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TRENDS AND CYCLICAL CHANGES IN NATURAL FIR-BEECH FORESTS AT THE NORTH-WESTERN EDGE OF THE CARPATHIANS

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Abstract: The vegetation of natural fir-beech forests on the western edge of the Carpathians was repeatedly surveyed in 1972(4) and 1994(5) on 34 plots in the Razula and Salajka reserves. Concurrently repeated whole-area dendrometric measurements of all live and dead trees were made together with maps of forest development stages. The maps were used to compare vegetation changes. The objective was to assess the tree layer dynamics, to discern vegetation development trends from cyclical changes, and to assess the changes of site conditions through phytoindication.

The fir (*Abies alba*) population showed disrupted continuity of development associated with its pronounced withdrawal and replacement by beech (*Fagus sylvatica*). Rather than a cyclical change, the phenomenon is a trend that can be expected to become more dominant in the future. The reason for the interchange of the two species is seen in a fading response to the medieval colonization of Carpathian ridges connected with the exploitation of local forests for grazing and intensive litter raking.

The herb layer was significantly modelled by changes occurring over time and by the dynamics of forest development stages. Species diversity in Razula was observed to increase. Salajka exhibited an invasion of acidophilous taxa (*Luzula luzuloides*, *Vaccinium myrtillus*) and decreased frequency of demanding taxa (*Galeobdolon montanum*, *Dentaria enneaphyllos*, *Galium odoratum*).

Changes in the coverage of *Dryopteris filix-mas*, *Rubus idaeus* and *Senecio ovatus* were interpreted as cyclical changes. No significant shifts were found in the species diversity between the stages. The herb layer at a disintegration stage was homogenized and exhibited the lowest tendency to gain relative control of the undergrowth; the tendency was highest at the optimum stage.

The stages of forest development exhibited changes in soil nitrogen and soil reaction.

Keywords: *Abies alba*, Developmental dynamics, Ellenberg indicator value, *Fagus sylvatica*, Natural forest

Nomenclature: KUBÁT et al. (2002)

INTRODUCTION

Beech and fir-beech forests represent the dominant community of the potential natural vegetation from the planar to montane zones of Central European temperate forests (BOHN et al. 2002/2003). The main species of these forests are European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* MILL.). The alternation of their dominance is documented to have occurred already in the period of 6900–6000 BP (VAN DER KNAAP et al. 2004). A further dominance (3000–4000 BP) of *Fagus sylvatica* and *Abies alba* in the mid-elevations of Central Europe and in the concerned area (the Moravsko-Slezské Beskydy Mts.) was described by RYBNÍČEK & RYBNÍČKOVÁ (1995, 2004) and by POKORNÝ (2002) on the basis of palaeobotanical data.

Based on tree layer studies in near-natural fir-beech forests a theory of the "small developmental cycle" of the temperate mixed forest was developed (LEIBUNDGUT 1993, OTTO 1994, KORPEĽ 1995). The model was further slightly modified according to regional conditions (cf. PODLASKI 2004). The field distinction of developmental stages and phases dwells on the tree layer dynamics (LEIBUNDGUT 1993, OTTO 1994, KORPEĽ 1995). In the climax type of natural fir-beech forest, three developmental stages are distinguished, which markedly differ in live-dead wood volumes and in their proportions. At the growth stage (duration ca. 50–100 years) the volume of live wood is increasing and the volume of dead wood is decreasing. At the optimum stage (duration ca. 40–80 years) the volume of live wood is culminating while the volume of dead wood is at minimum. At the disintegration stage (duration ca. 50–100 years) the volume of dead wood is gradually increasing and the volume of live wood is decreasing. The stages of development break further down into phases that characterize different variants of development within the respective stages (e.g., disintegration stage – phase of expiration) (OTTO 1994, KORPEĽ 1995, PODLASKI 2004). The distinction of developmental stages and phases has been made by visual estimation until the 1990s (LEIBUNDGUT 1959). The procedures we use today are more exact; they include e.g., dendrochronological analyses (PODLASKI 2004) and statistical methods (PODLASKI 2006). The latest methods make use of maps of repeatedly measured trees (VRŠKA et al. 2006) in which the tree layer (dendromass) dynamics can be visualized. It is exactly the tree layer dynamics that is a determining factor in the distinction of individual stages and their partial phases.

Fundamental works concerned with the cyclical development of fir-beech forests dwelled on the study of tree layer dynamics. LEIBUNDGUT (1993) for example studied tree layer dynamics in four fir-beech localities of European importance (Boubín – Czech Republic, Dobroč – Slovak Republic, Pečka – Slovenia, Peručica – Bosnia and Herzegovina), demonstrating beech/fir alternation and the decreasing representation of fir. Similarly, KORPEĽ (1995) evaluated a 40-year series of repeated measurements in the four most preserved fir-beech forest reserves in the Northern and Western Carpathians, documenting an overall decrease of fir and increasing representation of beech and understanding the exchange as a part of the cyclical development. Vegetation changes in the same localities were also studied by UJHÁZY et al. (2005) who demonstrated a correlation of some herb layer species with the developmental stages of the natural fir-beech forest. Of the latest works, PODLASKI (2004), JAWORSKI et al. (2002) and SZWAGRZYK & SZEWCZYK (2001) showed the decreasing representation of fir and the invasion of beech in the Polish part of the Carpathians, interpreting the change as a cyclical development.

A range of studies on the dynamics of beech- and fir-beech forests, based on phytosociological relevés, have brought new information about developmental trends. However, the studies have been made not only in natural forests but also in forests under long-term management schemes. For example VIEWEGH (1999) demonstrated changes in forest vegetation composition in the Western Carpathians, interpreting them as a trend caused by anthropogenic impacts. MAYCOCK et al. (2000) described trends in the changing representation of fir, beech and spruce in relation to individual ecological factors, which are not of a cyclical character and cannot be unambiguously limited in time. HÉDL (2004a) assessed vegetation changes occurring in the long-term managed beech woods of the Rychlebské hory Mts. after 60 years and interpreted them as the consequence of change in ecological conditions – mainly soil acidification and nutrient leaching.

The works dealing with the developmental trends do not assess cyclical changes – and can hardly do so, being worked out as syntheses from managed forests. Conversely, it is evident that most works dealing with the cyclical development of natural forests do not assess possible linear trends in the development of communities. Only in one case the distinction of trends and (cyclical) developmental processes was studied by LIU & BRAKENHIELM (1996) who repeatedly studied the vegetation of natural mixed and coniferous forests in Sweden, interpreting the detected changes largely as being under the influence of natural processes (cyclical development) – not a trend.

However, the above works (exception LIU & BRAKENHIELM 1996) concerned with the cyclical development of the forest did not take into account either the former human impact (grazing in the forest, litter raking) or the existing secondary impacts (depositions of sulphur and nitrogen compounds in the soil, excessive game stock, minimum number of predators, etc.). Especially the natural fir-beech forests of the Carpathians, and hence also their dynamics within the small developmental cycle, have been considerably affected by humans since the medieval times. The Wallachian colonization that progressed along the rounded Western Carpathian ridges, the greater part of which did not reach the upper forest boundary (unlike the sharp peaks of the Alps beyond the upper forest boundary), had a specific impact. The Wallachian colonization was associated with the pasture of large herds of sheep for which forests on the mountain ridges were stumped. However, the grazing took place also in the surrounding forests that also became subject to litter raking (ZLATNÍK 1934, 1935, ŽALOUDÍK 1966, 1984). The Wallachian colonization of the western edge of the Carpathian belt is documented from the end of the 15th century (ŽALOUDÍK 1966, 1984). This could have had an impact on the course of the cyclical development in beech (*Fagus sylvatica*) and fir (*Abies alba*) forest.

The general hypothesis of the paper dwells on the presumption that it is not only the cyclical development that can be observed in the remainders of natural forests in the Western Carpathians but that there are also some "linear" trends to be discerned there. The paper focuses on (i) tree layer dynamics [changes of beech (*Fagus sylvatica*) and silver fir (*Abies alba*) representation especially], (ii) distinction of the "time-defined" cyclical changes from the "time-unlimited" developmental trends in the herb layer, and (iii) site condition changes detected through phytoindication.

MATERIALS AND METHODS

Study area

The surveys took place in two National Nature Reserves (NNR): Salajka (21.9 ha; under strict protection since 1937), and Razula (23.5 ha; under strict protection since 1933). Both reserves are the best remainders of natural silver fir-beech forests at the north-western edge of the Carpathians. According to long-term repeated measurements (since the 1970s) these reserves offered the best information about the spontaneous development of natural silver-fir beech forests in the Western Carpathians. Therefore, we assume that generalization about the natural processes is possible based on these two forests.

The Carpathians belong to the Central- and Eastern-European region of mixed broadleaved-coniferous forests (OTTO 1994). The westernmost ridges of the Carpathian massif (the Moravsko-Slezské Beskydy Mts. and the Javorníky Mts.; Fig. 1) are situated on the border of the Czech Republic with Slovakia. Average annual precipitation ranges from 1050–1370 mm, the mean annual temperature from 5–6°C (VESECKÝ et al. 1960; www.chmu.cz/meteo/ok/). The Moravsko-Slezské Beskydy Mts. and the Javorníky Mts. are a component part of the sizeable flysh belt of the Western Carpathians. Insertions of argillaceous shales exist between these layers. Skeletic Cambisols and Haplic Cambisols (ANONYMOUS 1998, DRIESSEN et al. 2001) are the predominant soils. The areas are situated on gentle to steep slopes oriented to NE and SE (Salajka), N and NW (Razula). Fir-beech stands are a dominant forest community in this area and contain the most valuable remnants of natural forests in the Western Carpathians. The phytocoenoses can be classified to the associations *Dentario enneaphylli-Fagetum* and *Dentario glandulosae-Fagetum* (ELLENBERG 1996).

Field sampling: developmental stages of the forest

In the tree layer all standing and lying trees with a diameter at breast height (DBH) > 10 cm were mapped across the entire areas of Salajka (1974) and Razula (1972) (PRŮŠA 1985). A comparison with repeated maps (1:1000) from the 1990s (Salajka – 1994, Razula – 1995) provides information about the dynamics of all trees in space and time (increase of living trees, decomposition of dead trees, etc.). It is the main level for the identification of developmental stages and its phases in the maps of trees (VRŠKA 1998, VRŠKA et al. 2001). This information was compared with the visual assessment in the field. After this the stages and phases were plotted into the maps (VRŠKA et al. 2001) over the whole area of the surveyed reserves. Individual permanent sample plots projected into the map of trees were allocated the respective stage. For more robust results, the assessment was made only for three stages of development with no further refinement into phases. The proportions between stages do not markedly differ between the two localities; the share of the disintegration stage slightly increased in the 1990s. The maps of tree positions and the developmental stages and phases were prepared in Arc GIS (http://www.esri.com/) software.

Field sampling: relevés

Vegetation data were collected in the field in the form of circular phytosociological relevés from permanent sample plots, each of 25 m in diameter. The number of plots in the Salajka NNR and Razula NNR was 19 and 15, respectively. The placement of the plots was chosen by E. Průša in the 1970s in such a way that the plots covered the ecological gradients and were therefore representative for the localities (PRŮŠA & HOLUŠA 1976, PRŮŠA 1985). The repeated surveys were made in Razula in 1972 and 1995 (VRŠKA et al. 2001), and in Salajka in 1974 and 1994 (VRŠKA 1998). The plots were precisely localized (with a plot centre determination accuracy of approx. 1 m) according to the maps of trees in the scale 1:1000.

Fig. 1. Location of study areas. Grey shading: the Protected Landscape Area Beskydy. Two studied forest reserves are shown.

Possible bias due to inaccurate relocation or incorrectly established size of plots was eliminated in this way (cf. CHYTRÝ 2001, HÉDL 2004a, VAN DER MAAREL 2005).

The vegetation was recorded in the 1990s using the 11-member ZLATNÍK (1953) scale (an adjusted Braun-Blanquet scale), in the 1970s using the coarser 7-member Braun-Blanquet scale (BRAUN-BLANQUET 1964). The vertical structure of phytocoenoses was classified as follows (cf. 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 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 of height ranging from 0.20 – 1.30 m); 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 further in the paper. Mosses and lichens were not recorded.

Data analysis

Vegetation changes were studied regarding the years of measurement (1970s or 1990s) and between the forest development stages (3 options) using the indices of floristic similarity, diversity, species fidelity, average cover and constancy, and applying multivariate ordination analyses. Species abundance-dominance was quantified using BRAUN-BLANQUET (1964) 7-degree scale.

The qualitative JACCARD (1901) similarity index and its quantitative modification (GLEASON 1920) were used to assess the difference between the years of measurement. Moreover, the Steinhaus quantitative similarity index (MOTYKA 1947) was used for the same purpose. This index effectively reacts to changes of dominant species.

Table 1. Settings of ordination analyses; 68 relevés in all analyses, $N_{species}$ – number of species, CCA – Canonical Correspondence Analysis, DCA – Detrended Correspondence Analysis; vegetation layers: 1 Tree layer – high, 2 Tree layer – middle, 3 Tree layer – low, 4 Shrub layer – high, 5 Shrub layer – low, 6 Seedling layer, 7 Herb layer (see text).

Analysis no.	Analyzed data	$N_{species}$	Analysis type	Transformation	Environmental data	Covariable data
1	All layers	90	CCA	Logarithmic	year of measurement	stage of development
2		90	CCA	Logarithmic	stage of development	year of measurement
3		90	CCA	Logarithmic	stage + year	none
4	Tree species layers	28	CCA	Logarithmic	year of measurement	stage of development
5		28	CCA	Logarithmic	stage of development	year of measurement
6		28	CCA	Logarithmic	stage + year	none
7	Herb layer	62	CCA	Logarithmic	year of measurement	stage of development
8		62	CCA	Logarithmic	stage of development	year of measurement
9		62	CCA	Logarithmic	stage + year	none
10		62	DCA	none	none	none

Taxon fidelity, "phi" coefficient – *sensu* CHYTRÝ et al. (2002), the value of constancy, average cover and the Shannon-Wiener index of diversity (e.g. BEGON et al. 1990) were computed using the Juice 6.2 software (TICHÝ 2002). Shannon-Wiener index values were tested for homogeneity (ANONYMOUS 2000) and then tested by *t*-test and ANOVA analysis (STATSOFT 2003), as well as the values of equitability and the species numbers in relevés.

Ordination analyses (Table 1) were processed in CANOCO for Windows 4.5 and CanoDraw for Windows 4.0 (TER BRAAK & ŠMILAUER 2002, LEPŠ & ŠMILAUER 2003). Tree layers were not compounded. Data transformation was made by a logarithmic transformation according to the formula: $y' = \log(y + 1)$ where " y' " is a quantitative variable of the given taxon introduced into the analysis, and " y " is a percentual value of the taxon coverage determined in the field. The y' values were centred and standardized according to the species and samples. With the exception of the environmental and covariable data application, supplementary data were used in DCA (Table 1, analysis 10); they were tree species layer coverages and year of measurement. The significance of variables was tested using the Monte Carlo test with 4999 permutations. Graphic outputs show scores on the first two axes. Only the most weighted species (inclusion rules in CanoDraw for Windows 4.0) in analyses are shown.

Changes of environmental conditions were studied between the years of measurement and between the stages of forest development using the calculation of Ellenberg indicator values (EIV). EIVs of taxa were used according to ELLENBERG et al. (1992). The possible indirect measurement of site conditions by means of econumbers was verified in a range of studies although the limitations of the approach have also been pointed out (SCHAFFERS & SÝKORA 2000, WAMELINK et al. 2002, 2005, CHYTRÝ et al. 2003, EWALD 2003, SMART & SCOTT 2004). EIVs were tested for homogeneity (ANONYMOUS 2000), the statistical significance of variables being subsequently tested using *t*-tests and ANOVA analysis using Statistica 6.0 (STATSOFT 2003) software.

The critical level of significance in all analyses was set at $\alpha = 0.05$.

Table 2. Variance and its partitioning by CCA explained by year of measurement and stage of development (see Table 1), including different sets of vegetation layers (1–7, delimitation see text). F – test statistics, P – level of significance (Monte Carlo permutation test), explained variabilities represent the partial effect of environmental variables (year, stage) in species data or the common effect of year and stage. Shared effect = common effect of year and stage – partial effect of stage – partial effect of year. The period of measurement and the forest development stage are significant variables in analyses of all vegetation layers, tree layers and herb layers.

Analysis no.	Analyzed data	Environmental data	Covariable data	Explained variability (%)	P-value	F-value
1	All layers	Year	Stage	4.70	0.0002	3.31
2	(1–7)	Stage	Year	4.05	0.0034	1.80
3		Year + stage	/	9.11		
		Shared effect	/	0.36		
4	Tree layers	Year	Stage	6.63	0.0002	4.68
5	(1–6)	Stage	Year	5.15	0.0182	2.09
6		Year + stage	/	12.42		
		Shared effect	/	0.64		
7	Herb layer	Year	Stage	2.95	0.0012	2.09
8	(7)	Stage	Year	3.99	0.0014	2.07
9		Year + stage	/	7.06		
		Shared effect	/	0.11		

RESULTS

Dynamics of tree species

The year of survey is a significant variable (Table 2). The increase of *Fagus sylvatica* frequency in tree layer-1 is markedly high (Table 3 - see Appendix, Fig. 2). Although the frequency of *Abies alba*, *Picea abies* and *Acer pseudoplatanus* slightly increased in this layer, their degrees of cover significantly decreased. The cover shrink is particularly obvious in *Abies alba* (Table 3, Fig. 2) with the species being bound in the tree level namely to the disintegration stage (Table 4). The stages of development are also one of the statistically significant variables (Table 2).

In the middle tree layer (2) the original and nearly equal position of *Fagus sylvatica* and *Abies alba* (assessed by the frequency of occurrence) changes into an unambiguous predominance of *Fagus sylvatica* (Table 3). In the middle tree layer beech is bound particularly to the growth stage and partly also to the disintegration stage (Table 4 – see Appendix, Fig. 3). This layer exhibited a profound decrease of *Picea abies* and *Acer pseudoplatanus* cover between the years of survey (Table 3).

The lower tree layer (3) shows a considerable decrease in the frequency of *Abies alba* in which a decreased degree of coverage was observed similarly as in *Picea abies* and *Fagus sylvatica* (Table 3, Fig. 2). However, the frequency of *Fagus sylvatica* markedly increased. Beech dominates the lower tree layer on nearly all plots in the 1990s. In this layer *Abies alba* is bound to the optimum stage where the values of its cover are very low (Table 4, Figs. 3, 4). Conversely, with its high degree of coverage, *Fagus sylvatica* dominates the lower tree layer at the disintegration stage (Table 4, Figs. 3, 4).

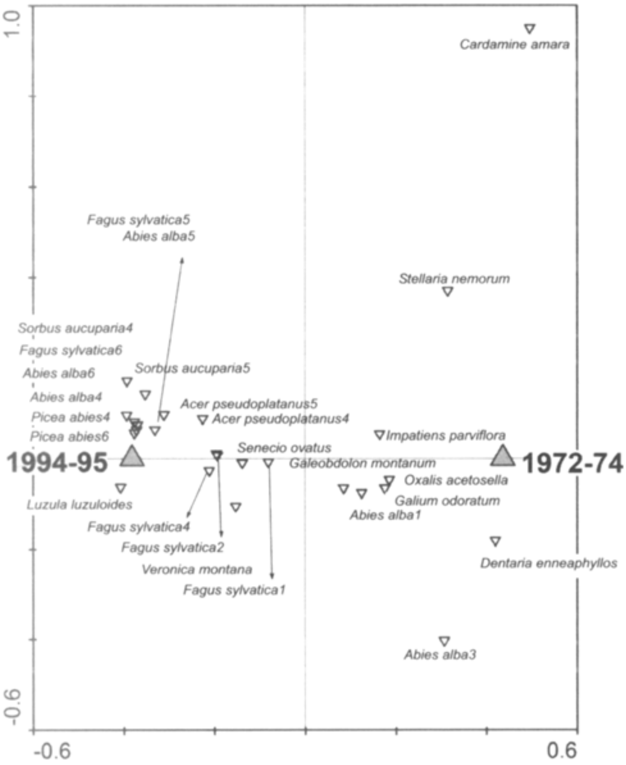

Fig. 2. Vegetation changes between two periods of measurement, with forest development stage as a covariable; CCA analysis of all vegetation layers (Table 1, analysis 1). Species with a fit ≥7% are shown, numbers 1–6 denote vegetation layers (see text). The increase in shrub and seedling (4–6) layers and the increase of *Fagus sylvatica* in tree layers are shown in the 1990s. In contrast, the share of *Abies alba* in the tree layers and the share of some taxa characteristic for base- and nutrient-rich soils (*Galeobdolon montanum*, *Dentaria enneaphyllos*) decrease in the 1990s.

The coverage of shrub layers (4 and 5) considerably increased in the 1990s (Table 3, Figs. 2, 4). Although *Fagus sylvatica* was still dominant, it was increasingly accompanied by *Acer pseudoplatanus*, *Sambucus racemosa* and *Sorbus aucuparia*, at some places newly also by *Abies alba*. A massive invasion of *Fagus sylvatica* was observed at the disintegration stage, the shrub layers however gaining ground also at other stages in the 1990s.

Similarly, the layer of seedlings (6) was taking ground throughout the area in the 1990s across the developmental stages with the frequency of occurrence being higher in *Abies alba* than in *Fagus sylvatica*. The range of species also includes *Acer pseudoplatanus* and *Picea abies*.

Obviously, the dendromass dynamics, and hence the dynamics of the forest developmental stages, is now moderated mainly by *Fagus sylvatica*. In this respect, the long-term gradual replacement of *Abies alba* by *Fagus sylvatica* is a trend possibly reaching beyond the span of the developmental stages. Taking into consideration the different age potential of the two main tree species, this exchange may affect the duration of developmental stages in the future.

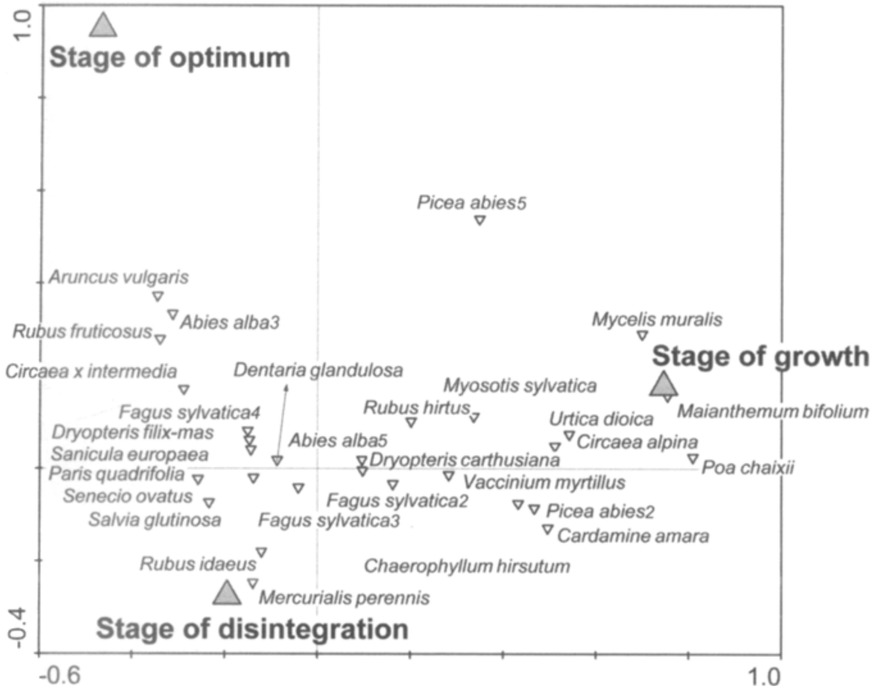

Fig. 3. Differences in vegetation among the forest development stages, with the period of measurement as a covariable; CCA analysis of all vegetation layers (Table 1, analysis 2). Species with a fit ≥ 4% are shown, numbers 1–6 denote vegetation layers (see text). The differences between the forest development stages were found not only in the vertical stand structure (e.g. *Fagus sylvatica* is bound in the middle and lower tree layers to the growth and disintegration stage) but also in the herb species coverage. The forest development cycle particularly connects with the changes in frequency and cover of *Senecio ovatus*, *Dryopteris filix-mas*, *Rubus idaeus*, *Mercurialis perennis* and *Maianthemum bifolium*.

Cyclical changes versus trends in the herb layer

Herb layer variability can be to a greater part explained by water regime and by the coverage of the tree layers (Fig. 5). Hygrophilous taxa occur in Fig. 5 on the 1st non-canonical (i.e., horizontal) axis furthest on the right. The horizontal axis in Fig. 5 covers 14.6% of the total variance. Species with the highest score on this axis are *Equisetum sylvaticum* and *Chaerophyllum hirsutum*, dominating the open and water-affected stands. At the other end, there are shade-tolerant *Oxalis acetosella* and *Dentaria enneaphyllos*. Subsequently, on the vertical axis, the herbaceous undergrowth is differentiated particularly according to the coverage of shrub layers and the year of survey (Fig. 5).

Year of measurement and stage of development were significant variables in the CCA (Table 2, analyses 7 and 8). Changes in the presence of plant taxa between the 1970s and the 1990s are smaller than those in their dominance (Table 7). Dominant species are usually present in relevés from both surveys – changing however profoundly their coverages and finally withdrawing (Steinhaus formula in Table 7). The decreased coverage of some

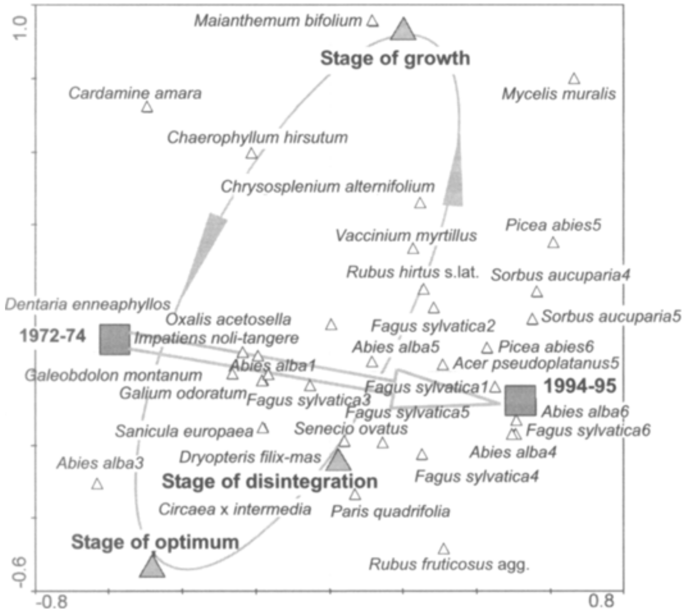

Fig. 4. Species composition explained by the joint effect of the period of measurement and the stage of forest development; CCA analysis of all vegetation layers (Table 1, analysis 3). The grey arrow denotes the trend between the 1970s and 1990s, and grey circle the cyclical change between the three forest stages. Species with a fit ≥ 7% are shown, numbers 1–6 denote vegetation layers (see text). The changes of shrub and seedling (4–6) layers, the changes of *Fagus sylvatica* and *Abies alba* in the tree layers, the changes in share of *Galeobdolon montanum*, *Dentaria enneaphyllos* and *Galium odoratum* relate to developmental trends. The forest development cycle particularly connects with the changes in the cover of tree layers and in the coverage of *Senecio ovatus*, *Dryopteris filix-mas*, *Rubus idaeus*, *Mercurialis perennis* and *Maianthemum bifolium*.

site-specific dominants (*Petasites albus*, *Oxalis acetosella*, *Impatiens noli-tangere*, *Chaerophyllum hirsutum*, Table 3) and the increased species diversity (Tables 3, 5) led to the plot approximation in ordination axes in Fig. 5. The relevés are more similar in the 1990s (Fig. 5). The localities do not develop quite consistently. Salajka shows greater qualitative and smaller quantitative changes than Razula (Table 7). Differences are found between the localities in the development of equitability and also in the number of species. The herb layer in the two localities exhibited an increase of Shannon-Wiener index between the years of survey (Fig. 6, Table 5). The decreasing frequency and cover of *Dentaria enneaphyllos*, *Galeobdolon montanum* and *Galium odoratum* can be considered a definite developmental trend (Table 3, Figs. 2, 4). Conversely, the frequency of *Veronica montana* and *Luzula luzuloides* is increasing (Table 3, Fig. 2).

The optimum stage is the worst floristically separated. Communities at the disintegration stage typically show higher values of Shannon-Wiener index (Table 6), which follows from the combination of higher species diversity and equitability. *Senecio ovatus*, *Dryopteris filix-mas* and *Mercurialis perennis* have a high value of fidelity in this stage (Table 4). In the herbaceous undergrowth of the growth stage, the values of Shannon-Wiener index are

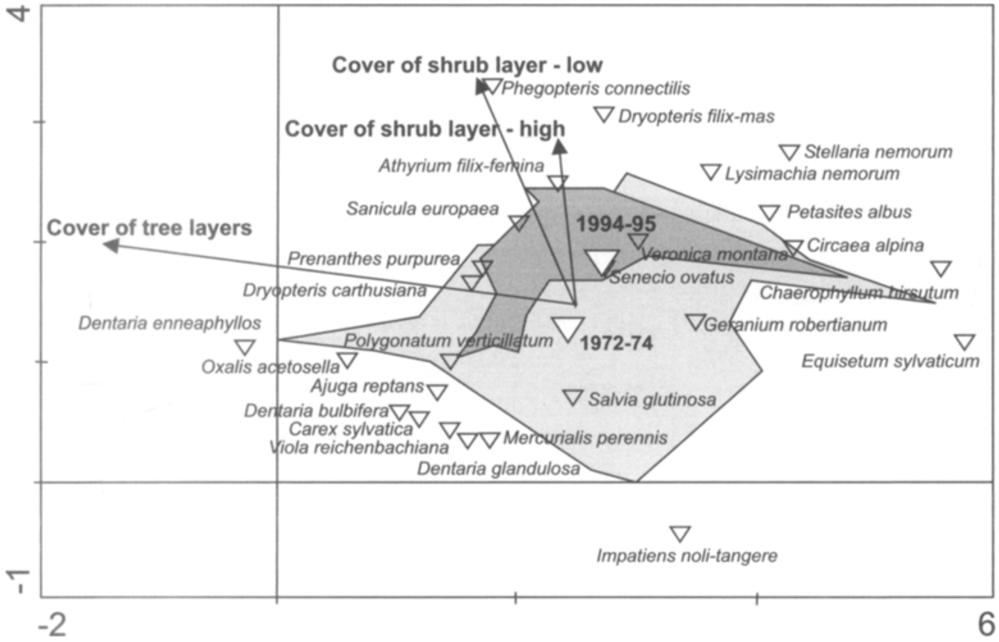

Fig. 5. The first two main directions of variance of the herb layer as plotted on horizontal and vertical axes, respectively, of DCA analysis (Table 1, analysis 10). Supplementary variables are year of measurement and coverage (%) of tree species layers. Species with a weight ≥ 4% are shown. Grey polygons outline the area occupied by the plots of the respective periods (dark grey – 1994–1995, light grey – 1972–1974). Herb layer variability can be particularly explained by water regime (hygrophilous taxa occur furthest to the right) and by the coverage of the tree layers. The relevés are more similar in the 1990s.

suppressed by low species diversity and in that of the optimum stage by low equitability (Table 6). However, none of the two variables was significant among the stages. The herb layer has the lowest average cover at the growth stage (Table 4). The forest development cycle particularly connects with the changes in frequency and cover of *Senecio ovatus*, *Dryopteris filix-mas*, *Rubus idaeus*, *Mercurialis perennis*, *Maianthemum bifolium* (Table 4, Figs. 3, 4).

Changes of environmental conditions

Based on the phytoindication, significantly decreased soil reaction and increased light and temperature were found between the periods of survey in Razula and/or Salajka. Significant changes were found in soil reaction and soil nitrogen between the stages of forest development.

Ellenberg indicator values for light increased between the 1970s and the 1990s at 24 plots, and dropped only in 9 plots. In accordance to this, EIV for temperature significantly increased in Salajka. The species composition of the vegetation does not indicate any changes in soil moisture or soil nitrogen content between the periods of survey. In the other EIVs the localities have not developed quite consistently. Ellenberg indicator values for soil reaction significantly decreased in Salajka (Fig. 6, Table 5). A range of taxa newly recorded in 1994 can be considered acidophytes (*Luzula luzuloides*). In contrast, a pronounced decrease was

Table 5. Parameters of the herb layer vegetation between the years of measurement; number of plots: Razula = 15, Salajka = 19; testing by *t*-test, s.d. – standard deviation, *P* – level of significance ($P < 0.05$ printed in bold), *t* – test statistics, EIV – Ellenberg indicator value. Significant changes were found between periods of measurement in the case of number of species, Shannon-Wiener index, equitability, light, temperature and soil reaction in Razula and/or Salajka.

Locality	Characteristic	Year					
		1972		1995			
		Mean	s.d.	Mean	s.d.	*t*-value	*P*-value
Razula	No. of species	11.1	3.9	15.2	5.4	-3.63	**0.0027**
	Equitability	54.7	5.4	55.0	5.9	-0.12	0.9041
	Shannon-Wiener index	1.9	0.4	2.1	0.4	-2.63	**0.0198**
	Light (EIV)	3.4	0.4	3.6	0.3	-2.26	**0.0401**
	Temperature (EIV)	4.7	0.2	4.8	0.1	-0.99	0.3404
	Moisture (EIV)	5.7	0.3	5.6	0.2	0.88	0.3963
	Soil reaction (EIV)	5.7	0.3	5.8	0.4	-1.31	0.2097
	Soil nitrogen (EIV)	5.7	0.3	5.8	0.2	-1.25	0.2311
		1974		1994			
		Mean	s.d.	Mean	s.d.	*t*-value	*P*-value
Salajka	No. of species	12.9	4.3	13.7	3.9	-0.67	0.5092
	Equitability	56.9	8.6	61.4	6.7	-2.45	**0.0236**
	Shannon-Wiener index	2.0	0.3	2.3	0.3	-2.63	**0.0161**
	Light (EIV)	3.7	0.6	3.9	0.3	-1.80	0.0867
	Temperature (EIV)	4.5	0.2	4.7	0.2	-2.49	**0.0215**
	Moisture (EIV)	5.9	0.6	5.8	0.4	1.24	0.2308
	Soil reaction (EIV)	5.9	0.6	5.3	0.7	4.49	**0.0002**
	Soil nitrogen (EIV)	5.8	0.3	5.7	0.4	0.80	04327

recorded in the frequency and coverage of some taxa characteristic for base- and nutrient-rich forest soils (*Galeobdolon montanum*, *Dentaria enneaphyllos*). The frequency of *Dentaria enneaphyllos* also markedly decreased in Razula but the general trend toward acidification was not demonstrated.

Statistically significant differences were revealed among the developmental stages by single-factor ANOVA analysis in the case of EIV values for nitrogen and soil reaction (Table 6). Similar results (statistically significant EIV for soil reaction and nitrogen) are also provided by the multi-factor ANOVA analysis using the locality or the year of survey as a second factor.

DISCUSSION

Changes of tree species

The results demonstrate a discontinued representation of fir (*Abies alba*) in the vertical stand structure and its long-term withdrawal and replacement by beech (*Fagus sylvatica*). The described changes are interpreted as a trend exceeding one cycle of the forest development. The changes originate from the historical impact of humans, more precisely in the inertial

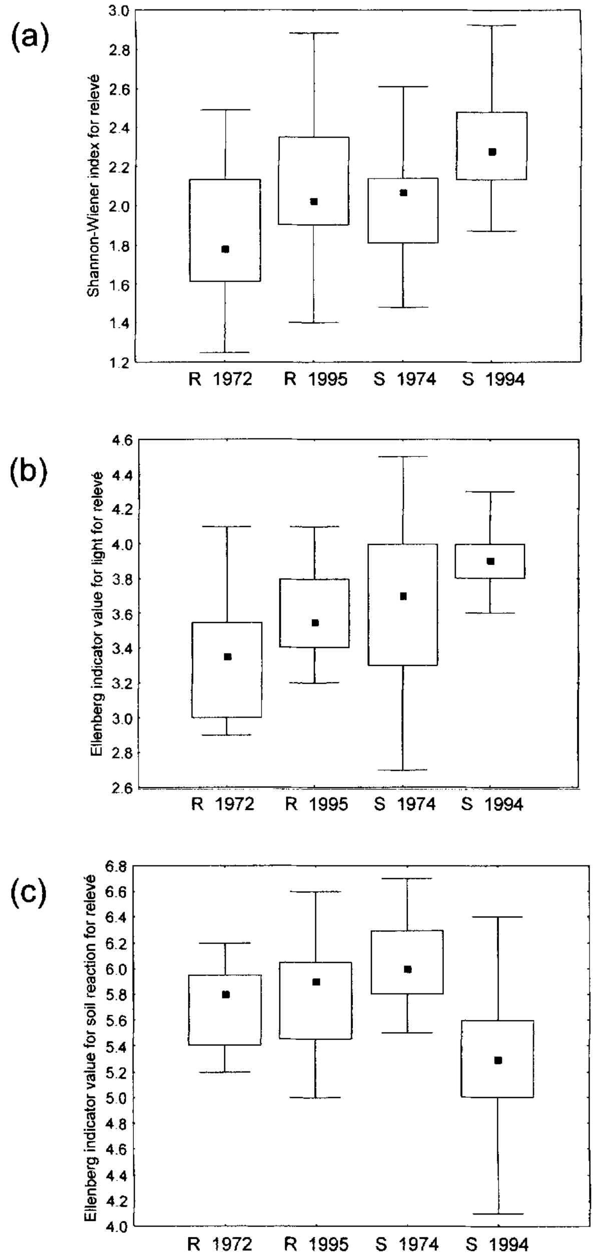

Fig. 6. Herb layer diversity and Ellenberg indicator values (EIV) in dependence on the year of measurement; number of plots: Razula (R) = 15, Salajka (S) = 19, (a) change of Shannon-Wiener index, (b) change of EIV for light, (c) change of EIV for soil reaction. Full squares – median, open boxes – interquartile range (25%–75%), whiskers – non-outlier range (coefficient 1). The herb layer in both localities exhibited an increase of Shannon-Wiener index and an increase of Ellenberg indicator values for light in the 1990s. Ellenberg indicator values for soil reaction significantly decreased in Salajka in the 1990s.

Table 6. Parameters of the herb layer vegetation jointly for Razula and Salajka, among stages of forest development; testing by ANOVA, number of cases: growth stage = 19, optimum stage = 9, disintegration stage = 40; s.d. – standard deviation, P – level of significance ($P < 0.05$ printed in bold), F – test statistics, EIV – Ellenberg indicator value. Significant changes were found between the forest development stages in the case of the soil reaction and soil nitrogen.

	Stage							
	Growth		Optimum		Disintegration			
Characteristic	Mean	s.d.	Mean	s.d.	Mean	s.d.	*F*-value	*P*-value
No. of species	11.2	3.3	13.9	5.0	13.8	4.8	2.376	0.101
Equitability	56.7	8.8	54.1	5.0	58.5	7.1	1.494	0.232
Shannon-Wiener index	1.9	0.3	2.0	0.4	2.2	0.4	3.077	0.053
Light (EIV)	3.6	0.4	3.5	0.3	3.7	0.4	0.965	0.386
Temperature (EIV)	4.6	0.3	4.7	0.1	4.7	0.2	0.480	0.621
Moisture (EIV)	5.8	0.5	5.6	0.2	5.6	0.3	1.575	0.215
Soil reaction (EIV)	5.3	0.7	5.8	0.4	5.7	0.5	3.959	**0.024**
Soil nitrogen (EIV)	5.6	0.4	5.8	0.3	5.8	0.2	5.231	**0.008**

effect of the Wallachian colonization in spite of the forests in question having been left to spontaneous development since the 1930s (PRŮŠA 1985).

Due to sheep grazing and litter raking in the period from the 15th to 19th centuries beech was replaced mostly by fir, which underwent a massive invasion and a rise in the so-called "grazing generation" of fir. Conversely, since the 19th century (actual end of litter gathering and grazing in the forest) fir has been replaced mostly by beech and in our opinion the decline in its representation still has not bottomed out. Moreover, the forest regeneration conditions experienced an essential change in the 19th century – with accumulating litterfall more favourable for beech (litter no longer raked) and hoofed game stock (no longer limited by predators) essentially hampering the natural regeneration of not only fir. The last forty years of the 20th century witnessed a process of fragmentation of the developmental stages – the stand texture was profoundly differentiated due to the disintegration of the "grazing" fir generation, and conditions arose that were favourable for the regeneration of both beech and fir, as seen from the increased cover of shrub layers in the whole-area. Another positive effect was the decrease in hoofed game stock after 1989 (VRŠKA et al. 2000). Other regions, e.g. northern Italy (MOTTA & GARBARINO 2003), or the middle of the Czech Republic (MÁLEK 1962, 1971, 1981) show a similar pattern where the historical disturbance of the developmental cycle of fir-beech forests by humans results in the current dominance of beech in forest stands on the sites of fir-beech forests.

The results found on the basis of repeated phytosociological relevés correlate with the results from the repeated dendrometric measurements of the tree layer (VRŠKA 1998, VRŠKA et al. 2000, 2001).

Cyclical changes versus developmental trend for the herb layer

The herb layer was significantly modelled by changes in time and by the dynamics of forest development changes, i.e., by the dynamics of dominant tree species. Developmental stages (OTTO 1994, KORPEĽ 1995) are a good concept for studying the woody component of the

Table 7. Floristic similarity of phytosociological relevés on plots in Razula and Salajka between the years of measurement; number of plots: 1970s = 34, 1990s = 34; indexes: Jaccard index of qualitative floristic similarity, Gleason index of quantitative floristic similarity, Steinhaus index of quantitative floristic similarity. s.d. – standard deviation. Changes in the presence of plant taxa between the 1970s and 1990s are smaller than those in their dominance. Salajka shows greater qualitative and smaller quantitative changes than Razula.

Locality	Razula		Salajka	
Index	Mean	s.d.	Mean	s.d.
Jaccard	45.47	11.31	41.70	10.54
Gleason	71.39	27.36	81.42	16.20
Steinhaus	37.47	18.50	38.47	21.16

ecosystem, and they seem to be a coarse framework that discloses the broader relations in a discrete study of the herbaceous layer.

Species diversity increased between the years of survey, which is in good agreement with the recent findings of WILD et al. (2004) from the Šumava Mts. but does not correspond with those of HÉDL (2004a), VIEWEGH (1994, 1996), VACEK & LEPŠ (1987, 1991, 1992) and VACEK et al. (1996, 1999) from other regions of the Czech Republic. The most frequently mentioned reason for the decreased species diversity is usually the air pollution load (SMITH 1974, 1981, SCHULTZE 1989, ØKLAND & EILERTSEN 1996, VACEK et al. 1999, NYGAARD & ØDEGAARD 1999). According to VACEK & MATĚJKA (2003), the decrease of species diversity between the years 1951–1970 was followed – after the reduced air pollution load – by the increase of species number. The trend established by us may also relate to the overall regeneration of forests in the study area (Razula) after the suppression of air-pollution concentrations after 1989. The close correlation between species diversity and the soil reaction (BRUNET et al. 1996, BORCHSENIUS et al. 2004) may also be the cause of only an insignificant increase in the species number in Salajka where the EIV value for soil reaction decreased.

No significant difference in species diversity was found among the forest development stages. Similar findings were presented by UJHÁZY et al. (2005) who demonstrated only a very limited turnover of species in the forest development cycle, and by COLLINS & PICKETT (1987) or MOORE & VANKAT (1986) who do not find in the gap (usually the disintegration stage) any markedly higher species diversity than in the none-gap (fully enclosed crown canopy). This does not answer the concepts of REMMERT (1991) who conversely anticipates a dramatically growing species number in the open beech stand at the disintegration stage. The insignificant increase in species between the stages may result from the limited size of gaps in the stands under study, which does not provide for direct insolation of the undergrowth (SAMEK & JAVŮREK 1964, BATELKA 1979, NAKASHIZUKA 1985, DRÖSSLER & VON LÜPKE 2005).

The herb layer at the disintegration stage exhibits the highest values of the Shannon-Wiener index. The tendency to gain the control of the undergrowth by a taxon is lowest here, which apparently demonstrate the results from a wider range of site conditions of these forest stands. Similar findings are reported by AUBERT et al. (2003). Such undergrowth with a number of common taxa appears more homogeneous in vegetation syntheses although the tree layer is considerably diversified. At the optimum stage, the individual taxa of the herb layer show the highest tendency to "relative" capturing of the undergrowth. Different species can dominate in different relevés. As a result of the described tendencies the optimum stage is as a whole the worst separating stage of the development.

The decreased presence and cover of *Dentaria enneaphyllos* is interpreted as a trend and corresponds well with the findings of HÉDL (2004a,b). It is likely to be caused by the change of site conditions (see below). A pronounced decrease was recorded in the share of *Galium odoratum* and *Galeobdolon montanum*, which are considered by UJHÁZY et al. (2005) to be taxa typical of the optimum stage. This was not corroborated by our findings; the decrease in their representation rather suggests a trend. The affinity of ferns toward the fir-beech woods at the growth stage (UJHÁZY et al. 2005) can be with respect to the analyses carried out defined as an affinity to forests with the developed shrub layers, i.e., also to forest stands at the disintegration stage. In line with the findings of UJHÁZY et al. (2005), an increase was observed in the representation of nitrophilous and heliophilous taxa at the disintegration stage (*Senecio ovatus*, *Rubus idaeus*). This change, too, is interpreted by us as a manifestation of the cyclical development of the forest.

Changes in environmental conditions

The significant increase of EIV for light in the 1990s across the developmental stages is likely to be related to trends in the development of tree layers. A total enclosure of the tree canopy has not occurred yet in the process of tree species exchange (namely with *Fagus sylvatica* replacing *Abies alba*), which is also corroborated by the development of shrub layers in the 1990s.

VAN DOBBEN et al. (1999) observed that the decrease of EIV values for soil reaction correlates with the actual course of soil acidification. According to SCHAFFERS & SÝKORA (2000), the course of EIV changes for soil reaction better correspond to Ca content (exchangeable Ca^{2+} plus Ca from carbonates) as compared to the measured soil reaction. The EIV decrease for soil reaction measured by us between the years of survey relates to the withdrawing *Dentaria enneaphyllos*, *Galeobdolon montanum* and *Galium odoratum*. In combination with the expanding *Vaccinium myrtillus* and *Luzula luzuloides* the development can be considered a manifestation of site acidification (Salajka). A similar valuation of the decreased representation of *Dentaria enneaphyllos* was published by HÉDL (2004a,b). FALKENGREN-GRERUP & TYLER (1991) and FALKENGREN-GRERUP (1995) found a positive correlation between soil reaction and the representations of *Galium odoratum*, *Dentaria bulbifera*, *Lamium galeobdolon* and *Mercurialis perennis*, too. In acidification, these taxa were observed to exhibit frequency curves extended towards the low pH sites (FALKENGREN-GRERUP 1990). The profound decrease in the frequency and cover of the mentioned taxa further supports the idea of soil acidification in Salajka. The actual proceeding acidification of forest soils (natural and/or human caused) is documented by the direct measurements of soil characteristics from a number of places in Europe (FALKENGREN-GRERUP & TYLER 1992, BORŮVKA et al. 2005, MLÁDKOVÁ et al. 2005).

VAN DOBBEN et al. (1999) and FALKENGREN-GRERUP & SCHÖTTELNDREIER (2004) observe a close dependence between the soil content of nitrogen (and its forms) and EIV for

N. Conversely, SCHAFFERS & SÝKORA (2000) find relations of low significance between EIV for N and soil characteristics. On the contrary, they can see an obvious dependence with respect to biomass production, which supports the opinion of HILL & CAREY (1997). A similar interpretation of EIV for N changes was published by HÉDL (2004a). The course of EIV values for N measured by us – with the minimum and maximum at the growth stage and at the disintegration stage, respectively – corresponds neither to the course of live dendromass volume nor to the live dendromass increment culmination, the changes being apparently related to the volume of dead wood and conditions of its decomposition (KORPEĽ 1982, KOOP 1989, VRŠKA 1998, VRŠKA et al. 2001). The N-content changes in soils and the changes of humus forms in dependence on the stages of development, age and forest stand structure were described by PONGE & DELHAYE (1995), ARPIN et al. (1998), FISCHER & BINKLEY (2000), AUBERT et al. (2004), GODEFROID et al. (2005), and PALUCH (2005). Similar behaviour to that of EIV values for nitrogen can be seen in EIV values for soil reaction. This apparently also corresponds to the course of dead wood decomposition and to changes in the thickness and forms of organic horizons.

No greater exercise of hygrophilous taxa at the disintegration stage was observed between the stages of forest development, which was supposed by REMMERT (1991). A mild but highly significant increase in EIV for temperature (Salajka) is likely to be caused by local changes the time course of which is not known, but similar trends were not found in Razula. It is unlikely that global warming would play a role in these changes as hypothesized by WILD et al. (2004) for Šumava forests.

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REFERENCES

ANONYMOUS (1998): World reference base for soil resources, ISSS-ISRIC-FAO. *World Soil Resources Reports* 84: 1–92.

ANONYMOUS (2000): *Unistat 5.0 – Statistical package for WindowsTM – User's Guide.* UNISTAT House, London.

ARPIN P., PONGE J.-F., FAILLE A. & BLANDIN P. (1998): Diversity and dynamics of eco-units in the biological reserves of the Fontainebleau (France): Contribution of soil biology to a functional approach. *Eur. J. Soil Biol.* 34: 167–177.

AUBERT M., ALARD D. & BUREAU F. (2003): Diversity of plant assemblages in managed temperate forests: a case study in Normandy (France). *Forest Ecol. Managem.* 175: 321–337.

AUBERT M., BUREAU F., ALARD D. & BARDAT J. (2004): Effect of tree mixture on the humic epipedon and vegetation diversity in managed beech forests (Normandy, France). *Canad. J. Forest Res.* 34: 233–248.

BATELKA J. (1979): Zhodnocení vývoje porostní struktury a dřevinné skladby pralesa Bumbálka (Assessment of the stand structure development and tree species composition in Bumbálka natural forest). *Lesnictví* 25: 531–550.

BEGON M., HARPER J.L. & TOWNSEND C.R. (1990): *Ecology: individuals, populations and communities.* Blackwell, Boston.

BOHN U., NEUHÄUSL R., GOLLUB G., HETTWER C., NEUHÄUSLOVÁ Z., SCHLÜTER H. & WEBER H. (2002/2003): *Karte der natürlichen Vegetation Europas / Map of the Natural Vegetation of Europe. Maßstab / Scale 1:2 500 000.* Landwirtschaftsverlag, Münster.

BORCHSENIUS F., NIELSEN P.K. & LAWESSON J.E. (2004): Vegetation structure and diversity of an ancient temperate deciduous forest in SW Denmark. *Pl. Ecol.* 175: 121–135.

BORŮVKA L., MLÁDKOVÁ L. & DRÁBEK O. (2005): Factors controlling spatial distribution of soil acidification and Al forms in forest soils. *J. Inorg. Biochem.* 99: 1796–1806.

BRAUN-BLANQUET J. (1964): *Pflanzensoziologie.* Springer Verlag, Wien-New York.

BRUNET J., FALKENGREN-GRERUP U. & TYLER G. (1996): Herb layer vegetation of south Swedish beech and oak forests – effects of management and soil acidity during one decade. *Forest Ecol. Managem.* 88: 259–272.

CHYTRÝ M. (2001): Phytosociological data give biased estimates of species richness. *J. Veg. Sci.* 12: 439–444.

CHYTRÝ M., TICHÝ L., HOLT J. & BOTTA-DUKÁT Z. (2002): Determination of diagnostic species with statistical fidelity measures. *J. Veg. Sci.* 13: 79–90.

CHYTRÝ M., TICHÝ L. & ROLEČEK J. (2003): Local and regional patterns of species richness in Central European vegetation types along the pH/calcium gradient. *Folia Geobot.* 38: 429–442.

COLLINS B.S. & PICKETT S.T.A. (1987): Influence of canopy opening on the environment and herb layer in a northern hardwoods forest. *Pl. Ecol.* 70: 3–10.

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.

DRÖSSLER L. & VON LÜPKE B. (2005): Canopy gaps in two virgin beech forest reserves in Slovakia. *J. Forest Sci.* 51: 446–457.

ELLENBERG H., WEBER H.E., DÜLL R., WIRTH W., WERNER W. & PAULIßEN D. (1992): Zeigerwerte von Pflanzen in Mitteleuropa. Ed. 2. *Scripta Geobot.* 18: 258.

ELLENBERG H. (1996): *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht.* Verlag Eugen Ulmer, Stuttgart.

EWALD J. (2003): The sensitivity of Ellenberg indicator values to the completeness of vegetation relevés. *Basic Appl. Ecol.* 4: 507–513.

FALKENGREN-GRERUP U. (1990): Distribution of field-layer species in Swedish deciduous forests in 1929–54 and 1979–88 as related to pH. *Vegetatio* 86: 146–150.

FALKENGREN-GRERUP U. (1995): Long-term changes in flora and vegetation in deciduous forests of southern Sweden. *Ecol. Bull.* 44: 215–226.

FALKENGREN-GRERUP U. & SCHÖTTELNDREIER M. (2004): Vascular plants as indicators of nitrogen enrichment in soil. *Pl. Ecol.* 172: 51–62.

FALKENGREN-GRERUP U. & TYLER G. (1991): Dynamic floristic changes of Swedish beech forest in reation to soil acidity and stand management. *Pl. Ecol.* 95: 149–158.

FALKENGREN-GRERUP U. & TYLER G. (1992): Changes since 1950 of mineral pools in the upper C-horizon of Swedish deciduous forest soils. *Water, Air & Soil pollution* 64: 495–501.

FISCHER R.F. & BINKLEY D. (2000): *Ecology and management of forest soils.* Wiley, New York.

GLEASON H.A. (1920): Some application of the quadrat method. *Bull. Torrey Bot. Club* 47: 21–33.

GODEFROID S., MASSANT W. & KOEDAM N. (2005): Variation in the herb species response and the humus quality across a 200-year chronosequence of beech and oak plantations in Belgium. *Ecography* 28: 223–235.

HÉDL R. (2004a): Vegetation of beech forests in the Rychlebské Mountains, Czech Republic re-inspected after 60 years with assessment of environmental changes. *Pl. Ecol.* 170: 243–265.

HÉDL R. (2004b): Retreat of *Dentaria enneaphyllos* in Rychlebské hory Mts. (Czech Republic) in perspective of habitat preference. *Biologia (Bratislava)* 59: 417–423.

HENNEKENS S.M. & SCHAMINÉE J.H.J. (2001): TURBOVEG, a comprehensive data base management system for vegetation data. *J. Veg. Sci.* 12: 589–591.

HILL M.O. & CAREY P.D. (1997): Prediction of yield in the Rothamsted Park grass experiment by Ellenberg indicator values. *J. Veg. Sci.* 8: 579–586.

JACCARD P. (1901): Étude comparative de la distribution florale dans une portion des Alpes et du Jura. *Bull. Soc. Vaud. Sci. Nat.* 37: 547–579.

JAWORSKI A., KOLODZIEJ Z. & PORADA K. (2002): Structure and dynamics of stands of primeval character in selected areas of the Bieszczady National Park. *J. Forest Sci.* 48: 185–201.

KOOP H. (1989): *Forest Dynamics. SILVI-STAR: A comprehensive monitoring system.* Springer, Berlin.

KORPEĽ Š. (1982): Degree of equilibrium and dynamical changes of the forest on example of natural forests of Slovakia. *Acta Fac. Forest. Zvolen* 24: 9–30.

KORPEĽ Š. (1995): *Die Urwälder der Westkarpaten.* Gustav FISCHER Verlag, Stuttgart-Jena-New York.

KUBÁT K. (ed.) et al. (2002): *Klíč ke květeně České republiky* (*Key to the Flora of the Czech Republic*). Academia, Praha.

LEIBUNDGUT H. (1993): *Europäische Urwälder*. Paul Haupt, Bern.

LEIBUNDGUT H. (1959): Über Zweck und Methodik der Struktur- und Zuwachsanalyse von Urwäldern. *Schweiz. Z. Forstwesen* 110: 111–124.

LEPŠ J. & ŠMILAUER P. (2003): *Multivariate analysis of ecological data using CANOCO*. University Press, Cambridge.

LIU O. & BRAKENHIELM S. (1996): Variability of plant species diversity in Swedish natural forest and its relation to atmospheric deposition. *Pl. Ecol.* 125: 63–72.

MÁLEK J. (1962): *Lesy jihozápadní Moravy* (*The forests of southwestern Moravia*). PhD. Thesis, Vysoká škola zemědělská, Brno.

MÁLEK J. (1971): Vliv pastvy dobytka na přežívání semenáčků a přirozenou obnovu jedle (The influence of livestock grazing on the survival of silver fir seedlings and on the natural regeneration of the silver fir). *Lesnická práce* 50: 543–546.

MÁLEK J. (1981): Problematik der Ökologie der Tanne (*Abies alba* MILL.) und ihres Sterbens in der ČSSR. *Forstwiss. Centralbl.* 100: 170–174.

MAYCOCK P.E., GUZIK J., JANKOVIC J., SHEVERA M. & CARLETON T.J. (2000): Composition, structure and ecological aspects of Mesic Old Growth Carpathian Deciduous Forests of Slovakia, Southern Poland and the Western Ukraine. *Fragm. Florist. Geobot.* 45: 281–321.

MLÁDKOVÁ L., BORŮVKA L. & DRÁBEK O. (2005): Soil properties and toxic aluminium forms in acid forest soils as influenced by the type of stand factors. *Soil Sci. Pl. Nutrition* 51: 741–744.

MOORE M.R. & VANKAT J.L. (1986): Responses of the herb layer to the gap dynamics of a mature beech-maple forest. *Amer. Midl. Naturalist* 115: 336–347.

MOTTA R. & GARBARINO F. (2003): Stand history and its consequence for the present and future dynamic in two silver fir (*Abies alba* MILL.) stands in the high Pesio Valley (Piedmont, Italy). *Ann. Forest Sci.* 60: 361–370.

MOTYKA J. (1947): O celach i metodach badań geobotanicznych (About the goals and methods of geobotanical studies). *Ann. Univ. Mariae Curie-Sklodowska, Sectio C, Supplementum I*, VIII: 1–168.

NAKASHIZUKA T. (1985): Diffused light conditions in canopy gaps in a beech (*Fagus crenata* BLUME) forest. *Oecologia* 66: 472–474.

NYGAARD P.H. & ØDEGAARD T. (1999): Sixty years of vegetation dynamics in a south boreal coniferous forest in southern Norway. *J. Veg. Sci.* 10: 5–16.

ØKLAND R.H. & EILERTSEN O. (1996): Dynamics of undestorey vegetation in a Norwegian boreal coniferous forest, 1988–1993. *J. Veg. Sci.* 7: 747–762.

OTTO H.-J. (1994): *Waldökologie*. Eugen Ulmer Verlag, Stuttgart.

PALUCH J. (2005): Spatial distribution of regeneration in West-Carpathian uneven-aged silver fir forests. *Eur. J. Forest Res.* 124: 47–54.

PODLASKI R. (2004): A development cycle of the forest with fir (*Abies alba* MILL.) and beech (*Fagus sylvatica* L.) in its species composition in the Swietokrzyski National Park. *J. Forest Sci.* 50: 55–66.

PODLASKI R. (2006): Suitability of the selected statistical distributions for fitting diameter data in distinguished development stages and phases of near-natural mixed forests in the Swietokrzyski National Park (Poland). *Forest Ecol. Managem.* 236: 393–402.

PONGE J.F. & DELHAYE L. (1995): The heterogeneity of humus profiles and earthworm communities in a virgin beech forest. *Biol. Fertil. Soils* 20: 20–24.

POKORNÝ P. (2002): Palaeogeography of forest trees in the Czech Republic around 2000 BP: Methodical approach and selected results. *Preslia* 74: 235–246.

PRŮŠA E. & HOLUŠA J. (1976): Prales Razula (Natural forest Razula). *Lesnictví* 22: 343–368.

PRŮŠA E. (1985): *Die böhmischen und mährischen Urwälder – ihre Struktur und Ökologie. Vegetace ČSSR A15*. Academia, Praha.

RANDUŠKA D., VOREL J. & PLÍVA K. (1986): *Fytocenológia a lesnicka typológia* (*Phytocoenology and forest typology*). Príroda, Bratislava.

REMMERT H. (1991): The mosaic-cycle concept of ecosystems – An overview. *Ecol. Stud.* 85: 1–21.

RYBNÍČKOVÁ K. & RYBNÍČKOVÁ E. (1995): Palaeoecological and phytosociological reconstruction of precultural vegetation in the Bílý Kříž area, the Moravskoslezské Beskydy Mts., Slovak Republic. *Veg. Hist. Archeobot.* 4: 161–170.

RYBNÍČEK K. & RYBNÍČKOVÁ E. (2004): Pollen analyses of sediments from the summit of the Praděd range in the Hrubý Jeseník Mts. (Eastern Sudetes). *Preslia* 76: 331–347.

SAMEK V. & JAVŮREK M. (1964): Lesní společenstva rezervace Mionší v Beskydách (Forest plant communities of the Mionší natural forest reserve). *Acta Mus. Silesiae*, series C, III: 11–31.

SCHAFFERS A.P. & SÝKORA K.V. (2000): Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: comparison with field measurements. *J. Veg. Sci.* 11: 225–244.

SCHULTZE E.-D. (1989): Air pollution and forest decline in a spruce (*Picea abies*) forest. *Science* 244: 776–783.

SMART S.M. & SCOTT W.A. (2004): Bias in Ellenberg indicator values – problems with detection of the effect of vegetation type. *J. Veg. Sci.* 15: 843–846.

SMITH W.H. (1974): Air pollution effects on the structure and function of temperate forest ecosystem. *Environm. Pollut.* 6: 111–129.

SMITH W.H. (1981): *Air pollution and forests*. Springer, New York.

STATSOFT INC. (2003): *STATISTICA Cz, version No. 6.* www.StatSoft.com, StatSoft, Inc., Tulsa.

SZWAGRZYK J. & SZEWCZYK J. (2001): Tree mortality and effect of release from competition in an old-growth *Fagus-Abies-Picea* stand. *J. Veg. Sci.* 12: 621–626.

TER BRAAK C.J.F. & ŠMILAUER P. (2002): *CANOCO reference manual and CanoDraw for Windows User's guide: Software for canonical community ordination (version 4.5).* Microcomputer Power, Ithaca.

TICHÝ L. (2002): JUICE, software for vegetation classification. *J. Veg. Sci.* 13: 451–453.

UJHÁZY K., KRIŽOVÁ E., VANČO M., FREŇÁKOVÁ E. & ONDRUŠ M. (2005): Herb layer dynamics of primeval fir-beech forests in central Slovakia. In: COMMARMOT B. & HAMOR F.D. (eds.), *Natural forests in the temperate zone of Europe – values and utilisation*, Swiss Federal Research Institute WSL, Birmensdorf & Carpathian Biosphere Reserve, Rakhiv, pp.193–202.

VACEK S. & LEPŠ J. (1987): Changes in the horizontal structure in a spruce forest over a 9-year period of pollutant exposure in the Krkonoše Mountains, Czechoslovakia. *Forest Ecol. Managem.* 22: 291–295.

VACEK S. & LEPŠ J. (1991): Analýza vegetačních změn v bukových porostech Orlických hor (The analysis of vegetation changes in the Orlické Mts. beech forests). *Lesnictví* 23: 993–1007.

VACEK S. & LEPŠ J. (1992): Analýza vegetačních změn ve smrkových porostech Orlických hor (The analysis of vegetation changes in the Orlické Mts. spruce forests). *Lesnictví* 38: 733–749.

VACEK S. & MATĚJKA K. (2003): Vegetation changes in beech and spruce stands in the Orlické hory Mts. in 1951–2001. *J. Forest Sci.* 49: 445–473.

VACEK S., BASTL M. & LEPŠ J. (1999): Vegetation changes in forests of the Krkonoše Mts. over a period of air pollution stress (1980–1995). *Pl. Ecol.* 143: 1–11.

VACEK S., LEPŠ J. & BASTL M. (1996): Vegetační změny na výzkumných plochách ve smrkových, smrkobukových a bukových porostech v Krkonoších (The Vegetation changes on experimental plots in spruce-beech and beech forests in the Krkonoše Mts.). In: VACEK S. (ed.), *Monitoring, výzkum a management ekosystémů na území Krkonošského národního parku* (*Monitoring, research and management of ecosystems in the Krkonoše Mts. National Park*), Správa Krkonošského národního parku (Krkonoše National Park Administration), Vrchlabí, pp. 114–124.

VAN DER KNAAP W.O., VAN LEEUWEN J.F.N. & AMMANN B. (2004): The first rise and fall of *Fagus sylvatica* and interactions with *Abies alba* at Faulenseemoos (Swiss Plateau) 6900–6000 cal yr BP. *Acta Palaeobot.* 44: 249–266.

VAN DER MAAREL E. (ed.) (2005): *Vegetation ecology*. Blackwell Publishing, Oxford.

VAN DOBBEN H.F., TER BRAAK C.J.F. & DIRKSE G.M. (1999): Undergrowth as a biomonitor for deposition of nitrogen and acidity in pine forest. *Forest Ecol. Managem.* 114: 83–95.

VESECKÝ A., BRIEDOŇ V., KARSKÝ V. & PETROVIČ Š. (1960): *Podnebí Československé socialistické republiky – Tabulky* (*The climate of the Czechoslovak Socialistic Republic – tables*). Hydrometeorologický ústav, Praha.

VIEWEGH J. (1994): Změny ve vegetaci některých přírodních rezervací Moravskoslezských Beskyd (Changes in vegetation of some natural forest reserves in the Moravskoslezské Beskydy Mts.). *Lesnictví-Forestry* 40: 523–536.

VIEWEGH J. (1996): Změny travních dominant v lesních společenstev Beskyd (Changes of grass dominant features in forest communities in the Moravskoslezské Beskydy Mts.). *Zpr. Čes. Bot. Spol. 31, Mater.* 13: 67–69.

VIEWEGH J. (1999): Změny lesních společenstev Moravskoslezských Beskyd v období mezi lety 1970–1986 (Changes of forest plant communities in the Moravskoslezské Beskydy Mts. between 1970–1986). *Zpr. Čes. Bot. Spol. 34, Mater. 17: 103–106.*

VRŠKA T. (1998): Prales Salajka po 20 letech (1974–1994) (Salajka natural forest after 20 years (1974–1994)). *Lesnictví-Forestry* 44: 153–181.

VRŠKA T., HORT L., ODEHNALOVÁ P., ADAM D. & HORAL D. (2000): Prales Mionší – historický vývoj a současný stav (Mionší natural forest – historical development and present state). *J. Forest Sci.* 46: 411–424.

VRŠKA T., HORT L., ODEHNALOVÁ P., ADAM D. & HORAL D. (2001): The Razula virgin forest after 23 years (1972–1995). *J. Forest Sci.* 47: 15–37.

VRŠKA T., HORT L., ODEHNALOVÁ P., ADAM D. & HORAL D. (2006): *Developmental dynamics of virgin forest reserves in the Czech Republic II – Floodplain forests (Cahnov-Soutok, Jiřina, Ranšpurk).* Academia, Praha.

WAMELINK G.W.W., JOOSTEN V., VAN DOBBEN H.F. & BERENDSE F. (2002): Validity of Ellenberg indicator values judged from physico-chemical field measurements. *J. Veg. Sci.* 13: 269–278.

WAMELINK G.W.W., GOEDHART P.W., VAN DOBBEN H.F. & BERENDSE F. (2005): Plant species as predictors of soil pH: Replacing expert judgement with measurements. *J. Veg. Sci.* 16: 461–470.

WILD J., NEUHÄUSLOVÁ Z. & SOFRON J. (2004): Changes of plant species composition in the Šumava spruce forests, SW Bohemia, since 1970. *Forest Ecol. Managem.* 187: 117–132.

ZLATNÍK A. (1934): *Studie o státních lesích na Podkarpatské Rusi. Díl první: Příspěvky k dějinám státních lesů a lesnictví na Podkarpatské Rusi (A study of state forests in Subcarpathian Russia, 1st part – The contributions to the history of state forests and forestry in Subcarpathian Russia).* Ministerstvo zemědělství ČSR, Praha.

ZLATNÍK A. (1935): *Studie o státních lesích na Podkarpatské Rusi. Díl třetí: Vývoj a složení přirozených lesů na Podkarpatské Rusi (A study of state forests in Subcarpathian Russia, 3rd part – Development and composition of natural forests in Subcarpathian Russia).* Ministerstvo zemědělství ČSR, Praha.

ZLATNÍK A. (1953): *Fytocenologie lesa – 1. část (Forest phytocoenology – 1st part).* SPN, Praha.

ŽALOUDÍK V. (1966): *Historie lesů Moravskoslezských Beskyd (A history of forests in the Moravskoslezské Beskydy Mts.).* Ústav pro hospodářskou úpravu lesů, Frýdek-Místek.

ŽALOUDÍK V. (1984): *Historický průzkum lesů bývalého těšínského panství (Historical study of forests of former domain Těšín).* Ústav pro hospodářskou úpravu lesů, Frýdek-Místek.

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Encl.: Appendix – Table 3: pp. 358–359, Table 4: pp. 360–361

Table 3. List of all found plant species sorted by the period of measurement and vegetation layers; species are ordered according to their fidelity. Number of relevés: 1970s = 34, 1990s = 34. Parameters: A – species constancy (%), B – species average cover (%) in non-zero relevés, C – species fidelity (phi coefficient). Fidelity values higher than 10.0 are in bold. In tree layers (1–3) changes particularly in constancy and coverage of *Fagus sylvatica*, *Abies alba* and *Acer pseudoplatanus* were found in the 1990s. In shrub and seedling layers the increase of diversity and coverage were found. In herb layers the increase of species diversity, increase of acidophilous taxa (*Luzula luzuloides*, *Vaccinium myrtillus*) and decrease of *Galeobdolon montanum*, *Dentaria enneaphyllos* and *Galium odoratum* were found in the 1990s.

Year of measurement	1972–74			1994–95		
	A	B	C	A	B	C
Tree layer – high (no. 1)						
Fagus sylvatica	56	27	-	92	31	**41.0**
Picea abies	14	16	-	25	11	**14.0**
Acer pseudoplatanus	3	38	-	6	6	7.0
Abies alba	58	30	-	64	9	5.7
Tree layer – middle (no. 2)						
Abies alba	22	14	3.4	19	3	-
Fagus sylvatica	28	26	-	92	26	**65.1**
Acer pseudoplatanus	3	13	-	6	3	7.0
Picea abies	6	26	-	6	3	-
Tree layer – low (no. 3)						
Abies alba	17	4	**23.4**	3	3	-
Picea abies	8	14	5.5	6	2	-
Fagus sylvatica	86	44	-	97	29	**20.1**
Shrub layer – high (no. 4)						
Fagus sylvatica	14	10	-	75	4	**61.5**
Abies alba	.	.	-	22	2	**35.4**
Acer pseudoplatanus	6	3	-	28	2	**29.8**
Sorbus aucuparia	.	.	-	11	2	**24.3**
Picea abies	.	.	-	8	1	**20.9**
Sambucus racemosa	6	1	-	8	2	5.5
Shrub layer – low (no. 5)						
Sambucus racemosa	3	2	**11.9**	.	.	-
Fagus sylvatica	6	2	-	72	2	**68.4**
Abies alba	8	2	-	75	2	**67.6**
Acer pseudoplatanus	6	2	-	33	1	**35.1**
Sorbus aucuparia	.	.	-	11	1	**24.3**
Picea abies	.	.	-	8	1	**20.9**
Lonicera nigra	3	2	-	6	2	7.0
Seedling layer (no. 6)						
Abies alba	.	.	-	64	2	**68.5**
Fagus sylvatica	.	.	-	53	2	**59.9**
Picea abies	.	.	-	19	1	**32.8**
Acer pseudoplatanus	.	.	-	6	1	**16.9**
Herb layer (no. 7)						
Dentaria enneaphyllos	31	13	**37.3**	3	1	-
Galeobdolon montanum	56	3	**28.2**	28	2	-
Cardamine amara	11	3	**24.3**	.	.	-
Stellaria nemorum	19	4	**21.0**	6	2	-
Luzula sylvatica	6	2	**16.9**	.	.	-
Ranunculus lanuginosus	6	2	**16.9**	.	.	-
Galium odoratum	86	6	**14.0**	75	3	-

Poa chaixii	3	1	**11.9**	.	.	-
Galeopsis speciosa	3	1	**11.9**	.	.	-
Geranium robertianum	31	3	9.5	22	2	-
Circaea × intermedia	14	2	8.8	8	2	-
Mercurialis perennis	22	6	7.0	17	4	-
Dentaria bulbifera	47	2	5.6	42	2	-
Chaerophyllum hirsutum	17	20	3.9	14	4	-
Carex sylvatica	31	3	3.1	28	2	-
Sanicula europaea	42	3	2.8	39	2	-
Senecio ovatus	42	2	-	83	3	**43.0**
Dryopteris filix-mas	31	4	-	61	2	**30.7**
Veronica montana	17	2	-	42	2	**27.5**
Luzula luzuloides	.	.	-	11	1	**24.3**
Dryopteris carthusiana	61	4	-	81	3	**21.4**
Rubus fruticosus agg.	3	1	-	14	1	**20.1**
Vaccinium myrtillus	8	2	-	22	2	**19.3**
Rubus hirtus s.lat.	8	2	-	22	2	**19.3**
Chrysosplenium alternifolium	6	2	-	17	2	**17.7**
Neottia nidus-avis	.	.	-	6	1	**16.9**
Mycelis muralis	.	.	-	6	1	**16.9**
Myosotis sylvatica	.	.	-	6	2	**16.9**
Epilobium montanum	.	.	-	6	1	**16.9**
Glechoma hederacea	.	.	-	6	2	**16.9**
Calamagrostis arundinacea	.	.	-	6	2	**16.9**
Oxalis acetosella	86	19	-	94	2	**14.1**
Stachys sylvatica	6	2	-	14	2	**14.1**
Lysimachia nemorum	14	4	-	25	4	**14.0**
Ajuga reptans	14	1	-	25	2	**14.0**
Athyrium filix-femina	92	9	-	97	8	**12.1**
Actaea spicata	3	3	-	8	1	**12.1**
Pulmonaria obscura	3	3	-	8	2	**12.1**
Thalictrum aquilegiifolium	3	3	-	8	2	**12.1**
Polypodium vulgare	.	.	-	3	1	**11.9**
Equisetum arvense	.	.	-	3	1	**11.9**
Fragaria vesca	.	.	-	3	1	**11.9**
Huperzia selago	.	.	-	3	2	**11.9**
Poa nemoralis	.	.	-	3	1	**11.9**
Brachypodium sylvaticum	.	.	-	3	1	**11.9**
Paris quadrifolia	11	2	-	19	2	**11.6**
Dentaria glandulosa	53	4	-	64	2	**11.3**
Prenanthes purpurea	44	2	-	56	1	**11.1**
Urtica dioica	6	2	-	11	4	**10.1**
Viola reichenbachiana	25	2	-	33	1	9.2
Phegopteris connectilis	8	2	-	14	5	8.8
Impatiens noli-tangere	56	21	-	64	2	8.5
Polygonatum verticilatum	36	2	-	44	2	8.5
Petasites albus	39	26	-	44	11	5.6
Rubus idaeus	19	2	-	22	2	3.4
Euphorbia amygdaloides	17	1	-	17	1	-
Salvia glutinosa	14	5	-	14	2	-
Polystichum aculeatum	11	2	-	11	2	-
Circaea alpina	8	6	-	8	5	-
Gymnocarpium dryopteris	6	1	-	6	2	-
Deschampsia cespitosa	3	2	-	3	2	-
Maianthemum bifolium	3	2	-	3	2	-

Table 4. A list of all plant species found sorted by the stages of forest development and vegetation layers; species are ordered according to their fidelity in stages. Number of relevés: growth stage = 19, optimum stage = 9, disintegration stage = 40. Parameters: A – species constancy (%), B – species average cover (%) in non-zero relevés, C – species fidelity (phi coefficient). Fidelity values higher than 10.0 are in bold. Marked changes in cover of tree and shrub layers were found between the stages of forest development cycle. The herb layer has the lowest average cover at the growth stage, while at the disintegration stage it has the highest species diversity.

Stage of development	Growth			Optimum			Disintegration		
	A	B	C	A	B	C	A	B	C
Tree layer – high (no. 1)									
Fagus sylvatica	74	34	-	78	39	3.8	72	24	-
Picea abies	21	11	-	22	26	1.6	20	11	-
Abies alba	47	16	-	56	33	-	70	18	**20.3**
Acer pseudoplatanus	.	.	-	.	.	-	8	17	**18.0**
Tree layer – middle (no. 2)									
Fagus sylvatica	79	36	**22.0**	11	3	-	65	21	8.0
Picea abies	11	20	**18.5**	.	.	-	2	13	-
Abies alba	16	15	-	.	.	-	30	82	**2.9**
Acer pseudoplatanus	.	.	-	.	.	-	8	61	**8.0**
Tree layer – low (no. 3)									
Abies alba	.	.	-	33	6	**33.7**	8	3	-
Picea abies	5	2	-	22	20	**22.3**	5	2	-
Fagus sylvatica	79	22	-	89	41	-	100	43	**33.7**
Shrub layer – high (no. 4)									
Sorbus aucuparia	11	2	**12.3**	.	.	-	5	2	-
Fagus sylvatica	26	2	-	44	12	-	52	5	**20.2**
Abies alba	5	2	-	.	.	-	15	2	**18.5**
Picea abies	.	.	-	.	.	-	8	1	**18.0**
Sambucus racemosa	5	1	-	.	.	-	10	2	**12.1**
Acer pseudoplatanus	16	2	-	11	1	-	20	2	7.4
Shrub layer – low (no. 5)									
Picea abies	11	2	**18.5**	11	1	**12.7**	.	.	-
Sorbus aucuparia	11	1	**12.3**	.	.	-	5	2	-
Fagus sylvatica	37	2	-	11	2	-	50	2	**21.4**
Lonicera nigra	.	.	-	.	.	-	8	2	**18.0**
Acer pseudoplatanus	21	2	-	.	.	-	25	2	**13.0**
Sambucus racemosa	.	.	-	.	.	-	2	2	**10.2**
Abies alba	53	2	**10.7**	11	2	-	48	2	8.1
Seedling layer (no. 6)									
Picea abies	16	1	**11.3**	.	.	-	10	1	-
Abies alba	26	2	-	11	2	-	40	2	**19.5**
Fagus sylvatica	21	2	-	11	2	-	35	2	**18.8**
Acer pseudoplatanus	.	.	-	.	.	-	5	1	**14.6**
Herb layer (no. 7)									
Mycelis muralis	11	1	**28.0**	.	.	-	.	.	-
Maianthemum bifolium	11	2	**28.0**	.	.	-	.	.	-
Phegopteris connectilis	21	2	**22.0**	.	.	-	8	7	-
Chaerophyllum hirsutum	21	12	**22.0**	.	.	-	8	5	-
Vaccinium myrtillus	26	2	**20.4**	.	.	-	12	2	-
Circaea alpina	16	9	**20.1**	.	.	-	5	2	-
Poa chaixii	5	1	**19.6**	.	.	-	.	.	-
Huperzia selago	5	2	**19.6**	.	.	-	.	.	-

Cardamine amara	11	3	**18.5**	.	.	-	2	3	-
Urtica dioica	11	2	**18.5**	.	.	-	2	1	-
Rubus hirtus s.lat.	26	2	**17.1**	11	2	-	12	2	-
Chrysosplenium alternifolium	16	3	**15.3**	.	.	-	8	1	-
Athyrium filix-femina	100	7	**13.4**	89	13	-	95	9	-
Gymnocarpium dryopteris	11	1	**12.3**	11	2	8.7	2	2	-
Neottia nidus-avis	5	1	8.6	.	.	-	2	1	-
Myosotis sylvatica	5	2	8.6	.	.	-	2	1	-
Ranunculus lanuginosus	5	2	8.6	11	1	**18.9**	.	.	-
Lysimachia nemorum	21	4	8.2	11	2	-	15	4	-
Dryopteris carthusiana	79	5	5.7	67	2	-	75	3	-
Veronica montana	32	2	3.0	22	2	-	30	2	1.5
Geranium robertianum	26	3	1.9	33	3	7.5	22	2	-
Galeopsis speciosa	.	.	-	11	1	**31.3**	.	.	-
Circaea × intermedia	.	.	-	33	2	**29.6**	10	2	-
Dentaria glandulosa	42	2	-	89	2	**21.8**	65	3	8.0
Galium odoratum	63	3	-	100	4	**19.0**	85	5	**12.5**
Luzula sylvatica	.	.	-	11	2	**18.9**	2	1	-
Stellaria nemorum	5	3	-	22	2	**18.4**	8	6	-
Rubus fruticosus agg.	.	.	-	22	2	**18.4**	10	1	5.0
Dentaria enneaphyllos	11	13	-	33	14	**16.1**	18	12	-
Petasites albus	32	28	-	56	12	**13.9**	38	14	-
Polystichum aculeatum	11	2	-	22	2	**12.7**	10	1	-
Prenanthes purpurea	53	2	-	67	2	**10.7**	50	2	-
Sanicula europaea	21	2	-	56	5	**10.2**	50	2	**17.8**
Oxalis acetosella	89	8	-	100	17	9.8	95	10	4.5
Galeobdolon montanum	32	2	-	56	2	9.0	48	3	8.1
Actaea spicata	5	1	-	11	3	8.7	5	2	-
Pulmonaria obscura	5	1	-	11	3	8.7	5	2	-
Salvia glutinosa	.	.	-	22	2	8.3	20	4	**17.9**
Impatiens noli-tangere	47	6	-	67	16	7.4	60	11	6.4
Dentaria bulbifera	37	2	-	56	2	6.6	50	2	7.0
Paris quadrifolia	.	.	-	22	2	6.4	22	2	**20.5**
Euphorbia amygdaloides	16	1	-	22	1	4.7	18	1	-
Viola reichenbachiana	21	2	-	33	2	2.1	35	2	**10.7**
Ajuga reptans	11	2	-	22	1	1.6	25	2	**13.0**
Stachys sylvatica	5	2	-	11	2	1.1	12	2	8.7
Senecio ovatus	32	2	-	44	7	-	80	3	**44.8**
Mercurialis perennis	5	2	-	11	2	-	30	6	**27.8**
Dryopteris filix-mas	26	2	-	44	8	-	60	2	**27.4**
Rubus idaeus	11	1	-	11	1	-	30	2	**22.9**
Thalictrum aquilegiifolium	.	.	-	.	.	-	10	2	**20.9**
Luzula luzuloides	.	.	-	.	.	-	8	1	**18.0**
Epilobium montanum	.	.	-	.	.	-	5	1	**14.6**
Glechoma hederacea	.	.	-	.	.	-	5	2	**14.6**
Calamagrostis arundinacea	.	.	-	.	.	-	5	2	**14.6**
Carex sylvatica	26	2	-	22	8	-	35	2	**10.7**
Polypodium vulgare	.	.	-	.	.	-	2	1	**10.2**
Equisetum arvense	.	.	-	.	.	-	2	1	**10.2**
Fragaria vesca	.	.	-	.	.	-	2	1	**10.2**
Deschampsia cespitosa	.	.	-	.	.	-	2	2	**10.2**
Brachypodium sylvaticum	.	.	-	.	.	-	2	1	**10.2**
Poa nemoralis	.	.	-	.	.	-	2	1	**10.2**
Polygonatum verticillatum	42	2	-	33	2	-	45	2	5.7