	.---	.---	.---	8 25.3
Carpinus betulus	.---	71 29.0	58 14.5	54 9.7
Crataegus laevigata	.---	4 17.8	.---	.---
Crataegus monogyna	.---	33 11.1	29 5.6	38 16.7
Euonymus europaea	8---	8---	.---	21 22.7
Fraxinus angustifolia subsp. *danubialis*	.---	67 13.3	83 32.7	71 18.1
Juglans nigra	.---	.---	4 17.8	.---
Parthenocissus quinquefolia	.---	.---	4 17.8	.---
Quercus robur	.---	12---	50 43.8	17---
Rhamnus cathartica	.---	4 17.8	.---	.---
Rosa canina	.---	4---	8 2.3	17 20.8
Sambucus nigra	.---	17 36.1	.---	.---
Tilia cordata	4---	50 21.9	29---	46 16.7
Ulmus laevis	.---	.---	25 19.3	29 26.4
Ulmus minor	.---	4 17.8	.---	.---
Layer 6				
Acer campestre	.---	8---	29 26.4	17 5.3
Carpinus betulus	.---	67 53.4	8---	29 4.1
Crataegus monogyna	.---	.---	4 17.8	.---
Fraxinus angustifolia subsp. *danubialis*	.---	8---	17 17.4	8---
Quercus robur	.---	.---	4 17.8	.---
Tilia cordata	.---	33 9.6	21---	50 31.5
Synusia of herbal species				
Layer 7				
Aegopodium podagraria	12---	21 3.1	21 3.1	21 3.1
Agrostis stolonifera	8 5.0	4---	8 5.0	4---
Ajuga reptans	46 18.2	29---	17---	33 2.6
Alliaria petiolata	21---	38 21.8	.---	29 10.2

Table 2 to be continued

Year (No. of relevés)	1973–74 (24)	1994 (24)	2000 (24)	2005 (24)
Allium ursinum	8 25.3	.---	.---	.---
Anemone ranunculoides	4 17.8	.---	.---	.---
Arctium minus	.---	21 22.7	.---	17 14.4
Aristolochia clematitis	12---	17---	21 3.1	25 9.2
Aster lanceolatus	4---	12---	29 13.6	33 19.6
Astragalus glycyphyllos	.---	8 17.3	.---	4 3.5
Atriplex patula	.---	4 8.4	4 8.4	.---
Bidens frondosa	4---	12---	21 10.2	21 10.2
Brachypodium sylvaticum	46---	88 23.4	67---	75 7.8
Calamagrostis epigejos	.---	4 3.5	.---	8 17.3
Caltha palustris	8 12.0	4---	.---	4---
Campanula trachelium	.---	21 26.1	.---	12 8.7
Cardamine impatiens	8---	54 21.2	8---	75 46.2
Cardamine pratensis	50 8.5	54 13.4	21---	46 3.6
Carex acuta	25 44.7	.---	.---	.---
Carex acutiformis	4 17.8	.---	.---	.---
Carex divulsa	.---	8 25.3	.---	.---
Carex montana	4 17.8	.---	.---	.---
Carex muricata agg.	.---	17---	17---	42 33.9
Carex remota	54---	38---	75 20.7	62 6.1
Carex riparia	.---	8---	17 9.4	21 17.0
Carex sylvatica	29 2.7	.---	21---	58 40.6
Carex vulpina agg.	.---	4 17.8	.---	.---
Cerastium holosteoides subsp. *triviale*	.---	29 19.4	12---	25 12.9
Chaerophyllum aromaticum	.---	12 31.1	.---	.---
Chaerophyllum temulum	8---	58 23.5	25---	62 28.4
Chelidonium majus	4---	12 8.7	4---	12 8.7
Circaea lutetiana	50---	75---	83 11.1	92 22.2
Cirsium arvense	.---	.---	.---	4 17.8
Cirsium palustre	.---	4 17.8	.---	.---
Convallaria majalis	4---	4---	12 11.6	8 2.3
Cuscuta europaea	.---	8 17.3	4 3.5	.---
Dactylis polygama	21---	75 26.5	54 2.4	58 7.2
Deschampsia cespitosa	83 3.1	75---	79---	88 9.2
Dryopteris carthusiana	.---	4---	8 5.0	12 14.9
Elymus caninus	.---	.---	8 17.3	4 3.5
Epilobium collinum	.---	4 17.8	.---	.---
Epilobium montanum	.---	4 17.8	.---	.---
Epilobium roseum	---	4 17.8	.---	.---
Fallopia dumetorum	.---	.---	4---	21 34.8
Festuca gigantea	42---	46 3.6	33---	50 8.5
Ficaria verna subsp. *bulbifera*	4---	8 8.1	4---	4---
Galeopsis pubescens	17 3.4	4---	12---	25 17.0
Galium album	.---	.---	.---	8 25.3

Table 2 to be continued

Year (No. of relevés)	1973–74 (24)	1994 (24)	2000 (24)	2005 (24)
Galium aparine	58 22.1	29–––	.–––	71 36.9
Galium odoratum	12–––	25 11.0	12–––	21 4.7
Galium palustre	33 11.1	25–––	21–––	21–––
Geranium robertianum	21–––	42 2.5	50 12.3	46 7.4
Geum urbanum	42–––	92 20.0	79 2.9	96 25.8
Glechoma hederacea	83 8.6	42–––	96 25.8	88 14.3
Glechoma hirsuta	.–––	.–––	.–––	4 17.8
Hedera helix	4–––	8 2.3	8 2.3	8 2.3
Heracleum sphondylium	.–––	.–––	4 8.4	4 8.4
Hypericum hirsutum	.–––	.–––	.–––	4 17.8
Impatiens parviflora	.–––	71 25.3	58 10.8	67 20.5
Iris pseudacorus	29 23.9	4–––	8–––	17 3.4
Lactuca serriola	.–––	.–––	.–––	4 17.8
Lamium maculatum	21–––	58 9.6	54 4.8	67 19.2
Lapsana communis	17–––	75 43.2	21–––	42 3.7
Lathyrus vernus	17–––	17–––	17–––	29 13.6
Leonurus marrubiastrum	.–––	.–––	.–––	8 25.3
Leucojum aestivum	4 17.8	.–––	.–––	.–––
Lychnis flos-cuculi	.–––	.–––	8 8.1	12 18.9
Lycopus europaeus	12 6.2	4–––	8–––	12 6.2
Lysimachia nummularia	33–––	67 19.2	50–––	50–––
Lysimachia vulgaris	8–––	4–––	8–––	12 8.7
Lythrum salicaria	4 8.4	.–––	.–––	4 8.4
Maianthemum bifolium	25–––	12–––	29 5.6	33 11.1
Mentha aquatica	4 17.8	.–––	.–––	.–––
Mentha arvensis	.–––	.–––	4–––	17 29.8
Milium effusum	38 3.8	25–––	29–––	46 13.9
Moehringia trinervia	12–––	8–––	21–––	42 29.6
Myosotis palustris agg.	17 24.8	.–––	8 5.0	.–––
Myosotis palustris subsp. *laxiflora*	.–––	4 17.8	.–––	.–––
Myosoton aquaticum	.–––	25 17.0	12–––	21 10.2
Oenanthe aquatica	.–––	.–––	.–––	4 17.8
Paris quadrifolia	.–––	4–––	8–––	21 26.1
Persicaria hydropiper	42 44.3	.–––	4–––	12–––
Persicaria mitis	–––	21 22.7	17 14.4	.–––
Phalaris arundinacea	29 13.6	17–––	8–––	25 7.5
Plantago major	.–––	8–––	17 11.8	17 11.8
Poa annua	4 17.8	.–––	.–––	.–––
Poa nemoralis	.–––	.–––	.–––	12 31.1
Poa palustris	.–––	8–––	12 6.2	17 14.4
Poa trivialis	12 31.1	.–––	.–––	.–––
Polygonatum multiflorum	.–––	.–––	4 3.5	8 17.3
Potentilla reptans	.–––	4 17.8	.–––	.–––
Prunella vulgaris	.–––	33 16.0	21–––	33 16.0

Table 2 to be continued

Year (No. of relevés)	1973–74 (24)	1994 (24)	2000 (24)	2005 (24)
Pulmonaria officinalis	25---	29---	46 8.6	54 18.5
Ranunculus acris	12 31.1	.---	.---	.---
Ranunculus repens	58 58.6	.---	4---	12---
Rubus caesius	67---	92 8.8	88 1.8	100 22.8
Rumex conglomeratus	92 77.3	12---	8---	8---
Rumex sanguineus	.---	67 22.9	62 18.1	58 13.3
Scrophularia nodosa	4---	17 24.8	.---	4---
Scutellaria galericulata	17 7.3	.---	12---	21 14.5
Senecio erraticus	.---	.---	4---	17 29.8
Silene vulgaris	.---	4 17.8	.---	.---
Solidago canadensis	4 17.8	.---	.---	.---
Solidago gigantea	.---	.---	8 25.3	.---
Stachys palustris	12---	21 6.5	17---	17---
Stachys sylvatica	33---	46 6.1	42 1.2	42 1.2
Stellaria holostea	4 17.8	.---	.---	.---
Stellaria media	.---	4---	8---	29 35.4
Stellaria nemorum	.---	4 3.5	8 17.3	.---
Symphytum officinale	42 11.6	29---	29---	29---
Taraxacum sect. *Ruderalia*	.---	8---	4---	25 30.9
Torilis japonica	.---	38 12.0	42 17.4	33 6.7
Triticum aestivum	.---	.---	.---	4 17.8
Urtica dioica	92---	92---	88---	96 8.7
Veronica chamaedrys	25---	58 32.2	29---	17---
Vicia species	.---	.---	.---	4 17.8
Viola reichenbachiana	38---	62---	83 21.5	79 16.5

In terms of phytocoenological classification the plant communities mostly belong to the drier type of association *Fraxino pannonicae-Ulmetum* Soó in Aszód 1936 corr. Soó 1963 described as the sub-association *Fraxino pannonicae-Ulmetum carpinetosum* (Simon 1957) Džatko 1972. Only in damp hollows, the plant communities incline to the sub-association *Fraxineto pannonicae-Ulmetum caricetosum* Soó in Aszód 1963 corr. Soó 1964. At the elevated and only exceptionally flooded sites (hrudy), diagnostic species of the *Carpinion* Issler 1931 association can be found.

The general overview of the studied species is listed in a phytocoenological table (Table 2). The table does not list any species of the vernal aspect. However, the surveys carried out in 1994–2005 included their inventory as well. Vernal plants characteristic for this area are for instance *Ficaria verna* subsp. *bulbifera*, *Anemone ranunculoides*, *Gagea lutea*, *Pulmonaria officinalis*, *Allium ursinum* as well as *Isopyrum thalictroides*.

Data acquisition

The primary phytocoenological surveys were carried out by Průša in 1973 (Cahnov-Soutok) and 1974 (Ranšpurk) (Průša 1985). Permanent research plots (PRP) were subjectively located in order to cover the site variability of the forest reserves. A total of 15 PRP were located in Ranšpurk and 9 in Cahnov-Soutok. Their position was fixed by drawing in the tree situation map, which enables their identification with approximately 2 m accuracy. The plots are circular, 25 m in diameter. In 1994, 2000, and 2005, phytocoenological relevés were repeatedly carried out for these plots.

In the 1970's, vegetation records were made using the Braun-Blanquet 7-point scale (Braun-Blanquet 1964) of abundance and dominance, later followed by the 11-point Zlatník scale (adjusted Braun-Blanquet scale) (Zlatník 1953). The vertical structure of phytocoenoses was classified as follows

(Randuška et al. 1986; Hennekens, Schaminée 2001): (1) Tree layer – high (dominant and co-dominant trees); (2) Tree layer – middle (sub-dominant trees, higher than a half-height of the trees in the main level); (3) Tree layer – low (tree height ranging from 1.30 m to a half-height of co-dominant trees); (4) Shrub layer – high (woody species from 0.20 to 1.30 m in height); (5) Shrub layer – low (woody species up to a height of 0.20 m, individual conifers with at least one lateral shoot, individual broadleaves without cotyledons); (6) Seedling layer; (7) Herb layer. This numerical marking of vegetation layers is used below in this paper. Mosses and lichens were not included.

Data analysis

The changes in phytocoenoses are described at two levels. The first level represents changes in the vertical structure and presence of species from the woody synusia including their projection onto the herb layer. The evolution of the forest structure was described by quantification of the cover of the individual woody levels. The cover of the herb layer and total cover of the woody species were estimated on the site when making the records. The cover ratios of other woody levels were determined by adding up the cover ratios of the species present in relation to the total woody synusia cover. That means $d_1 + d_2 + d_n < C$. The d_{1-n} variables represent the percentage cover of species recorded at the given level, and "C" stands for the overall cover of the trees. Programme Juice 6.4 (Tichý 2002), which enables the merging of species within levels with calculated algorithm assessing the degree of mutual overlap, was not used in this case. The reason is the necessity of converting the cover data into the seven-point Braun-Blanquet scale. While working at the site, the cover ratios of the individual species in the woody levels were estimated with approximately 1% accuracy. Especially on the coarser abundance and dominance scale, the disproportion of species and level coverage is often lost; in the original records, it yields as a result though with a certain inaccuracy due to the estimate. Although the summation of the woody species cover expressed in percentage is rather non-standard, it enables a more detailed recording of the variance of the given level's cover in the given year of survey. To record the onset or decline of the individual woody species within the defined levels, the CCA (canonical correspondence analysis) direct ordinance method was used with the time factor ordinate as a continuous environmental variable. The time determinant was the year in which the given relevé was recorded, and the plot mark served as a covariant variable. This setting of the ordination analysis removed variability between the plots while preserving only variability within the individual plots in time.

The projection of variability in the woody synusia onto the herb synusia was done through relevé scores on 4 ordination axes of DCA (detrended correspondence analysis). For this analysis, woody synusiae of all relevés were used as species data. The woody synusiae were analyzed in the complex level structure of the synusia. The co-ordinate values of relevés on the respective axes were studied relative

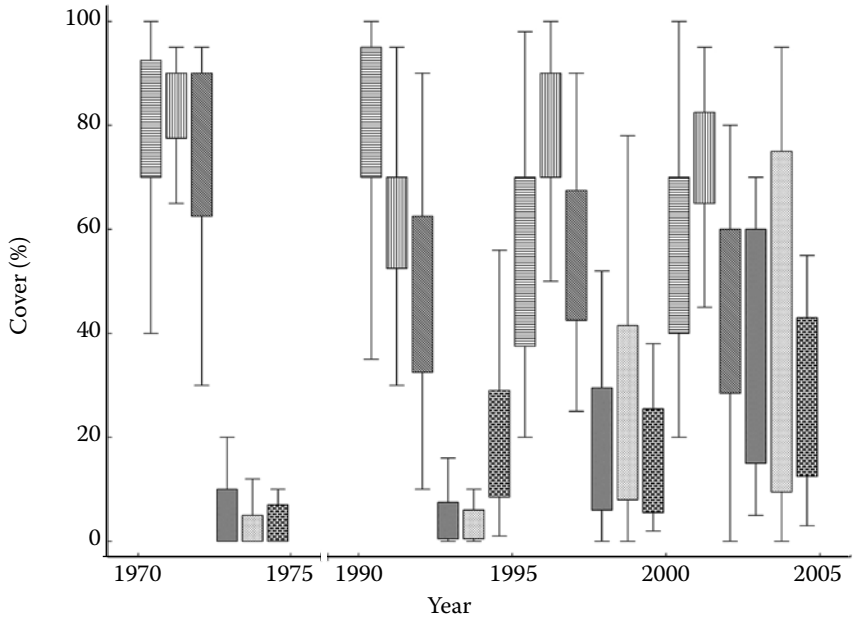

Fig. 1. Percentage values of the herb synusia cover and levels of the woody synusia in the years of repeated surveys. Each survey year is represented by six boxes. Horizontal lining – the extent of recorded covers of the herb layer, vertical lining – the extent of total cover of woody plants, diagonal lining – cover of level 1, grid – cover of level 2, dots – cover of level 3, zip – cover of levels 4 and 5

to the abundance of selected woody species, cover of the individual woody synusia levels, average *EIV*, and Shannon-Wiener index separately for woody and herb synusiae. For this purpose, the unweighted mean of Ellenberg indicator values (*EIV*) calculated by Juice 6.5 was used. The comparison of relevé scores with the characteristics of the woody synusiae suggested which part of the relevé variability is explained by which ordination axis. The values of correlation coefficients of relevé scores on the ordination axes versus herb synusiae characteristics indicate the impact of the given fact on this part of phytocoenosis. The degree of statistical significance was determined by means of *F*-statistics.

The second level represents changes in the herb synusia. The shift of the herb synusia composition over time was studied by CCA in the same way as described above. To determine the potential vegetation change relative to soil water content, the coordinates of individual species on the canonical axis were set out against the respective *EIV* for moisture. By fitting the trend curve, the vegetation shift in time was recorded relative to soil moisture. The mutual dependence of the Ellenberg indicator value of the species and the scores of the given species on the first canonical axis is expressed by the correlation coefficient. The statistical significance was assessed using the *F*-statistics.

A certain complication in the relationship studied in this way is a difference in the quantity of recorded species on the same plots in different years of the survey (Fig. 6), which is sometimes rather large. Generally, it can be stated that most species are characterized by a sensitivity value to the given abiotic factor that is close to the middle of the set scale. With an increasing number of the species, the probability of higher occurrence of *EIV* values signalling minimal or no relation to the given factor is also therefore increasing. That means the study of the phytocoenosis development trends can be influenced by the changing number of species. The unweighted arithmetical mean of *EIV* of the species in the phytocoenological relevé may also, under the given circumstances, suppress the information borne by several more sensitive species. For this reason, the following method was used for the calculation of relevé *EIV*. It counts with the frequency of occurrence of the indicator value as the valuing factor for the calculation of the weighted arithmetical mean of the indicator values of species recorded in the phytocoenological relevé (Schaffers, Sýkora 2000). The *EIV* of relevé herb layers obtained in this way were used for the comparison of values reached in the survey years (Fig. 5). The dependence of the altitude of PRP centres and moisture expressed through the herb synusia *EIV* (Figs. 7 and 8) is also based on the given conversion.

$$EIV_F = \frac{\sum \frac{a_j}{\mathrm{F_j}} I_j}{\sum \frac{a_j}{F_j}}$$

The Ellenberg indicator value of the given relevé EIV_F depends on the value of abundance of each species a_j, its indicator value I_j and frequency of the respective indicator value of the species in the set of all species recorded within the survey F_j.

Although the observed floodplain forest communities grow in the flat broad plain at the confluence of rivers, they differ especially in the composition of the herb layers, according to the degree of their being influenced by the water table height and length of time when water stagnates once the floods drop. The full-area surveys including the updating of maps where the position of standing and fallen trees is indicated (Průša 1985; Vrška et al. 2006), which was carried out using Field Map Technology (www.fieldmap.cz), enabled to create digital terrain models of the studied areas. The accurate data of the measured points (standing tree, ends of fallen trunk, etc.) using stakes of stable height create a network of points (Ranšpurk 7,294 points, Cahnov-Soutok 4,832 points), which

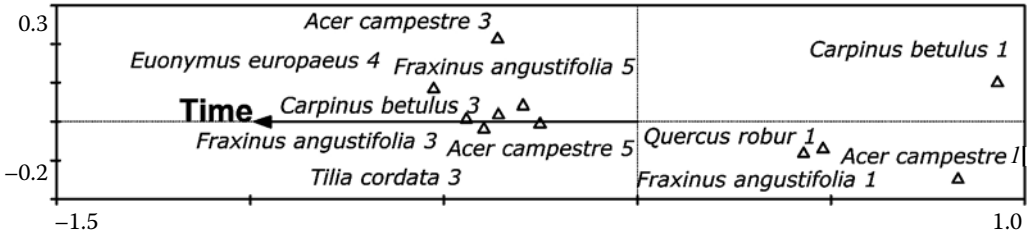

Fig. 2. CCA of woody synusia with the time factor ordinated as a continuous explanatory variable of the environment. Statistical significance of the canonical axis was verified (P = 0.0002). The presence of trees in lower levels increases over time. The continuous main level of the forest, characteristic of the primary survey, gradually disintegrates. The number following the species name stands for the woody synusia layer

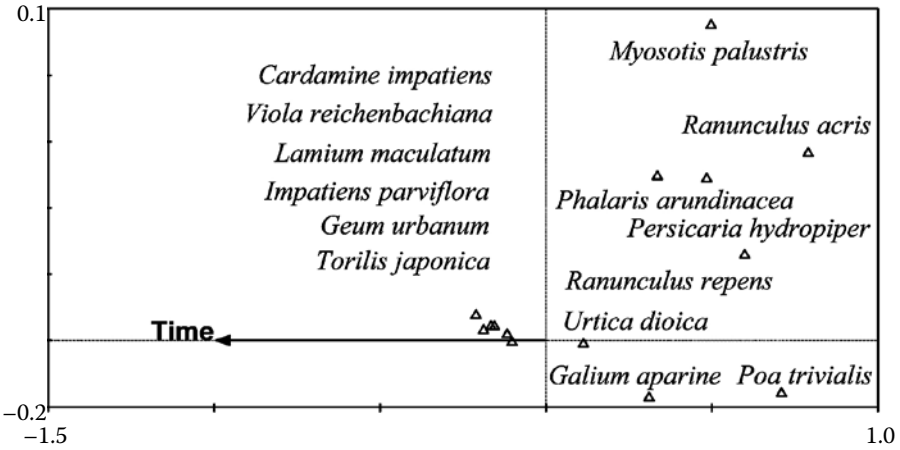

Fig. 3. CCA of herb synusia with the time factor ordinated as a continuous explanatory variable of the environment. Statistical significance of the canonical axis was verified $P = 0.0002$. In the diagram, species with higher demands for water content in soil are usually situated against the direction of time

copy the terrain in a 3D image. The altitude of PRP centres was read off from terrain models produced in this way. Mean *EIV* for relevé herb layers were projected against them, separately for each year of the survey. The trend of herb synusia evolution relative to increasing altitude and time was studied for both areas separately due to a substantial difference in the altitudes of the studied reserves. The statistical significance of differences between the sets of *EIV* values for moisture in survey years was analyzed by one-factor analysis of variance ANOVA.

For the work with phytocoenological data, the software Turboveg for Windows 2.0 (Hennekens, Schaminée 2001) and Juice 6.4 (Tichý 2002) was used. Ordination analyses were carried out in Canoco for Windows 4.5 (ter Braak, Šmilauer 2002; Lepš, Šmilauer 2003) and statistical calculations and their graphical interpretation were done using specialized software Statistica (StatSoft 2004).

RESULTS

Synusia of woody plants and vertical structure of the forest over time

In the 1970's, the woody synusia consisted only of the highest tree level. The other levels usually reached less than 10% cover. Since 1994, the onset of the lowest woody level can be observed, and later surveys show a gradual filling of the vertical structure of the forest (Fig. 1). While the presence of tree species in levels 2–5 increases over time, the presence and woody cover of level 1 drop. The presence of most shrub species does not change significantly over time (Fig. 2). This development is reflected also in the herb layer. The herb cover is initially on the same level of total cover as woody plants. Later on, herbs cover a higher percentage of the forest floor in the PRP than the disintegrating main tree level, as well as the entire woody synusia. The herb synusia reacts to the development of the upper forest levels with a decrease in its cover (Fig. 1).

The woody synusia in the full structure of the partial levels suggests the scores of the individual relevés indicated on the DCA axes. These co-ordinates were studied in relation to selected characteristics of the woody synusia and the herb layer (Table 1). The first axis is characterized by the presence of *Juglans nigra* – it was planted only on a small plot within Ranšpurk. The fourth axis can be characterized in a similar way; it explains the variability of relevés from the perspective of *Quercus robur* presence. Its decreasing distribution is accompanied by a higher share of level 3. The third axis creates a boundary between the two sites. With the increasing share of *Quercus robur* in Cahnov-Soutok compared to Ranšpurk, the share of *EIV* for the moisture and light of woody synusia increases. The reaction of the herb layer to the development of the third ordination axis is statistically insignificant.

From the viewpoint of changes in phytocoenoses over the repeated surveys, the second axis is crucial. It is characterized by increasing diversity in both the woody and the herb synusia. In relation to the structure of the forest, it suggests the recession of layer 1 and a significant increase in the lower levels. When projected onto the herb synusia, the increase in species diversity is clear, as well as the decrease in mean *EIV* relevés in relation to moisture and light.

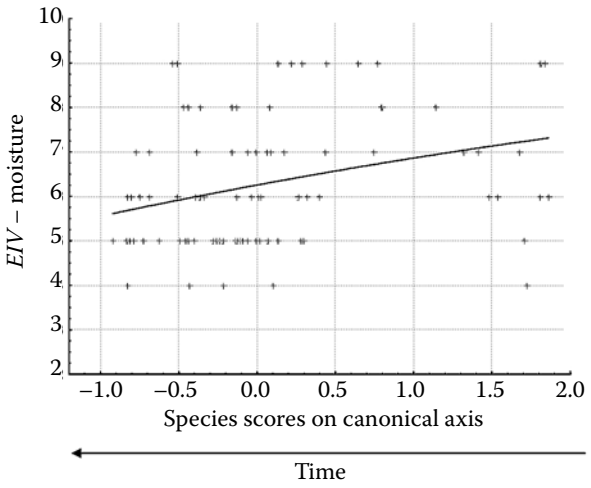

Fig. 4. The co-ordinates of recorded herb species on the canonical axis (time) projected against *EIV* for the moisture of the given species. The fitting of the resulting field of points shows a shift in the species composition of the herb layer. The relation of the species position on the *x* axis and its *EIV* for moisture is statistically significant (correlation coefficient 0.3; $P = 0.002$). An increase in the species number recorded over time is substantial. The more frequent occurrence of species with the value of *EIV* for moisture close to the middle of the assessment scale may significantly influence the development of the represented trend

Changes in the herb synusia

The significant factors influencing the species composition of the herb layer include the height of water table, duration of floods, and length of time when water stagnates at the site after floods recede. The ordination analysis (Fig. 3) suggests the recession of water-demanding species in time, and on the other hand, also an increase in the wood flora species on sites not influenced by water. The drop in soil moisture and its reflection in the species composition of the herb layer are illustrated in Fig. 4.

The relation of *EIV* to the moisture of herbaceous species and their position within the ordination diagram (Fig. 4) is statistically significant (correlation coefficient = 0.3; $P = 0.003$). A decreasing trend is also visible in the *EIV* of herb layers of relevés taken in the sequence of individual survey years (Fig. 5). The degree of their variance decreases in relation to higher *EIV* values. The bottom threshold of the reached *EIV*, however, changes only very slightly. The *EIV*s of phytocoenological relevés were calculated for this purpose in order to eliminate the influence of the varying number of recorded species in the herb layer in different years of the survey (Fig. 6).

The evolution of the herb layer at the sites shows internal differences. It depends on the altitude of the sites and the altitude difference of PRP within the sites. These variables have a significant influence on the water regime at the given micro-site. In Cahnov-Soutok, the converted *EIV* values for moisture in relation to PRP altitude show a similar development in the individual surveys (Fig. 7). In the given respect, none of the input *EIV* value sets represents a statistically significant deviation.

In Ranšpurk, on the other hand, a decrease of the *EIV* values for moisture over time is clearly visible. The most significant is the difference between the values from 1974 and 2005 on sites influenced by water to the greatest extent (Fig. 8). The statistical

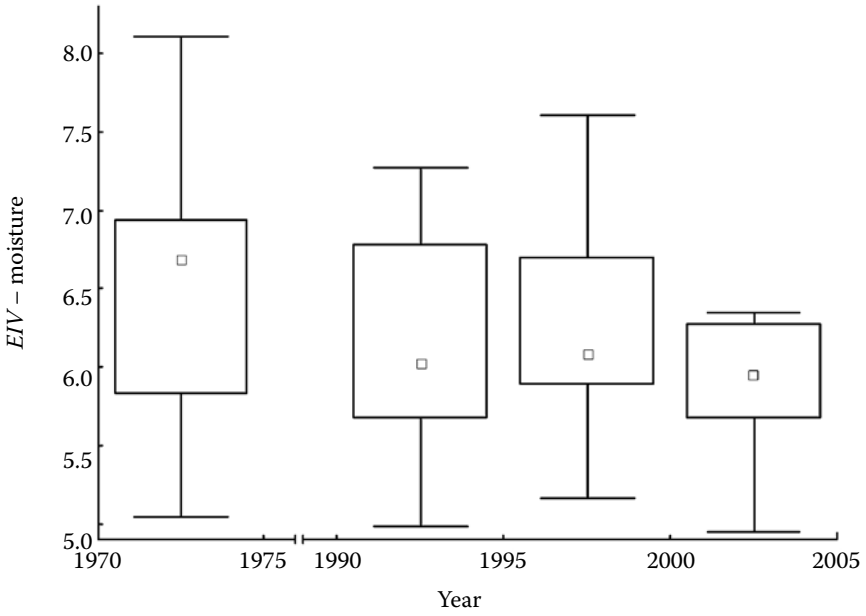

Fig. 5. *EIV* for the moisture of phytocoenological relevés in the survey years. The method used to compose them counted on the frequency of occurrence of the indicator value as a weighting factor for the calculation of weighted arithmetical mean of the indicator values of species recorded in the relevé (Schaffers, Sýkora 2000)

Fig. 6. The difference in the number of recorded species of the herb layer within PRP in the individual survey years exceeds the value of statistical significance ($P < 0.001$)

significance of the difference in input data was verified ($P = 0.01$). Only the surveys carried out in the years 1994 and 2000 are homogeneous.

DISCUSSION

From the perspective of the studied forests, the period between 1973 and 2005 can be described as the time of differentiation of the woody synusia. Its spontaneous onset can be optically visible already during the first years after game was fenced out. The frequently discussed question is the absence of *Quercus robur* regenerating in a natural way. This fact was also highlighted by previous research (Průša 1974; Staněk, Barták 1989). Some authors explain this fact by frequent floods, coming especially in summer (Vyskot 1959; Průša 1974). Surveys carried out 20 and more years after the regular floods ceased, however, have never recorded any growing seedlings of *Quercus robur*. The presence of this tree in lower woody levels therefore remains close to zero. The presence of *Quercus robur* in layer 1 could be explained by its preference by animals grazing in the forest in the past. The speculations whether and to what extent the present view of the natural species composition of the hardwood floodplain forest

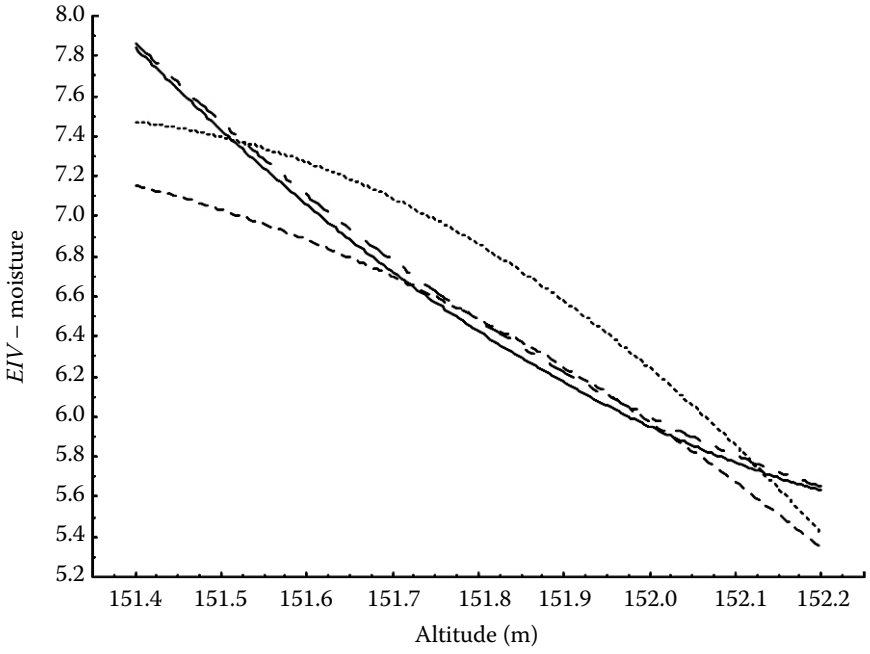

Fig. 7. *EIV* for the moisture of phytocoenological relevés from the Cahnov-Soutok site projected against the altitude of the respective PRP's centres. The curves represent the polynomial fitting of values from the studied years. Full line – 1973, dashed line – 1994, dotted line – 2000, and dash-and-dot line – 2005. To determine *EIV*, the method counted with the frequency of the indicator value occurrence as a weighting factor for the calculation of weighted arithmetical mean of the indicator values of species recorded in the relevé (Schaffers, Sýkora 2000)

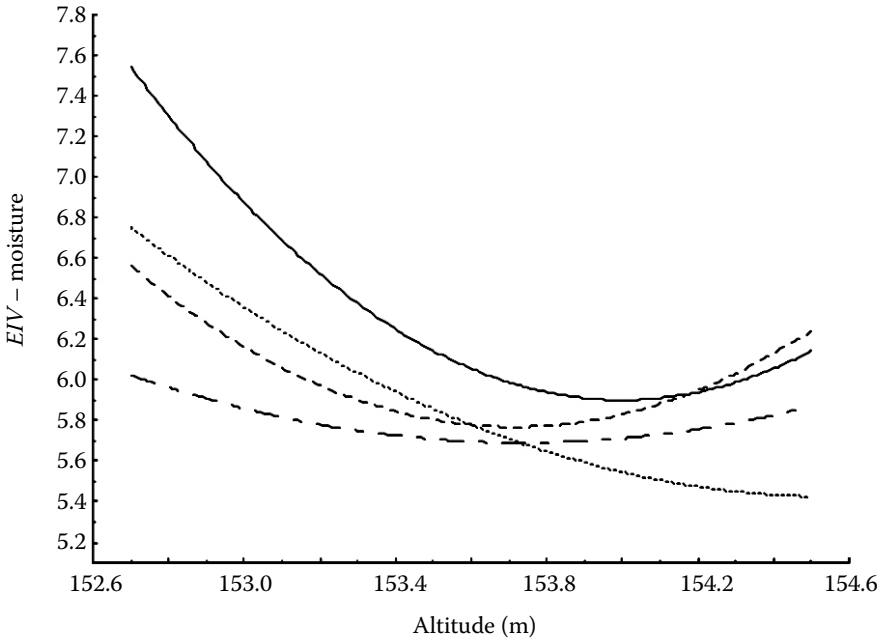

Fig. 8. *EIV* for the moisture of phytocoenological relevés from the Ranšpurk site projected against the altitude of the respective PRPs' centres. The curves represent the polynomial fitting of values from the studied years. Full line – 1973, dashed line – 1994, dotted line – 2000, and dash-and-dot line – 2005. To determine *EIV*, the method counted with the frequency of the indicator value occurrence as a weighting factor for the calculation of weighted arithmetic mean of the indicator values of species recorded in the relevé (Schaffers, Sýkora 2000)

should be reviewed or not are still premature. The species composition of tree regeneration in the studied plots, however, suggests a substantial reduction in the share of *Quercus robur*, at least in the new generation of the main tree level. On the other hand, the presence of other species – *Acer campestre*, *Carpinus betulus*, *Fraxinus angustifolia* subsp. *danubialis,* and *Tilia cordata* in levels 3–5 increases over time. These levels nowadays cover most of the forest floor within the study plots.

The herb synusia, although it lost some of its total cover, shows an increase in the number of recorded species. This could be caused by the climatic development in the respective vegetation seasons as well as mistakes made by those who processed the relevés. The increasing trend in the number of recorded species may, however, also mean the movement of some of the ecological factors. In the case of floodplain forests, one of the most important factors is the height of the water table. The changing character of some of the sites due to its fluctuation may result in increasing space available for the species of a wider range of environmental conditions.

Despite the recorded changes in the species composition of the aestival aspect, there remains a relatively stable vernal aspect. Species such as *Anemone nemorosa, Corydalis cava, Ficaria calthifolia,* or even *Primula veris, Scilla drunensis,* and *Galanthus nivalis,* which are crucial for the determination of the association *Fraxino-pannonicae-Carpinetum* Soó et Borhidi in Soó 1962, were not recorded during the survey. The presence of the given phytocoenological unit in Ranšpurk (Vicherek et al. 2000) therefore cannot be proved.

The assessment of changes in environmental conditions influencing the given forest communities is based on the indicator values of the recorded species relative to the given ecological factors. The results show that the altitude differences between PRP are limiting for the differentiation of the sites within study plots. On the other hand, the speed and intensity with which the phytocoenosis responds to the hydrological conditions of the area depend on the altitude of the locality (Figs. 7 and 8).

Some relations and processes inside the ecosystem were identified through phytoindication (Table 1). The geographically non-fitting *Juglans nigra* was planted only on one of the "hrudy" hillocks in Ranšpurk. With its decreasing presence, *EIV* for moisture and light in the herb synusia increase. The reason is the scarce presence of *Juglans nigra* outside the area of concentrated plantings in Ranšpurk and its total absence in damper and lighter Cahnov-Soutok. A decrease in the presence of *Quercus robur* is accompanied by massive regeneration of *Acer campestre*. The loosening of the canopy due to dying and fall of some of the large oaks is a condition crucial for the development of level 3. The increasing *EIV* for the light and moisture of the herb layer are probably caused by the absence of *Quercus robur* in the open parts of the dampest segments of the studied areas. Changes in the forest structure represented by the second DCA axis are reflected in the herb synusia through the more intensive shading of the forest floor. In reaction to this, species requiring

more light tend to recess. The drop in the presence of species bound to damp areas and increase in the species diversity correspond with the results of the other analyses that were carried out.

References

ANONYMOUS, 1998. World Reference Base for Soil Resources. ISSS-ISRIC-FAO. World Soil Resources Reports, *84*: 1–92.

BRAUN-BLANQUET J., 1964. Pflanzensoziologie. Wien, New York, Springer Verlag.

DEMEK J. et al., 1987. Zeměpisný lexikon ČSR, Hory a nížiny. Praha, Academia.

DRIESSEN P., DECKERS J., SPAARGAREN O., NACHTERGAELE F., 2001. Lecture notes on the major soils of the world. World Soil Resources Reports, *94*: 1–334.

HEJNÝ S., SLAVÍK B. (eds) et al., 1997. Květena České republiky 1. Praha, Academia.

HENNEKENS S.M., SCHAMINÉE J.H.J., 2001. TURBOVEG, a comprehensive data base management system for vegetation data. Journal of Vegetation Science, *12*: 589–591.

HORÁK J., 1969. Rezervace lužního lesa na soutoku Moravy a Dyje. Příloha časopisu Ochrana přírody.

MADĚRA P., 2001. Response of the floodplain forest communities' herb layer to changes in the water regime. Biologia (Bratislava), *56*: 63–72.

MEZERA A., 1956. Středoevropské nížinné luhy I. Praha, ČSAZV, SZN.

MEZERA A., 1958. Středoevropské nížinné luhy II. Praha, ČSAZV, SZN.

MICHÉLI E., SCHAD P. et al., 2006. World reference base for soil resources 2006. World Soil Resources Reports, *103*: 128.

LEPŠ J., ŠMILAUER P., 2003. Multivariate analysis of ecological data using CANOCO. Cambridge, University Press.

PRŮŠA E., 1974. Prales Cahnov. Lesnictví, *20*: 731–756.

PRŮŠA E., 1985. Die böhmischen und mährischen Urwälder. Praha, Academia.

RANDUŠKA D., VOREL J., PLÍVA K., 1986. Fytocenológia a lesnícka typológia. Bratislava, Príroda.

SCHAFFERS A.P., SÝKORA K.V., 2000. Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. Journal of Vegetation Science, *11*: 225–244.

STANĚK T., BARTÁK M., 1989. Strukturální analýza pralesa Cahnov v ekosystému jihomoravského lužního lesa. Lesnictví, *35*: 507–520.

TER BRAAK C.J.F, ŠMILAUER P., 2002. CANOCO Reference manual and CanoDraw for Windows Users guide: Software for Canonical Community Ordination (version 4.5). Ithaca, Microcomputer Power.

TICHÝ L., 2002. JUICE, software for vegetation classification. Journal of Vegetation Science, *13*: 451–453.

VIEWEGH J., 2002. South-Moravian floodplain forest herb vegetation in the period 1978–1997. Journal of Forest Science, *48*: 88–92.

VICHEREK J. et al., 2000. Flóra a vegetace na soutoku Moravy a Dyje. Brno, Masarykova univerzita.

VRŠKA T., 1997. Prales Cahnov po 21 letech (1973–1994). Lesnictví-Forestry, *43*: 155–180.

VRŠKA T., 1998. Prales Ranšpurk po 21 letech (1973–1994). Lesnictví-Forestry, *44*: 440–453.

VRŠKA T., ADAM D., HORT L., ODEHNALOVÁ P., HORAL D., KRÁL K., 2006. Dynamika vývoje pralesovitých rezervací v ČR II. Praha, Academia.

VYSKOT M., 1959. Druhová a prostorová skladba Lanžhotského pralesa a poměry přirozené obnovy. Lesnictví, *5*: 157–174.

ZLATNÍK A., 1953. Fytocenologie lesa. Praha, SPN.

Received for publication February 26, 2008

Accepted after corrections June 3, 2008

Vývoj přirozených lužních lesů na jižní Moravě v období let 1973–2005

ABSTRAKT: Krajina soutoku řek Moravy a Dyje prochází od poloviny 70. let minulého století výraznými změnami spojenými s poklesem hladiny podzemní vody v důsledku vodohospodářských úprav na obou tocích. I fenomén periodických jarních záplav patří od ukončení melioračních prací minulosti. Reakce lesních ekosystémů na úbytek půdní vlhkosti je v práci hodnocena prostřednictvím změn v druhovém složení bylinného patra a známých nároků jednotlivých zaznamenaných taxonů i celé synuzie bylin na obsah vody v půdě. Výsledky potvrzují, že v čase dochází k úbytku druhů, které jsou na vodu nejnáročnější. Tendence poklesu Ellenbergových indikačních hodnot bylinného patra fytocenologických snímků je pozorovatelná i při zohlednění vlivu rozdílného počtu druhů zaznamenaných na stejných plochách v různých letech šetření. Nejvýraznější změny vykazují nejvlhčí stanoviště, naopak nejstabilnější jsou vyvýšené polohy, tzv. hrúdy. Intenzita změn vegetace roste přímo úměrně s nadmořskou výškou lokalit. Proces proměny některých stanovišť vyvolaný změnou vodního režimu je třeba oddělit od opticky snáze pozorovatelných

změn porostní struktury. Limitním faktorem jejího rozvoje je v daných podmínkách lesní zvěř. Po vyloučení jejího vlivu dochází k výškové diferenciaci synuzie dřevin. Kvalitativní posun představuje ústup dříve dominantního *Quercus robur* v hlavní etáži a jeho postupné nahrazování ostatními druhy. Dopady změn probíhajících v synuzii dřevin na vybrané charakteristiky bylinného patra jsou součástí provedených analýz.

Klíčová slova: lužní les; fytocenóza; synuzie dřevin; synuzie bylin

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