

## THE STATE OF FOREST STANDS ON PERMANENT RESEARCH PLOTS IN THE KRKONOŠE MTS. IN YEARS 1976–1997

STAV LESNÍCH POROSTŮ NA VÝZKUMNÝCH PLOCHÁCH V KRKONOŠÍCH V LETECH 1976–1997

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**ABSTRACT:** Health state of maturing and mature Norway spruce (*Picea abies* L.), mixed spruce-beech and beech (*Fagus sylvatica* L.) stands was studied on 32 permanent plots (5th–8th altitudinal vegetation belt, pollution-damage zone A–C) in the Krkonoše Mts. during 1976–1997. Analysis of air pollution and ecological factors was based on reactions of all single trees in the plot stand. Damage (indicated by defoliation) of a tree was classified every year according to Tesař, Temmllová (1971) scale for spruce and to Vacek, Jurásek (1985) scale for beech respective. Changes in the structure of ground (herb and moss) vegetation were studied using classification (TWINSPAN) and ordination (DCA) methods. Results were related to the defoliation process of trees. Three periods of tree damage were distinguished. The first period (1976–1980) was characteristic by slow defoliation. The second one (1981–1988) was the main period of tree damage (increase of defoliation as well as of share of dead trees in the stand, total destruction of several stands was observed). In the last period since 1989, stabilisation of the defoliation increase has been observed. Highest resistance was documented in beech stands, lower in mixed spruce-beech stands, and the lowest in spruce stands. Tree damage was positively correlated with the altitude. Air pollution stress was strengthened by insect pest occurrence.

air pollution; classification; defoliation; *Fagus sylvatica* L.; ground vegetation; health state; mixed stands; ordination; *Picea abies* (L.) Karst.; statistics; transition matrices

**ABSTRAKT:** Zdravotní stav a vegetační dynamika dospívajících a dospělých smrkových, smrkobukových a bukových porostů byly studovány na 32 trvalých výzkumných plochách (5.–8. LVS, pásmo ohrožení A–C) v Krkonoších v letech 1976–1997. Analýza imisně ekologických vlivů vycházela z dendroekologických reakcí jednotlivých stromů v rámci textury porostů. Poškození bylo klasifikováno každoročně podle olistění. Olistění smrku bylo hodnoceno podle Tesaře, Temmllové (1971) a buku podle Vacka, Jurásky (1985) se zvláštním zřetelem na cenotické postavení. Změny přízemní vegetace (bylinné a mechové patro) byly sledovány při užití klasifikačních (TWINSPAN) a ordinačních (DCA) metod. Výsledky byly hodnoceny v souvislosti s probíhajícím procesem defoliace. Podle dynamiky olistění byla v průběhu sledovaných let vylišena tři charakteristická období. V prvním období (léta 1976–1980) došlo k mírnému nárůstu defoliace, ve druhém období (léta 1981–1988) došlo k výraznému poškození stromů a porostů (k nárůstu defoliace stejně jako ke zvětšení podílu mrtvých stromů v porostu, byla pozorována úplná destrukce několika porostů). V posledním období od roku 1989 byla pozorována stabilizace zdravotního stavu. Největší toleranci jevíly bukové porosty, jen mírně nižší smrkobukové porosty a nejmenší smrkové porosty. Poškození porostů většinou narůstalo se stoupající nadmořskou výškou. Imisní stres byl provázen zvýšeným výskytem hmyzích škůdců.

imise; klasifikace; defoliace; *Fagus sylvatica* L.; přízemní vegetace; zdravotní stav; smíšené porosty; ordinace; *Picea abies* (L.) Karst.; statistika; přechodové matice

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## INTRODUCTION

Forests in the Krkonoše National Park have been influenced by air-pollution stresses for almost four decades as it can be supposed from the origin, position and size of pollutant sources. A pollutant stress in the western part of these mountains has probably existed since 1972 as a result of the operation of power stations in the environs of eastern German and south-western Polish frontiers. These power stations emitted ca. 900 kt per annum  $\text{SO}_2$  in the late eighties (Balcar et al., 1994). An increased air-pollution stress is supposed to have existed in the eastern Krkonoše Mts. since 1959 when a power station at Poříčí near Trutnov (EPO II) was launched into operation. Other pollutant sources have impacts on the Krkonoše nature as it is evident from calculations of the share of industrial areas and the particular operations in sulphur deposition in the Krkonoše National Park area (Kurfürst et al., 1991): Turow 18.5%, Počerady 3.6%, Lužice 21.8%, Tušimice I–II 6.4%, Belchatow 3.6%, Prunéřov I–II 7.1%, Walbrzych 1.1%, Komořany 1.5%, Trutnov-Poříčí 1.0%, Litvínov CHEZA 1.8%, Opatovice 0.9%, Leipzig, Halle, Dresden 6.9%, Chvaletice 4.4%, Mělník I–III 4.6%, other sources 16.8%.

The first greater damage to Krkonoše spruce stands appeared after climatic shocks in March 1977 and at the beginning of 1979, and also in connection with a larch bud moth outbreak in 1977–1981 (Vacek, Vašina, 1991). Pollutant effects, accompanied by other negative factors (pathogenic organisms and extreme climatic episodes) resulted in extensive forest decline in the next years (Vacek et al., 1994, 1996). A total of ca. 7000 ha forest stands were felled in the Krkonoše Mts. by so called salvage cuttings (Vacek et al., 1994).

Even though  $\text{SO}_2$  pollution has been decreasing and is expected to decrease in future, forest decline will continue in the next 10–15 years although the level of stand damage has stagnated since 1988–1989 (Vacek, 1995). Soil conditions were substantially altered (soil acidification) and ecological limits for the existence of the present forest stands were exceeded (Vacek, Podrázský, 1994, 1995; Podrázský, 1996). Therefore research on the dynamics of forest stand damage was undertaken. The knowledge of structural processes in forests induced by air-pollution stresses (cf. Vacek et al., 1987, 1988; Vacek, 1990) is necessary to define specific guidelines of their management (Vacek, 1984a).

The present paper is a follow-up of the preceding one (Matějka et al., 1998), in which trends of spruce stand damage in the territory concerned were described as determined by terrestrial observations and evaluated on the base of satellite imagery. Mathematico-statistical processing of data is also the core of this paper. Assessment of transition matrices describing the probability of a change in the evaluation of single tree defoliation from one to another defoliation class was the basic method. A similar procedure was used in preceding pa-

pers (Vacek, 1987a, 1989a; Vacek, Lepš, 1987, 1995, 1996).

Damage of the tree layer in forest stands should be parallelly understood as an element of the change in forest ecosystem influenced by air-pollution stress. Therefore the basic knowledge of the structure of primary producer cenoses which is indicated by vegetation assessment using plant coenological relevés was applied to evaluate defoliation.

## MATERIAL AND METHODS

### EXPERIMENTAL PLOTS

Thirty-two permanent research plots (PRP) established in 1976 and 1980 to study the structure and development of mountain forests were used to examine forest stand health. Research plots in maturing and mature spruce, spruce-beech and beech stands were selected in order to represent the growth conditions of the particular ecosystems (Vacek, 1986a). Tab. I shows basic data on research plots. PRPs are mostly 0.25 ha in size, only the area of PRP 7 is 1.0 ha and PRP 6 is 0.5 ha in size. All PRPs comply with the requirements for long-term research plots.

### VEGETATION CONDITIONS

Plant coenological relevés were obtained by routine procedures in 1976 and 1980 while eleven-grade Domin-Hadač combined scale for abundance and dominance was used. Relevés were taken regularly in five-year intervals in the course of plot observation (in 1980, 1985, 1990, 1995, on PRP 11–15 also in 1976); the respective periods are designated by Nos. 1–4 and 5, respectively). The values of the scale were replaced by the average values of coverage for the separate degrees. Relevés were evaluated by these methods:

1. Evaluation of species diversity indexes in the period of observation: general species diversity (Shannon-Wiener index of species diversity 'H'), total number of species (S) and equitability (e).
2. General developmental trends on groups of plots (spruce, mixed and beech stands, spruce plots PRP 11–15 were evaluated separately due to their different nature) were evaluated from "average" relevés in which the presentation of each species was calculated as average coverage on all plots of the group.
3. Classification of all phytocenological relevés by TWINSpan procedure (Hill, 1979a).
4. Hierarchical agglomerative classification of relevés, average-linkage method; Euclidean distance was used as the dissimilarity measure.
5. Relevé ordination by DCA method (Hill, 1979b); relevés from all plots were used. The most different plots were excluded during the second run of the procedure to avoid inappropriate deformation of ordination space.

I. Summary of the basic properties of permanent research plots (according to working plans, state by 1981)

| Plot name | Forest establishment | Stand     | Woody species (sm - Norway spruce, bk - beech) | Age (years) | Mean height (m) | Mean diameter (cm) | Yield class | Growing stock (m <sup>3</sup> ha <sup>-1</sup> ) | Altitude (m) | Orientation (S - north, V - east, J - south, Z - west) | Inclination (°) | Forest type  | Forest stand group | Pollution-damage zone | Rock                  | Soil type          |
|-----------|----------------------|-----------|--|-------------|-----------------|--------------------|-------------|--|--------------|--|-----------------|--------------|--------------------|-----------------------|-----------------------|--------------------|
| 1+        | U tunelu             | 221 A8    | sm bk  | 105         | 23              | 25                 | 5           | 390  | 730          | JZ   | 26              | 6K5          | 01                 | C                     | biotite granite       | cambisol           |
| 2         | Vilemov              | 415 B16   | sm bk  | 105         | 20              | 20                 | 6           | 40   | 600          | JZ   | 22              | 5Y1          | 01                 | C                     | mica schist phyllite  | ranker             |
| 3++       | U Lubošské bystřiny  | 514 A1    | sm   | 216         | 22              | 32                 | 9           | 185  | 1150         | JZ   | 22              | 8Z1          | 02                 | A                     | granite               | podzol             |
| 4         | Pod Voseckou boudou  | 511 A17   | sm   | 196         | 18              | 30                 | 9           | 250  | 1180         | JZ   | 12              | 8T2          | 02                 | B                     | biotite granite       | organosol, gleysol |
| 5         | Pod Lysou horou      | 508 B17   | sm   | 216         | 22              | 32                 | 9           | 185  | 1130         | S  | 17              | 7T1          | 02                 | B                     | biotite granite       | organosol, gleysol |
| 6         | Bažinky 2            | 311 A17   | sm bk  | 205         | 28              | 48                 | 6           | 260  | 1060         | V  | 22              | 8K3          | 72                 | C                     | gneiss, phyllite      | cambisol           |
| 7         | Bažinky 1            | 311 A17   | sm bk  | 205         | 33              | 58                 | 5           | 110  | 940          | V  | 24              | 6S2 (6H, V2) | 54                 | C                     | gneiss                | cambisol           |
| 8         | Nad Benžinou 2       | 306 C14   | sm bk  | 131         | 24              | 36                 | 6           | 20   | 1190         | JZ   | 24              | 6A6          | 02                 | B                     | biotite granite       | cambisol           |
| 9         | Nad Benžinou 1       | 306 C17   | sm bk  | 141         | 24              | 36                 | 6           | 20   | 1170         | JZ   | 17              | 6A6          | 02                 | B                     | biotite granite       | cambisol           |
| 10        | Pod Vysokým kolem    | 103 E17   | sm   | 185         | 14              | 30                 | 9           | 120  | 1240         | J  | 16              | 8K2 (8R1)    | 02                 | B                     | biotite granite       | podzol, gleysol    |
| 11        | Strná stráň A        | 117 B17   | sm   | 188         | 18              | 30                 | 9           | 170  | 1220         | SV   | 29              | 8Z4          | 02                 | A                     | biotite granite       | podzol             |
| 12        | Strná stráň B        | 117 B17   | sm   | 188         | 18              | 30                 | 9           | 170  | 1170         | SV   | 26              | 8Z4          | 02                 | A                     | biotite granite       | podzol             |
| 13        | Strná stráň C        | 117 C17   | sm   | 186         | 26              | 30                 | 9           | 350  | 1120         | SV   | 23              | 8N1          | 01                 | B                     | biotite granite       | podzol             |
| 14        | Strná stráň D        | 117 C17   | sm   | 186         | 26              | 30                 | 9           | 350  | 1050         | SV   | 24              | 8N1          | 01                 | B                     | biotite granite       | podzol             |
| 15        | Strná stráň E        | 117 C17   | sm   | 186         | 26              | 30                 | 9           | 350  | 990          | SV   | 22              | 8N1          | 01                 | B                     | biotite granite       | podzol             |
| 16        | Pod Martinovkou      | 105 D16   | sm   | 145         | 18              | 27                 | 9           | 250  | 1170         | JV   | 16              | 8K2          | 02                 | B                     | biotite granite       | podzol             |
| 17++      | U Bílého Labe        | 219 A14   | sm   | 122         | 21              | 27                 | 9           | 320  | 1070         | SV   | 29              | 7N1 (8N1)    | 01                 | A                     | biotite granite       | podzol             |
| 18        | U Čertovy strouhy    | 213 A17   | sm   | 169         | 19              | 30                 | 9           | 260  | 1200         | JZ   | 23              | 8N1          | 01                 | A                     | granite               | podzol             |
| 19        | U Klinové boudy      | 310 A16   | sm   | 141         | 19              | 20                 | 8           | 260  | 1170         | JV   | 22              | 8K4 (8Z3)    | 02                 | B                     | mica schist, phyllite | podzol             |
| 20        | Pod Liště horou      | 237 A17   | sm   | 144         | 17              | 34                 | 9           | 150  | 1260         | JZ   | 19              | 8Z4          | 02                 | A                     | mica schist, phyllite | podzol             |
| 21        | Modrý důl            | 233 A13   | sm   | 107         | 13              | 28                 | 9           | 160  | 1230         | J  | 21              | 8Z4 (9K)     | 02                 | B                     | mica schist, phyllite | podzol             |
| 22        | Obří důl             | 234 B16   | sm   | 122         | 15              | 30                 | 9           | 170  | 1160         | V  | 32              | 8Z4 (9K)     | 02                 | B                     | mica schist, phyllite | podzol             |
| 23        | Václavák             | 101 B17   | sm   | 160         | 13              | 29                 | 9           | 100  | 1190         | SV   | 4               | 8R1          | 02                 | B                     | mica schist, phyllite | podzol             |
| 24        | Střední hora         | 330 D17   | sm   | 164         | 21              | 28                 | 8           | 360  | 1250         | JV   | 20              | 8Z3          | 02                 | B                     | mica schist, phyllite | podzol             |
| 25        | Pod Koulí            | 331 A17   | sm   | 165         | 21              | 28                 | 7           | 365  | 1140         | SV   | 28              | 8K9          | 01                 | B                     | mica schist, phyllite | podzol             |
| 26++      | Lysečinský hřeben    | 303 D1    | sm   | 142         | 14              | 18                 | 9           | 248  | 1170         | Z  | 3               | 8Z3          | 02                 | A                     | orthogneiss           | podzol             |
| 27        | U bukoveho pralesa A | 525 C16   | bk   | 147         | 10              | 21                 | 9           | 190  | 1030         | JZ   | 3               | 7K2 (7K3)    | 72                 | B                     | phyllite              | cambisol           |
| 28        | U bukoveho pralesa C | 536 A19   | bk   | 121         | 21              | 33                 | 7           | 280  | 940          | JV   | 15              | 6K5          | 52                 | C                     | phyllite              | cambisol           |
| 29        | U bukoveho pralesa B | 536 A16   | sm bk  | 142         | 25              | 54                 | 5           | 59   | 950          | JV   | 16              | 6S2          | 54                 | C                     | phyllite              | cambisol           |
| 30        | U hadí cesty D       | 542 D16   | bk   | 141         | 27              | 30                 | 6           | 140  | 790          | SV   | 24              | 6D4          | 55                 | C                     | metadiabase           | cambisol           |
| 31        | U hadí cesty F       | 542 C14   | sm bk  | 124         | 24              | 34                 | 6           | 20   | 740          | SV   | 23              | 6B1          | 54                 | C                     | metadiabase           | cambisol           |
| 32        | U hadí cesty E       | 542 B13/5 | sm bk  | 107         | 24              | 25                 | 5           | 5  | 760          | SV   | 35              | 6B9 (6A1)    | 54                 | C                     | metadiabase           | cambisol           |

++ - clear-cutting and reforestation with spruce

Note: + - partial cutting (plot 1 in 1991)

6. The level of vegetation change during the observation period (beginning in 1980) was calculated as the sum of variances of the first DCA  $n$ -axes (one to four axes) (results of relevé ordination from all plots were used) – applying the expression

$$\sqrt{\sum_{i=1}^n \text{var}(DCA_{.ij})}$$

Random changes occurring on every plot during development and not corresponding to general trends of cenotic structure changes were eliminated in this way.

## STAND HEALTH

The health of forest stands was evaluated with respect to foliage every year in the period (1976)–1981–1997. The method of Tesař, Temmllová (1971) was used for spruce evaluation while classification developed by Vacek, Jurásek (1985) was used for beech evaluation. Average foliage of stand is expressed as an arithmetical mean of foliage of all trees on a plot. Defoliation (complement of foliage to 100%) with special regard to the cenotic position and morphological type of tree-crown was estimated and recorded using six classes of defoliation that correspond to degrees of tree damage:

| Defoliation | Defoliation interval (%) | Average defoliation (%) | Tree attribute     |
|-------------|--------------------------|-------------------------|--------------------|
| 0           | (0–10)                   | 5                       | health             |
| 1           | (10–30)                  | 20                      | moderately damaged |
| 2           | (30–50)                  | 40                      | medium damaged     |
| 3           | (50–70)                  | 60                      | greatly damaged    |
| 4           | (70–100)                 | 85                      | dying back         |
| 5           | 100                      | 100                     | dead               |

Traits describing tree-crown health were also evaluated (damage caused by snow, frost, wood-decaying fungi and insects; cf. Vacek, 1992, 1993).

Degrees of damage were transformed to percent values of defoliation for the purposes of further calculations (average values for a defoliation class). Plot evaluation was based on trends of arithmetical means of defoliation (in per cent) of all living trees present on a plot at the same time (means for defoliation classes 0–4), standard deviations of defoliation and share of dead trees (totally defoliated trees). Each tree species was evaluated separately. General means of foliage of all trees including trees with total defoliation were calculated to evaluate the stand state in general.

Processes of defoliation changes and decline were studied on the basis of calculating transition matrices (cf. Matějka et al., 1998) for the particular defoliation classes, for two successive years in all cases. The matrices (6 x 6 in size) were classified by a hierarchical agglomerative average linkage method while Euclidean

distance of transition matrices was taken as the level of dissimilarity. With regard to the construction and basic characteristics of transition matrices, a maximum theoretically possible distance of two transition matrices is limited by the value

$$D_{\max} = p^{(0)} \sqrt{10}$$

where  $p^{(0)}$  is theoretical maximum of any element of transition matrix (it equals 1; 100 when it is expressed in per cent).

It is to note that there is some probability ( $2\alpha$ ) a tree is classified to the nearest class not to its proper class (Vacek et al., 1996b). Let us consider the situation of two successive years when trees were classified to their “proper classes” in the first year, and with the above mentioned error in the next year while their health state did not change. Transition matrix  $P_\alpha$  instead of the expected unit matrix  $I$  is produced in this case. Their Euclidean distance,  $D(P_\alpha, I)$  is the value insignificant for the difference in two transition matrices evaluated:

$$D(P_\alpha, I) = \alpha \sqrt{22}$$

Classification of transition matrices enabled to determine their types corresponding to classes of the process of defoliation changes and tree dieback. It was important to ask about the sequence of these processes, whether it was possible to define some periods with typical processes (occurring on all plots under observation or on most of them), and about differences in their sequences on the separate plots. The first question is answered by simply describing the separate sequences. Frequencies of the separate types over the years were described to answer the second question. The following statistical analysis of identified sequences was made to answer the last question:

Let  $c_{py}$  be the type of transition matrix on plot  $p$  in year  $y$  (comparing years  $y$  with  $y + 1$ ),  $f_Y(c, y)$  is frequency of type  $c$  in year  $y$  (on all plots) and  $f_p(c, p)$  is frequency of type  $c$  on plot  $p$  (in all years). Let's equate

$$F_Y(y) = \sum_c f_Y(c, y)$$

and

$$F_p(p) = \sum_c f_p(c, p)$$

the sum is calculated through all types  $c$ . The probability  $P(c_{py} = c)$  that the type  $c$  of transition matrix will occur on plot  $p$  in year  $y$  can be expressed by the equation

$$P(c_{py}) = 1 - \left( 1 - \frac{f_Y(c_{py}, y)}{F_Y(y)} \right) \cdot \left( 1 - \frac{f_p(c_{py}, p)}{F_p(p)} \right)$$

It is possible to test a null hypothesis that the sequence of types of transition matrices on plot  $p$  corresponds to the generally occurring sequence within the whole set of plots under observation, in contrast with a hypothesis that this sequence is different. The null





III. Mean relevés for the plot groups: ss (plots 11 to 15), Pi (the other plots with spruce), x (mixed stands) and Fa (plots with beech). Samplings were done in four or five periods

| Abbre-<br>viation                | ss<br>1 | ss<br>2 | ss<br>3 | ss<br>4 | ss<br>5 | Pi<br>1 | Pi<br>2 | Pi<br>3 | Pi<br>4 | x<br>1 | x<br>2 | x<br>3 | x<br>4 | Fa<br>1 | Fa<br>2 | Fa<br>3 | Fa<br>4 |
|----------------------------------|---------|---------|---------|---------|---------|---------|---------|---------|---------|--------|--------|--------|--------|---------|---------|---------|---------|
| <i>Abies alba</i>                | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0.03    |
| <i>Acer pseudoplatanus</i>       | 0.1     | 0.1     | 0.1     | 0.4     | 0.4     | 0       | 0       | 0       | 0       | 0.27   | 0.18   | 0      | 0      | 0.28    | 0.15    | 0.37    | 3.12    |
| <i>Actea spicata</i>             | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.33    | 0.33    | 0.05    | 0.05    |
| <i>Adenostyles alliariae</i>     | 5.9     | 5.9     | 3.7     | 1.8     | 1.2     | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Anthoxanthum odoratum</i>     | 0       | 0       | 0       | 0       | 0       | 0.06    | 0.03    | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Asperula odorata</i>          | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.05   | 0.02   | 0      | 0      | 0.37    | 0.37    | 0.33    | 0.33    |
| <i>Asplenium trichomanes</i>     | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.05    | 0.02    | 0.02    | 0       |
| <i>Athyrium distentifolium</i>   | 18.9    | 19.2    | 25.7    | 29      | 31.3    | 1.35    | 1.49    | 1.77    | 1.79    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Athyrium filix-femina</i>     | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.73   | 0.28   | 0.07   | 0.13   | 1       | 1.07    | 1.53    | 1.93    |
| <i>Betula pendula</i>            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Blechnum spicant</i>          | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.37   | 0.28   | 0.1    | 0.03   | 0       | 0       | 0       | 0       |
| <i>Brachypodium sylvaticum</i>   | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.6     | 1       | 1.75    | 3.25    |
| <i>Calamagrostis arundinacea</i> | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.27   | 0.07   | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Calamagrostis villosa</i>     | 13.6    | 13.6    | 14.8    | 13.2    | 15.4    | 28.61   | 29.26   | 30.24   | 29.31   | 16.15  | 14.27  | 14.18  | 13.1   | 0.13    | 0.35    | 1.22    | 3.25    |
| <i>Caluna vulgaris</i>           | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.06    | 0.14    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Campanula latifolia</i>       | 0       | 0       | 0       | 0       | 0       | 0.04    | 0.01    | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Carex limosa</i>              | 0       | 0       | 0       | 0       | 0       | 0.05    | 0.05    | 0.05    | 0.05    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Carex pauciflora</i>          | 0       | 0       | 0       | 0       | 0       | 0.02    | 0.02    | 0.13    | 0.13    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Carex pilosa</i>              | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0.02   | 0.05   | 0.05   | 0       | 0       | 0       | 0       |
| <i>Cicerbita alpina</i>          | 0.2     | 0.2     | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.07   | 0.02   | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Circaea intermedia</i>        | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0.02   | 0.05   | 0.05   | 0.33    | 0.33    | 0.05    | 0       |
| <i>Dentaria bulbifera</i>        | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0.02   | 0.13    | 0.07    | 0.05    | 0.07    |
| <i>Dentaria enneaphyllos</i>     | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.13   | 0.02   | 0.02   | 0      | 0.52    | 0.52    | 0.2     | 0.17    |
| <i>Deschampsia caespitosa</i>    | 0.1     | 0.1     | 0.8     | 0.8     | 0.8     | 0.66    | 0.77    | 1.15    | 1.49    | 0.13   | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Deschampsia flexuosa</i>      | 9.8     | 9.9     | 8.3     | 7.8     | 5.6     | 23.17   | 20.09   | 20.58   | 20.6    | 6.4    | 4.48   | 5.42   | 3.58   | 2.3     | 2.3     | 4.15    | 4.15    |
| <i>Digitalis purpurea</i>        | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0.05   | 0.02   | 0       | 0       | 0       | 0       |
| <i>Dryopteris dilatata</i>       | 11.4    | 11.4    | 11.4    | 8.2     | 6.9     | 4.22    | 4.03    | 2.27    | 2.49    | 9.47   | 7.58   | 5      | 4.05   | 4.1     | 2.27    | 1.8     | 3.3     |
| <i>Dryopteris filix-mas</i>      | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 1.13   | 0.73   | 0.52   | 0.33   | 9.73    | 8.05    | 5.08    | 5.08    |
| <i>Epilobium montanum</i>        | 0       | 0       | 0       | 0       | 0       | 0       | 0.05    | 0.02    | 0.01    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Eriophorum angustifolium</i>  | 0       | 0       | 0       | 0       | 0       | 0.43    | 0.13    | 0.13    | 0.13    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Eriophorum vaginatum</i>      | 0       | 0       | 0       | 0       | 0       | 0.02    | 0.02    | 0.02    | 0.02    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Fagus sylvatica</i>           | 0.1     | 0.1     | 0.1     | 0       | 0       | 0       | 0       | 0       | 0       | 6.77   | 6.77   | 4.18   | 9.42   | 1.07    | 1.15    | 1.52    | 6.08    |
| <i>Fraxinus excelsior</i>        | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.13    | 0.33    | 0.33    | 0.33    |
| <i>Galeopsis speciosa</i>        | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.02    | 0       | 0       | 0       |
| <i>Galium hercynicum</i>         | 0.4     | 0.4     | 0.6     | 0.9     | 0.8     | 0.25    | 0.22    | 0.11    | 0.11    | 0.05   | 0.05   | 0.05   | 0.02   | 0       | 0       | 0       | 0       |
| <i>Galium saxatile</i>           | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.05   | 0.05   | 0      | 0      | 0       | 0       | 0       | 0       |

Continuation of Tab. II

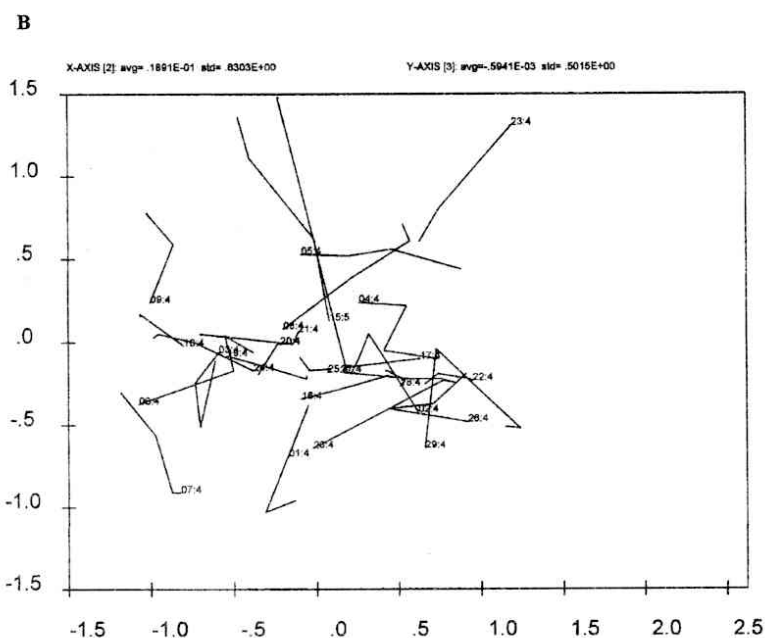
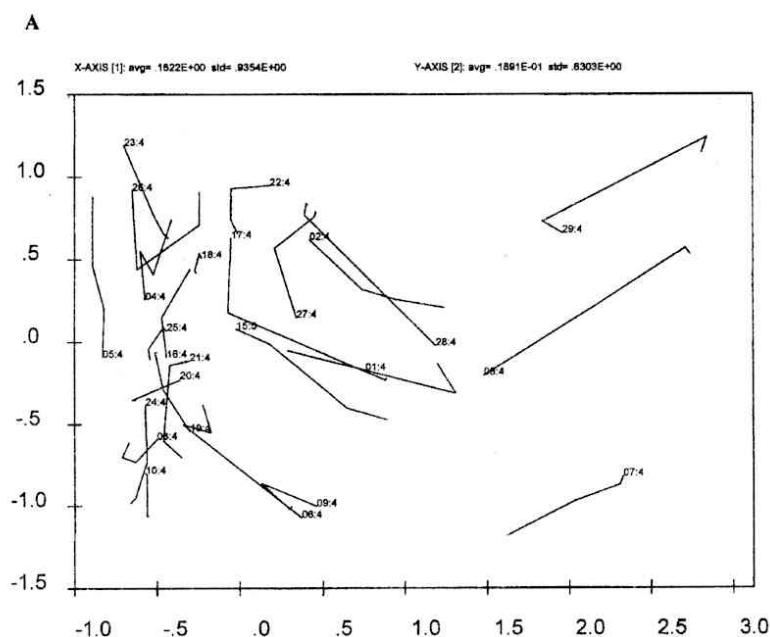
|                                   | Abbre-<br>viation | ss<br>1 | ss<br>2 | ss<br>3 | ss<br>4 | ss<br>5 | Pi<br>1 | Pi<br>2 | Pi<br>3 | Pi<br>4 | x<br>1 | x<br>2 | x<br>3 | x<br>4 | Fa<br>1 | Fa<br>2 | Fa<br>3 | Fa<br>4 |
|-----------------------------------|-------------------|---------|---------|---------|---------|---------|---------|---------|---------|---------|--------|--------|--------|--------|---------|---------|---------|---------|
| <i>Galium sylvaticum</i>          | Galsyl            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.13    | 0.02    | 0       | 0       |
| <i>Gentiana asclepiadea</i>       | Genasc            | 0       | 0       | 0       | 0.1     | 0.8     | 2.79    | 2.87    | 2.37    | 3.41    | 1.13   | 1.33   | 1.33   | 2.08   | 0       | 0       | 0       | 0       |
| <i>Gymnocarpium dryopteris</i>    | Gyndry            | 0.2     | 0.2     | 0.2     | 0       | 0       | 0.01    | 0.01    | 0       | 0       | 4.72   | 4.52   | 1.73   | 1.53   | 1.4     | 1.6     | 1.05    | 1.05    |
| <i>Hieracium laevigatum</i>       | Hielae            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.02    | 0.02    | 0       | 0       |
| <i>Hieracium sylvaticum</i>       | Hiesyl            | 0       | 0       | 0       | 0       | 0       | 0.09    | 0.01    | 0       | 0       | 0.07   | 0.05   | 0      | 0      | 0.42    | 0.13    | 0.05    | 0.02    |
| <i>Homogyne alpina</i>            | Hornalp           | 0.8     | 0.8     | 0.7     | 0.9     | 0.8     | 1.36    | 1.37    | 0.84    | 0.83    | 1.6    | 1.6    | 0.6    | 0.6    | 0.47    | 0.38    | 0.33    | 0.33    |
| <i>Huperzia selago</i>            | Hupsel            | 0.1     | 0.1     | 0.1     | 0       | 0       | 0.23    | 0.05    | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Chaerophyllum hirsutum</i>     | Chahir            | 0.4     | 0.4     | 0.1     | 0       | 0       | 0       | 0       | 0       | 0       | 0.02   | 0.02   | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Chamaenerium angustifolium</i> | Chaaang           | 0       | 0       | 0       | 0.1     | 0.4     | 0       | 0.51    | 0.53    | 0.45    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Juncus effusus</i>             | Juneff            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0.05   | 0.02   | 0       | 0       | 0       | 0       |
| <i>Juncus filiformis</i>          | Junfil            | 0       | 0       | 0       | 0       | 0       | 0.02    | 0.13    | 0.13    | 0.43    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Lanum galeobdolon</i>          | Langal            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.27    | 0.07    | 0.02    | 0.02    |
| <i>Lanum maculatum</i>            | Lannac            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.05   | 0.05   | 0      | 0      | 0.47    | 0.13    | 0.05    | 0       |
| <i>Lanum montanum</i>             | Lannon            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.05   | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Larix decidua</i>              | Lardec            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Lilium martagon</i>            | Lilmar            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.13    | 0.13    | 0.13    | 0.05    |
| <i>Lunaria rediviva</i>           | Lunred            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.05    | 0.05    | 0.02    | 0       |
| <i>Luzula nemorosa</i>            | Luznem            | 0       | 0       | 0       | 0       | 0       | 0.34    | 0.39    | 0.43    | 0.56    | 0.5    | 0.42   | 0.52   | 0.67   | 0.27    | 0.18    | 0.1     | 0.05    |
| <i>Luzula pilosa</i>              | Luzpil            | 0.2     | 0.2     | 0       | 0       | 0       | 0.21    | 0.07    | 0       | 0       | 0      | 0      | 0      | 0      | 0.02    | 0.02    | 0       | 0       |
| <i>Luzula sylvatica</i>           | Luzsyl            | 0       | 0       | 0       | 0       | 0       | 0.18    | 0.15    | 0.21    | 0.28    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Lycopodium annotinum</i>       | Lycann            | 0.2     | 0.2     | 0.2     | 0.4     | 0.4     | 0.48    | 0.19    | 0.17    | 0.27    | 0.33   | 0.33   | 0.33   | 0.33   | 0       | 0       | 0       | 0       |
| <i>Lysimachia nemorum</i>         | Lysnem            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.13   | 0.13   | 0.05   | 0      | 0.35    | 0.35    | 0.05    | 0.05    |
| <i>Maianthemum bifolium</i>       | Maibif            | 0.2     | 0.2     | 0.2     | 0.1     | 0.1     | 0.38    | 0.35    | 0.17    | 0.13    | 1.4    | 1.4    | 0.67   | 0.35   | 2.08    | 2.1     | 2.18    | 2.15    |
| <i>Milium effusum</i>             | Mileff            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0.02   | 0.05   | 10.88   | 10.88   | 6.97    | 6.97    |
| <i>Moehringia trinervia</i>       | Moetri            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.13    | 0.05    | 0       | 0       |
| <i>Mycelis muralis</i>            | Mycnur            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.18   | 0.18   | 0.38   | 0.33   | 0.45    | 0.2     | 0.1     | 0.03    |
| <i>Oxalis acetosella</i>          | Oxaace            | 2.1     | 2.1     | 0.9     | 0.5     | 0.4     | 0.56    | 0.56    | 0.31    | 0.25    | 1.75   | 0.92   | 1.12   | 1.08   | 1.6     | 1.32    | 0.92    | 1.08    |
| <i>Paris quadrifolia</i>          | Parqua            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.05   | 0.05   | 0.05   | 0.05   | 0.17    | 0.15    | 0.13    | 0.13    |
| <i>Phegopteris connectilis</i>    | Phecon            | 0.8     | 0.9     | 0.9     | 0.9     | 0.9     | 0.05    | 0.02    | 0.01    | 0       | 1.33   | 0.93   | 0.38   | 0.33   | 0       | 0       | 0       | 0       |
| <i>Phyteuma spicatum</i>          | Physpi            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.02   | 0.02   | 0      | 0      | 0.05    | 0.05    | 0.05    | 0       |
| <i>Picea abies</i>                | Picabi            | 0.8     | 0.8     | 0.6     | 0.7     | 2.4     | 0.79    | 1.23    | 1.01    | 1.67    | 3.37   | 3.23   | 1.18   | 1.43   | 0.15    | 0.08    | 0.12    | 0.17    |
| <i>Picea pungens</i>              | Piepun            | 0       | 0       | 0       | 0       | 0       | 0       | 0.43    | 0.13    | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Poa remota</i>                 | Poarem            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.05    | 0.02    | 0       | 0       |
| <i>Polygonatum multiflorum</i>    | Polmul            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0.02    | 0.02    | 0.05    |
| <i>Polygonatum verticillatum</i>  | Polver            | 0       | 0       | 0       | 0       | 0       | 0.06    | 0.02    | 0.01    | 0.01    | 0.83   | 0.83   | 0.67   | 0.53   | 2.07    | 2.07    | 1.23    | 2.15    |
| <i>Prenanthes purpurea</i>        | Prepur            | 0.1     | 0.1     | 0       | 0       | 0       | 0       | 0       | 0.03    | 0.14    | 1.12   | 1.03   | 0.95   | 1.1    | 2.47    | 2.38    | 1.07    | 1.07    |

| Abbre-<br>viation                  | ss<br>1 | ss<br>2 | ss<br>3 | ss<br>4 | ss<br>5 | Pi<br>1 | Pi<br>2 | Pi<br>3 | Pi<br>4 | x<br>1 | x<br>2 | x<br>3 | x<br>4 | Fa<br>1 | Fa<br>2 | Fa<br>3 | Fa<br>4 |
|------------------------------------|---------|---------|---------|---------|---------|---------|---------|---------|---------|--------|--------|--------|--------|---------|---------|---------|---------|
| <i>Pulmonaria officinalis</i>      | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.05    | 0.05    | 0.05    | 0.02    |
| <i>Ranunculus platanifolius</i>    | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.05   | 0.02   | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Rubus fruticosus</i>            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0.02   | 0.05   | 0.18    | 0.33    | 0.33    | 0.33    |
| <i>Rubus idaeus</i>                | 0       | 0       | 0       | 0.1     | 0.4     | 0.07    | 0.16    | 0.07    | 0.14    | 0.62   | 0.82   | 0.52   | 0.43   | 3.23    | 3.07    | 2.92    | 2.92    |
| <i>Rumex acetosa</i>               | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.01    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Rumex arifolius</i>             | 0       | 0       | 0       | 0       | 0       | 0.08    | 0.03    | 0.02    | 0.02    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Salix caprea</i>                | 0       | 0       | 0       | 0       | 0       | 0       | 0.13    | 0.05    | 0.01    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Sambucus racemosa</i>           | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.1    | 0.02   | 0      | 0      | 0.38    | 0.1     | 0.18    | 0.35    |
| <i>Senecio fuchsii</i>             | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.05   | 0.05   | 0      | 0      | 0.05    | 0.02    | 0.05    | 0.02    |
| <i>Senecio nemorensis</i>          | 0.2     | 0.2     | 0       | 0       | 0       | 0.07    | 0.57    | 0.47    | 0.63    | 0.78   | 0.42   | 0.35   | 0.18   | 0.85    | 0.43    | 0.45    | 0.37    |
| <i>Sorbus aucuparia</i>            | 0.3     | 0.4     | 0.1     | 0.1     | 0.1     | 0.62    | 0.52    | 0.33    | 0.32    | 0.65   | 0.23   | 0.33   | 0.35   | 1.2     | 0.75    | 0.27    | 0.17    |
| <i>Stachys sylvatica</i>           | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.13    | 0       | 0       | 0       |
| <i>Stellaria nemorum</i>           | 0.2     | 0.2     | 0.1     | 0       | 0       | 0.09    | 0.05    | 0.02    | 0       | 0.52   | 0.43   | 0.4    | 0.35   | 0.4     | 0.4     | 0.37    | 0.35    |
| <i>Streptopus amplexifolius</i>    | 0.5     | 0.5     | 0.4     | 0.3     | 0.3     | 0.25    | 0.16    | 0.07    | 0.04    | 0.02   | 0.02   | 0      | 0.02   | 0       | 0       | 0       | 0       |
| <i>Trientalis europaea</i>         | 0.7     | 0.8     | 1.3     | 2       | 2       | 1.19    | 1.01    | 1.01    | 1.13    | 0.13   | 0.05   | 0      | 0      | 0.33    | 0.33    | 0.05    | 0.02    |
| <i>Trichophorum caespitosum</i>    | 0       | 0       | 0       | 0       | 0       | 0.05    | 0.13    | 0.13    | 0.43    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Urtica dioica</i>               | 0       | 0       | 0       | 0       | 0       | 0       | 0.02    | 0.02    | 0.01    | 0      | 0      | 0      | 0      | 0.13    | 0.05    | 0       | 0       |
| <i>Vaccinium myrtillus</i>         | 13.1    | 13.1    | 11.9    | 16.6    | 17.5    | 15.77   | 14.71   | 17.76   | 21.47   | 11.35  | 9.27   | 10.03  | 10.02  | 21.92   | 21.92   | 14.85   | 12.77   |
| <i>Vaccinium vitis-idaea</i>       | 0.2     | 0.2     | 0.1     | 0       | 0       | 0.24    | 0.16    | 0.08    | 0.15    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Veratrum lobelianum</i>         | 0.2     | 0.2     | 0.1     | 0       | 0       | 0.15    | 0.11    | 0.05    | 0.03    | 0.1    | 0.03   | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Viola biflora</i>               | 0.6     | 0.6     | 0.1     | 0       | 0       | 0.05    | 0.02    | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Viola sylvatica</i>             | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.05   | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Anastrepta ocradensis</i>       | 0       | 0       | 0       | 0       | 0       | 0.05    | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Barbilophozia attenuata</i>     | 0.15    | 0.06    | 0.06    | 0       | 0       | 0.02    | 0.02    | 0.02    | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Barbilophozia floerkei</i>      | 0.02    | 0.02    | 0.02    | 0       | 0       | 0.05    | 0.01    | 0.01    | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Barbilophozia lycopodioides</i> | 0       | 0       | 0       | 0       | 0       | 0.05    | 0.01    | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Bazania trilobata</i>           | 0       | 0       | 0       | 0       | 0       | 0.02    | 0.02    | 0.01    | 0.01    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Blepharostoma trichophyllum</i> | 0.15    | 0.06    | 0.02    | 0       | 0       | 0.02    | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Bryum erythrocarpum</i>         | 0.14    | 0.06    | 0       | 0       | 0       | 0.03    | 0.01    | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Calypogeia integristipula</i>   | 0.06    | 0.02    | 0       | 0       | 0       | 0.02    | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Calypogeia neesiana</i>         | 0       | 0       | 0       | 0       | 0       | 0.02    | 0.01    | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Calypogeia trichomanis</i>      | 0.42    | 0.29    | 0.04    | 0.02    | 0       | 0.18    | 0.09    | 0.01    | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Cephalozia bispinidata</i>      | 0.18    | 0.14    | 0.08    | 0       | 0       | 0.02    | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Cetraria islandica</i>          | 0.02    | 0.02    | 0.02    | 0       | 0       | 0.01    | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Dicranella heteromalla</i>      | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.33   | 0.29   | 0.23   | 0.2    | 0.29    | 0.29    | 0.26    | 0.24    |
| <i>Dicranodontium denudatum</i>    | 0.15    | 0.15    | 0.06    | 0.06    | 0.02    | 0.41    | 0.31    | 0.13    | 0.19    | 0      | 0      | 0      | 0      | 0.14    | 0       | 0.02    | 0       |



Continuation of Tab. II

|                                   | Abbre-<br>viation | ss<br>1 | ss<br>2 | ss<br>3 | ss<br>4 | ss<br>5 | Pi<br>1 | Pi<br>2 | Pi<br>3 | Pi<br>4 | x<br>1 | x<br>2 | x<br>3 | x<br>4 | Fa<br>1 | Fa<br>2 | Fa<br>3 | Fa<br>4 |
|-----------------------------------|-------------------|---------|---------|---------|---------|---------|---------|---------|---------|---------|--------|--------|--------|--------|---------|---------|---------|---------|
| <i>Dicranum scoparium</i>         | Diesco            | 2.56    | 2.56    | 2.9     | 2.9     | 2.9     | 3.47    | 2.82    | 3.03    | 2.34    | 1.77   | 1.56   | 0.57   | 0.75   | 1.46    | 0.84    | 0.56    | 0.35    |
| <i>Diplophyllum obusifolium</i>   | Dipobt            | 0.06    | 0       | 0       | 0       | 0       | 0.01    | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Hylocomium splendens</i>       | Hylspl            | 0.17    | 0.06    | 0.04    | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Jungfermania sphaerocarpa</i>  | Junsph            | 0.06    | 0.02    | 0       | 0       | 0       | 0.02    | 0.02    | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Lepidozia reptans</i>          | Leprep            | 0.12    | 0.08    | 0.02    | 0       | 0       | 0.01    | 0.01    | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Lophozia ventricosa</i>        | Lopven            | 0       | 0       | 0       | 0       | 0       | 0.01    | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Mniium hornum</i>              | Mnihor            | 0.15    | 0.15    | 0.06    | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Mylia taylorii</i>             | Myltay            | 0.48    | 0.52    | 0.52    | 0.06    | 0.1     | 0.18    | 0.15    | 0.11    | 0.1     | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Orthodicranum montanum</i>     | Ortmon            | 0.06    | 0.02    | 0       | 0       | 0       | 0.02    | 0.02    | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Pellia neesiana</i>            | Pelnee            | 0.63    | 0.63    | 0.27    | 0.08    | 0.04    | 0.39    | 0.29    | 0.33    | 0.22    | 0.1    | 0.1    | 0.02   | 0      | 0       | 0       | 0       | 0       |
| <i>Philonotis fontana</i>         | Phifon            | 0.15    | 0.06    | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Plagiominium affine</i>        | Plaaff            | 0.55    | 0.55    | 0.21    | 0.08    | 0.15    | 0.25    | 0.25    | 0.16    | 0.14    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Plagiothecium curvifolium</i>  | Placur            | 0.06    | 0.06    | 0.02    | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0.12    | 0.02    | 0.02    | 0       |
| <i>Plagiothecium denticulatum</i> | Pladen            | 0.15    | 0.06    | 0.06    | 0       | 0       | 0.02    | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Plagiothecium laetum</i>       | Plalae            | 0.06    | 0.06    | 0       | 0       | 0       | 0.17    | 0.14    | 0.02    | 0.02    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Plagiothecium roseanum</i>     | Plaroe            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.02   | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Plagiothecium undulatum</i>    | Plaund            | 1.66    | 1.66    | 0.63    | 0.48    | 0.46    | 0.8     | 0.72    | 0.5     | 0.46    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Pleurozium schreberi</i>       | Plesch            | 0       | 0       | 0       | 0       | 0       | 0.06    | 0.05    | 0.02    | 0.02    | 0      | 0      | 0      | 0      | 0       | 0.24    | 0.03    | 0       |
| <i>Pohlia nutans</i>              | Pohnut            | 0.45    | 0.45    | 0.21    | 0.08    | 0.06    | 0.11    | 0.1     | 0.06    | 0.05    | 0.15   | 0.07   | 0      | 0      | 0.07    | 0.07    | 0.03    | 0.02    |
| <i>Polytrichastrum formosum</i>   | Polfor            | 17.55   | 17.55   | 15.3    | 8.7     | 8.7     | 12.48   | 7.37    | 5.17    | 4.57    | 4.58   | 4.58   | 2.54   | 2.23   | 2.75    | 2.75    | 2       | 2       |
| <i>Polytrichum commune</i>        | Polcom            | 0.15    | 0.15    | 0.02    | 0       | 0       | 0.29    | 0.26    | 0.13    | 0.2     | 0      | 0      | 0      | 0      | 0.02    | 0.02    | 0       | 0       |
| <i>Polytrichum gracile</i>        | Polgra            | 0       | 0       | 0       | 0       | 0       | 0.01    | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Polytrichum juniperinum</i>    | Poljun            | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0.05   | 0.05   | 0      | 0      | 0.12    | 0.02    | 0       | 0       |
| <i>Polytrichum strictum</i>       | Polstr            | 0       | 0       | 0       | 0       | 0       | 0.13    | 0.13    | 0.13    | 0.13    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Rhizomnium punctatum</i>       | Rhipun            | 0.55    | 0.55    | 0.08    | 0.08    | 0.08    | 0.2     | 0.17    | 0.02    | 0       | 0.07   | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Rhynchostegium confertum</i>   | Rhycon            | 0.21    | 0.15    | 0.08    | 0       | 0       | 0.07    | 0.01    | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Rhytidiadelphus loreus</i>     | Rhylor            | 0       | 0       | 0       | 0       | 0       | 0.05    | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Rhytidiadelphus squarrosus</i> | Rhysqu            | 0       | 0       | 0       | 0       | 0       | 0.04    | 0.01    | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Scapania undulata</i>          | Scaund            | 0.36    | 0.36    | 0.14    | 0       | 0       | 0.26    | 0.12    | 0.03    | 0.01    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Sphagnum girgensohnii</i>      | Sphgir            | 9.8     | 9.8     | 7.46    | 3.06    | 3       | 2.47    | 2.06    | 2.6     | 2.57    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Sphagnum nemoreum</i>          | Sphnem            | 0.06    | 0.06    | 0       | 0       | 0       | 0       | 0       | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Sphagnum quinquefarium</i>     | Sphqui            | 0.21    | 0.21    | 0.15    | 0.15    | 0.15    | 0.07    | 0.04    | 0.02    | 0.02    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Sphagnum recurvum</i>          | Sphrec            | 0       | 0       | 0       | 0       | 0       | 2.75    | 2.75    | 1.92    | 1.92    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Sphagnum robustum</i>          | Sphrob            | 0.21    | 0.21    | 0.12    | 0       | 0       | 0.43    | 0.43    | 0.13    | 0.13    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Sphagnum squarrosum</i>        | Sphsqu            | 0.52    | 0.48    | 0.08    | 0       | 0       | 0.91    | 0.71    | 0.52    | 0.54    | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |
| <i>Tetraphis pellucida</i>        | Tetpel            | 0.46    | 0.4     | 0.15    | 0       | 0       | 0.25    | 0.06    | 0       | 0       | 0      | 0      | 0      | 0      | 0       | 0       | 0       | 0       |



3. DCA ordination of the relevés without the most different plots (11–14, 30–32), axis 1 and 2 (A), 2 and 3 (B) respective. Position of the relevé at single periods 1 to 4, 5 respective is distinguished by breaking points of the trajectory, its end is described by number of the plot and the last period of sampling

hypothesis is rejected if the variable  $\chi^2$  has been higher than the relevant critical value of  $\chi^2$ -distribution:

$$\chi^2 = \sum_y \frac{(1 - P(c_{py}))^2}{P(c_{py})}$$

The probability  $P(c_{py})$  was calculated on the basis of frequencies of types within the whole set of plots, and for a set of plots from which plot  $p$  was excluded. The presented algorithm is a part of new program DVCLASS for sequence study.

## RESULTS AND DISCUSSION

### VEGETATION CONDITIONS

Vegetation of the groups of forest stands (spruce, beech and mixed ones) was described on the basis of

“mean“ relevés for each of the periods evaluated (Tab. II). These data were used for classification (Fig. 1) and ordination (Fig. 2). Variability of the separate plots under observation with respect to their development is indicated by ordination of the relevés (Fig. 3). The results document evident differences between the groups of plots and their different behaviour during succession.

The smallest changes in the herb layer were observed in spruce stands (except PRP 11–15) while the changes in mixed stands were greater, and they were greatest in beech stands (assessed from the classification of mean relevés) (compare V a c e k et al., 1996c).

### Spruce stands

Relatively small changes can be commonly described e.g. by a decrease in the coverage of *Dryopteris*

*dilatata* or by complete disappearance of *Blechnum spicant*, *Luzula pilosa* and *Viola biflora*. On the contrary, the coverage of *Vaccinium myrtillus* and *Deschampsia caespitosa* was increasing, some clear-cut species appeared as the new ones (*Chamaenerium angustifolium* or *Prenanthes purpurea*).

Development on PRP 11–15 was different: e.g. *Adenostyles alliariae* and *Dryopteris dilatata* receded while the representation of *Athyrium distentifolium* increased (cf. Vacek, 1984b).

coverage of *Blechnum spicant*, *Dentaria enneaphyllos*, *Dryopteris dilatata*, *Dryopteris filix-mas*, *Gymnocarpium dryopteris* and *Trientalis europaea*, and complete disappearance of *Asperula odorata* and *Ranunculus platanifolius*. On the other hand, the species occurring more frequently on clear-cut areas or in open forest stands increased their coverage or appeared as new species: *Digitalis purpurea*, *Juncus effusus*, *Rubus fruticosus* agg., *Carex pilosa*. The coverage of *Fagus sylvatica* in the herb layer augmented.

#### Mixed stands

Changes in the average coverage of many species were relatively low – they involved e.g. reduction in the

#### Beech stands

The average coverage of many species decreased (*Dentaria enneaphyllos*, *Dryopteris filix-mas*, *Hiera-*

III. Development of the species diversity ('H) and its components during single periods of sampling according to the groups of plots, herb layer. avg – average, std – standard deviation

| Period                 | 1    |       |       | 2    |       |       | 3    |       |       | 4    |       |       | 5    |       |       |
|------------------------|------|-------|-------|------|-------|-------|------|-------|-------|------|-------|-------|------|-------|-------|
| Parameter of diversity | S    | e     | 'H    | S    | e     | 'H    | S    | e     | 'H    | S    | e     | 'H    | S    | e     | 'H    |
| TVP 11–15              |      |       |       |      |       |       |      |       |       |      |       |       |      |       |       |
| avg                    | 16.0 | 0.545 | 1.480 | 16.6 | 0.541 | 1.504 | 16.6 | 0.581 | 1.598 | 14.8 | 0.637 | 1.704 | 14.6 | 0.661 | 1.774 |
| std                    | 4.5  | 0.050 | 0.172 | 3.5  | 0.054 | 0.156 | 4.0  | 0.076 | 0.122 | 2.0  | 0.094 | 0.237 | 1.9  | 0.075 | 0.257 |
| <i>Picea</i>           |      |       |       |      |       |       |      |       |       |      |       |       |      |       |       |
| avg                    |      |       |       | 15.1 | 0.550 | 1.473 | 15.9 | 0.559 | 1.537 | 14.1 | 0.581 | 1.525 | 12.8 | 0.597 | 1.504 |
| std                    |      |       |       | 4.5  | 0.099 | 0.350 | 3.3  | 0.078 | 0.268 | 3.1  | 0.091 | 0.291 | 3.3  | 0.110 | 0.338 |
| Mixed stands           |      |       |       |      |       |       |      |       |       |      |       |       |      |       |       |
| avg                    |      |       |       | 22.7 | 0.661 | 2.056 | 21.7 | 0.652 | 2.001 | 18.2 | 0.666 | 1.932 | 16.8 | 0.674 | 1.907 |
| std                    |      |       |       | 2.9  | 0.063 | 0.190 | 2.4  | 0.045 | 0.145 | 2.3  | 0.098 | 0.338 | 2.4  | 0.094 | 0.341 |
| <i>Fagus</i>           |      |       |       |      |       |       |      |       |       |      |       |       |      |       |       |
| avg                    |      |       |       | 21.8 | 0.585 | 1.778 | 21.7 | 0.565 | 1.700 | 19.2 | 0.615 | 1.793 | 18.3 | 0.687 | 1.963 |
| std                    |      |       |       | 8.5  | 0.141 | 0.530 | 9.4  | 0.141 | 0.540 | 7.9  | 0.101 | 0.496 | 7.2  | 0.070 | 0.390 |

S – number of species, e – equitability, 'H – Shannon-Wiener index of diversity

IV. Development of the species diversity ('H) and its components during single periods of sampling according to the groups of plots, moss layer. avg – average, std – standard deviation

| Period                 | 1    |       |       | 2    |       |       | 3    |       |       | 4   |       |       | 5   |       |       |
|------------------------|------|-------|-------|------|-------|-------|------|-------|-------|-----|-------|-------|-----|-------|-------|
| Parameter of diversity | S    | e     | 'H    | S    | e     | 'H    | S    | e     | 'H    | S   | e     | 'H    | S   | e     | 'H    |
| TVP 11–15              |      |       |       |      |       |       |      |       |       |     |       |       |     |       |       |
| avg                    | 15.2 | 0.525 | 1.432 | 14.0 | 0.497 | 1.319 | 11.4 | 0.478 | 1.169 | 6.2 | 0.597 | 1.044 | 5.2 | 0.654 | 1.007 |
| std                    | 4.0  | 0.085 | 0.364 | 4.0  | 0.096 | 0.398 | 3.6  | 0.104 | 0.408 | 1.9 | 0.063 | 0.222 | 1.9 | 0.105 | 0.228 |
| <i>Picea</i>           |      |       |       |      |       |       |      |       |       |     |       |       |     |       |       |
| avg                    |      |       |       | 10.1 | 0.585 | 1.353 | 8.3  | 0.647 | 1.310 | 6.4 | 0.610 | 1.075 | 5.1 | 0.629 | 0.954 |
| std                    |      |       |       | 2.3  | 0.150 | 0.417 | 2.9  | 0.118 | 0.326 | 2.5 | 0.098 | 0.319 | 2.6 | 0.086 | 0.435 |
| Mixed stands           |      |       |       |      |       |       |      |       |       |     |       |       |     |       |       |
| avg                    |      |       |       | 4.3  | 0.629 | 0.895 | 3.7  | 0.598 | 0.761 | 3.0 | 0.601 | 0.621 | 2.8 | 0.665 | 0.672 |
| std                    |      |       |       | 0.7  | 0.126 | 0.142 | 0.5  | 0.151 | 0.174 | 0.6 | 0.157 | 0.094 | 0.4 | 0.160 | 0.150 |
| <i>Fagus</i>           |      |       |       |      |       |       |      |       |       |     |       |       |     |       |       |
| avg                    |      |       |       | 5.2  | 0.691 | 1.113 | 4.0  | 0.637 | 0.868 | 3.5 | 0.548 | 0.686 | 2.8 | 0.577 | 0.591 |
| std                    |      |       |       | 1.2  | 0.034 | 0.156 | 0.8  | 0.088 | 0.156 | 1.3 | 0.169 | 0.307 | 0.7 | 0.195 | 0.214 |

S – number of species, e – equitability, 'H – Shannon-Wiener index of diversity

V. Results of the classification of relevés by TWINSpan procedure. Used cut-levels: 0.00, 1.00, 10.00, 31.60, 56.20, 75.00. Indicator species of the classification groups are presented (number by the species abbreviation represents cover according to the number of the cut-level)

|  |   |   |   |                            |                                  |   |                                   |        |
|--|---|---|---|----------------------------|----------------------------------|---|-----------------------------------|--------|
| 0<br>Des fle 2<br>Tri eur 1              | 00<br>Ath dis 1<br>Str amp 1<br>Des cae 1<br>Gal her 1<br>Ver lob 1 | 000<br>Car lim 1  |   |                            |                                  |   |                                   |        |
|  |   | 001   | 0010<br>Ade all 1   | 00100<br>Cha hir 1         |                                  |   |                                   |        |
|  |   |   |   | 00101                      | 001010<br>Cic alp 1              |   |                                   |        |
|  |   |   |   |                            | 001011                           |   |                                   |        |
|  |   |   | 0011  | 00110<br>Vac myr 3         | 001100<br>Gal her 2              | 0011000<br>Gen asc 2  |                                   |        |
|  |   |   |   |                            |                                  | 0011001   |                                   |        |
|  |   |   |   |                            | 001101<br>Des fle 3<br>Des cae 1 | 0011010   |                                   |        |
|  |   |   |   | 0011011<br>Des cae 1       |                                  |   |                                   |        |
|  |   |   |   | 00111                      | 001110<br>Ath dis 1              |   |                                   |        |
|  |   |   |   |                            | 001111                           |   |                                   |        |
|  |   |   |   | 01<br>Oxa ace 1<br>Luz nem | 010<br>Tri eur 1                 | 0100<br>Str amp 1<br>Gen asc 2<br>Cal vil 4<br>Ble spi 1<br>Des cae 1 | 01000<br>Sen nem 1                | 010000 |
|  | 01001   | 010001<br>Des cae 1                                       |   |                            |                                  |   |                                   |        |
|  |   | 010010<br>Luz syl 1                                       |   |                            |                                  |   |                                   |        |
|  |   | 010011  | 0100110<br>Gal her 1<br>Str amp 1<br>Cal vil 5<br>Des cae 1 |                            |                                  |   |                                   |        |
|  |   |   | 0100111<br>Vac myr 3<br>Gen asc 1                           |                            |                                  |   |                                   |        |
|  | 0101<br>Vac myr 3<br>Cha ang 1                                      | 01010<br>Oxa ace 1<br>Lyc ann 1                           | 010100  |                            |                                  |   | 0101000<br>Lyc ann 1<br>Mai bif 1 |        |
|  |   |   | 010101<br>Ath dis 1   |                            |                                  |   | 0101001                           |        |
|  |   |   |   |                            |                                  |   | 0101010                           |        |
|  |   | 01011<br>Sen nem 1<br>Bet pen 1<br>Cha ang 2<br>Cal vil 4 | 010110<br>Ath dis 1   |                            |                                  |   | 0101011<br>Abi alb 1              |        |
|  |   |   |   |                            |                                  |   | 0101100                           |        |
|  |   |   | 0101101<br>Ath dis 1  |                            |                                  |   |                                   |        |
|  | 011<br>Pre pur 1<br>Fag syl 1<br>Pol ver 1                          | 0110  | 01100   |                            |                                  | 011000  | 0110000<br>Luz pil 1              |        |
|  |   |   |   |                            |                                  | 0110001   |                                   |        |
|  |   |   | 011001<br>Gym dry 1   |                            |                                  |   |                                   |        |
|  |   | 01101<br>Bet pen 1  |   |                            |                                  |   |                                   |        |
|  |   | 01110   |   |                            |                                  |   |                                   |        |
|  |   | 0111<br>Gen asc 1   | 01111<br>Pre pur 2  |                            |                                  | 011110  | 0111100                           |        |
|  |   |   |   | 0111101<br>Ble spi 1       |                                  |   |                                   |        |
| 011111                                   |   |   |   |                            |                                  |   |                                   |        |
| 1<br>Gym dry 1<br>Dry fil 1<br>Ath fil 1 | 10  | 100<br>Des fle 1<br>Fag syl 3                             | 1000<br>Ace pse 1   |                            |                                  |   |                                   |        |
|  |   |   | 1001  |                            |                                  |   |                                   |        |
|  |   | 101   | 1010  |                            |                                  |   |                                   |        |
|  |   |   | 1011<br>Ble spi 1   |                            |                                  |   |                                   |        |
|  | 11<br>Bra syl 1   | 110   | 1100  | 11000<br>Asp odo 1         |                                  |   |                                   |        |
|  |   |   |   | 11001                      |                                  |   |                                   |        |
|  |   | 1101<br>Lam gal 1   |   |                            |                                  |   |                                   |        |
|  |   | 111<br>Act spi 1  |   |                            |                                  |   |                                   |        |



*cium sylvaticum*, *Luzula nemorosa*, *Milium effusum*, *Vaccinium myrtillus*) or some species fully disappeared (*Circaea intermedia*, *Lamium maculatum*). The coverage of some grasses increased (*Brachypodium sylvaticum* and *Calamagrostis villosa*). The coverage of *Acer pseudoplatanus* in the herb layer also augmented.

#### GENERAL TRENDS

Changes in species diversity and vegetation richness were great (Tabs. III, IV): the numbers of species in herb ( $E_1$ ) and moss ( $E_0$ ) layers declined in all groups of plots, overall species diversity of moss layer was also substantially reduced. Its changes in herb layer were specific of the groups of plots: it increased on PRP 11–15 (spruce stands with subalpine elements) and partly in beech stands, but it decreased in mixed stands or there were basically no changes in the other spruce stands. Both components of diversity influenced species equitability which was mostly improved.

The relevés were classified and evaluated by ordination analysis (Fig. 3). Classification by TWINSpan program provided identification of typical groups of species (Tab. V). Such classification indicated the existence of a "core" consisting of relevés from spruce stands. Other relevés were 'chain-linked' to the core, among them those from mixed and beech stands. Vegetation on PRP 14 was the most different of all.

Ordination (DCA) of all relevés indicated perceptibly different vegetation of some beech stands (PRP 30, 31, 32; localities in the 6th altitudinal zone) in a direction of the first ordination axis. The second ordination axis pointed to the different character of herbaceous vegetation at four localities with spruce stand (PRP 11–14; these were stands with significant participation of species occurring in sub-alpine tall-herbaceous meadows).

In order to evaluate vegetation changes without influence of the ordination space distortion caused by these most differing relevés, second run of ordination was carried out excluding the seven mentioned localities. It was possible to draw a conclusion from positions of various species in the resultant ordination space and from their requirements that the first axis applied to soil richness (nutrient contents, mainly of nitrogen) while the second showed soil moisture.

The question about the existence of any general trends in species composition on the plots was answered by analysis of variance used to interpret ordination scores of plots along the first to the fourth axis when the year of relevé was taken as a parameter of classification to groups. It is to state that no trends were determined that would support the hypothesis of the existence of these trends – either within the whole group of plots or for the separate groups (with spruce, beech and mixed stands).

Moss layer composition and its changes during succession were evaluated separately. The changes in the

species composition of moss layer did not appear to be so important as the changes in its whole coverage that were great in some cases (but it was necessary to compare trends of the species diversity in moss layer). After the tree layer of spruce stands was disturbed (where  $E_0$  coverage was primarily high),  $E_1$  coverage increased – mainly grasses vehemently competed with bryophytes, which can fully disappear as a result of this competition (cf. PRP 26). The species composition of bryophytes in spruce stands and in beech stands did not differ significantly. Water supply and potential peatification are the most important factors of moss layer development (see PRP 23 with  $E_0$  coverage 65–75%). Classification indicated the existence of two large and relatively homogeneous groups of relevés, and of several very different relevés (except the above-mentioned PRP 23, these were relevés from localities PRP 13, 14, 16, 21 and 25 – with spruce stand and moss layer of great cover; the greatest changes in  $E_0$  occurred at these localities after tree layer destruction). Ordination of relevés on the basis of moss layer composition confirmed an important role of peatification (PRP 23) largely distorting the ordination space. This is the reason why changes during succession should be evaluated when the position in the projection of second and third ordination axes was available: the second axis indicated moderate differences between five spruce stands (PRP 4, 5, 13, 14 and 21). A greater change in the moss layer structure was established from a shift along the third ordination axis in spruce-beech and beech stands on PRP 2, 8, 9, 30 and 32.

Tab. VI documents the level of changes in herb layer from the early eighties to 1995 (evaluation by variability in ordination space while various numbers – 1 to 4 – of the first ordination axes were used). Not absolute values of the indexes but their mutual comparison was important. Differences between the groups of forest ecosystems were perceptible – the greatest changes were determined in beech stands while changes in spruce stands were smaller. With respect to the position of these groups in ordination space, a change evaluated only from a shift along the first axis of ordination space could be considered as conclusive in beech stands but it was necessary to evaluate at least the first two axes in spruce stands. Changes in vegetation evaluated by these indexes reflected global processes, scarce processes (including fluctuation) may have been neglected.

Similar comparisons were made to evaluate changes in the moss layer composition (Tab. VII). Comparison of the two tables showed that the level of successive changes was comparable in the two layers. Greatest changes in moss layer occurred mostly in mixed stands, that means in stands with relatively smaller changes in herb layer. Moss layer was more stable in the spruce stands.

Forest stands were divided into four groups with regard to the above-mentioned level of changes in the respective layers using medians calculated from all values (Tab. VIII). Plots with tree layer destruction were marked for illustration; they occur in all these groups.

## TREE LAYER DAMAGE

### Spruce stands

Tab. IX shows foliage dynamics of spruce stands, and it is plotted in Fig. 4 using an example of PRP 11 and 13. The values document that foliage trends on the separate plots were largely different, in relative terms corresponding to environmental pollution stress, state, structure and origin of forest stand, and to cultural and protective treatments of forest managers. While the average regional foliage of spruce stands was about 83.9% in 1976, it was only 39.7% in 1997, it implied an average annual increase in defoliation of 2.1%. Three typical periods were identified on the basis of different trends of foliage dynamics. In the period of first signs of damage (1976–1980), average foliage ranged from 84.9 to 85.4% at lower mountain altitudes (below 1100 m above sea level) and between 79.2 and 81.8% at higher altitudes (above 1100 m a.s.l.) (average annual

increase in defoliation of 0.1% and 0.6%, respectively). In the period of great damage (1981–1988), average foliage ranged from 48.2 to 79.3% at lower altitudes and from 46.7 to 73.8% at higher altitudes (average annual increase in defoliation of 4.4 and 3.0%). If damage caused by bark beetle was excluded, average annual defoliation increase would be 2.3% at lower altitudes and 2.8% at higher altitudes. In the period of damage abatement (1989–1997), average foliage ranged from 19.9 to 47.5% at lower altitudes and from 42.8 to 52.6% at higher altitudes (average annual increase in defoliation was 3.5 and 1.2%), if damage caused by bark beetle was excluded, 0.2 and 0.4%. The years 1981, 1983, 1984 and 1986 were critical due to the environmental pollution stress, when defoliation was severe. PRP 3, 17 and 26 were felled in the period of heavy environmental pollution stress. PRP 15 was liquidated by bark beetle invasion and PRP 16 and 18 suffered great damage (cf. Vacek, 1996).

Maximum average defoliation of spruce-trees was 30–100% (average value 55.5%) in spruce stands and

VI. Change in the herb layer of the single plot groups expressed as sum of variances of ordination scores of several (one to four) first DCA axes

| Axes DCA             | [1]   | [1]+[2] | [1]+[2]+[3] | [1]+...+[4] |
|----------------------|-------|---------|-------------|-------------|
| <i>Fagus</i>         |       |         |             |             |
| Average              | 27.07 | 31.35   | 42.97       | 49.95       |
| min                  | 3.84  | 5.22    | 5.70        | 25.24       |
| max                  | 38.13 | 42.08   | 80.14       | 84.18       |
| <i>Fagus + Picea</i> |       |         |             |             |
| Average              | 21.10 | 25.89   | 26.76       | 32.84       |
| min                  | 5.59  | 7.47    | 7.81        | 16.22       |
| max                  | 40.92 | 46.95   | 49.73       | 52.47       |
| <i>Picea</i>         |       |         |             |             |
| Average              | 5.64  | 24.09   | 25.28       | 36.17       |
| min                  | 0.43  | 1.30    | 1.54        | 9.60        |
| max                  | 21.01 | 103.17  | 103.25      | 103.50      |

VII. Change in the moss layer of the single plot groups expressed as sum of variances of ordination scores of several (one to four) first DCA axes

| Axes DCA             | [1]  | [1]+[2] | [1]+[2]+[3] | [1]+...+[4] |
|----------------------|------|---------|-------------|-------------|
| <i>Fagus</i>         |      |         |             |             |
| Average              | 14.7 | 24.4    | 40.1        | 46.2        |
| min                  | 2.0  | 11.2    | 16.7        | 26.8        |
| max                  | 40.0 | 59.3    | 110.5       | 116.8       |
| <i>Fagus + Picea</i> |      |         |             |             |
| Average              | 2.5  | 14.9    | 48.1        | 55.7        |
| min                  | 1.2  | 4.5     | 14.1        | 19.7        |
| max                  | 3.8  | 38.3    | 120.5       | 134.9       |
| <i>Picea</i>         |      |         |             |             |
| Average              | 9.0  | 19.8    | 27.0        | 38.7        |
| min                  | 0.8  | 5.5     | 11.4        | 18.7        |
| max                  | 24.7 | 58.9    | 62.1        | 76.3        |

VIII. Division of the stands into groups according to the change in the herb and moss layer, respectively (see Tabs. VI and VII);  $\mu$  is median. Bold pressed are numbers of stands with total destruction of the tree layer

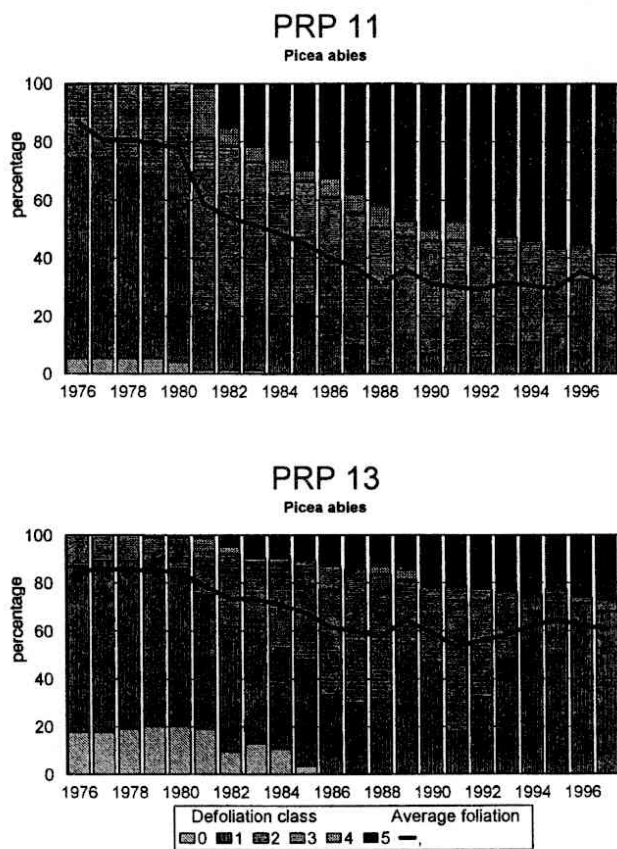
| A. Herb layer ( $E_1$ ); $\mu = 25.81$ |  |              |              |
|--|--|--------------|--------------|
| Change degree                          | Spruce stands  | Mixed stands | Beech stands |
| $<\mu/2$                               | <b>18</b> 20 25  |              |              |
| $\mu/2.. \mu$                          | <b>16</b> 22 19 3 <b>26</b> 10 23 21 24                  | 6 9          | 28           |
| $\mu..2\mu$                            | 4 5  | <b>1</b> 7 8 | 27 29        |
| $>2\mu$                                | <b>15</b> 12 17 13 14 11                                 | 2            | 31 32 30     |
| B. Moss layer ( $E_0$ ); $\mu = 35.59$ |  |              |              |
| Change degree                          | Spruce stands  | Mixed stands | Beech stands |
| $<\mu/2$                               |  |              |              |
| $\mu/2.. \mu$                          | 23 13 5 4 21 12 19 25 24                                 | <b>1</b> 7 6 | 30 29 27 28  |
| $\mu..2\mu$                            | <b>17</b> 10 22 <b>15</b> 20 <b>16</b> 11 <b>18</b> 14 3 | 2 9          | 31           |
| $>2\mu$                                | <b>26</b>  | 8            | 32           |

35–100% (average value 55.7%) in mixed spruce-beech stands in the period of observation.

Tab. X shows types of transition matrices for the separate localities. A typical sequence of transition matrices was (E)-A,F-(B)-(C)-(B)-G-A while the last two members were very doubtful, bracketed symbols indicated repetition of the type for two or more years (Fig. 5). Regular deterioration of spruce health was observed since 1981 or 1982, another turning point was the years 1986 and 1987 with peak of deterioration (the peak of damage was determined on some plots later), then the changes were not so abrupt, development was quite continuous [both in the sense of health improvement (e.g. PRP 5, 7) or total destruction of stand (PRP 14 or 1)].

Types of transition matrices can be divided into these groups (Fig. 6):

- decrease in average defoliation accompanied by a lower level of tree dieback (types M, K, B, D, F) – they describe the stages of stand health improvement;
- increase in average defoliation accompanied by a lower level of tree dieback (types A, E), the “first” stage of stand state deterioration;
- decrease in average defoliation accompanied by a higher level of tree dieback (types O, G, C) – the trees that cannot tolerate the given level of stress are eliminated in these stages; in case the period is not very long, there is a hope of conserving the stand without its total destruction if the number of surviving trees is sufficiently high;



4. Trend of average foliation and particular defoliation class of spruce on plots 11 and 13

- increase in defoliation accompanied by parallel intensive dieback of trees (types I, H, N) – stages of extreme damage to stand ending in its total destruction.

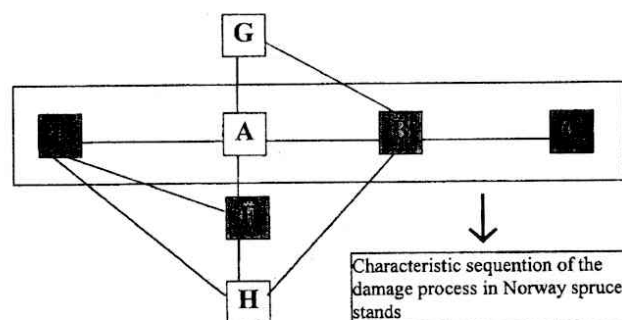
The presence of data on defoliation assessment at localities PRP 11–15 from the mid-seventies can allure to generalise the results from these localities for the whole area of the Krkonoše Mts. It is however necessary to be aware of the fact that these autochthonous spruce stands in extreme conditions of the Mumlava anemo-orographic system (cf. V a c e k, 1981) differ in some parameters from the other spruce stands – see vegetation evaluation.

## Beech stands

Tab. XI shows foliage dynamics of beech stands, and it is plotted in Fig. 7 using an example of PRP 27 and 31. The average regional foliage of beech stands was 94.2% in 1980 and only 62.7% in 1997, i.e. an average annual increase in defoliation was 1.9%. In the period of great damage (1981–1988) the average foliage of beech-trees ranged from 64.5 to 88.6%, i.e. an average annual increase in defoliation was 3.4%. If damage caused by beech scale and wood-destroying fungi were excluded, it would be about 2.0%. 1981, 1984 and 1986 were the years with critical environmental pollution stress, when an annual decrease in foliage was about 5.2–9.6% (cf. V a c e k, 1993). In the period of damage abatement (in 1989–1997), average beech foliage ranged between 62.7 and 68.0%, i.e. an average annual increase in defoliation was 0.7%. If damage caused by beech scale and lignicolous fungi were excluded, an annual increase in foliage would be about 0.4%.

Maximum average defoliation of beech was 24–46% (average 33.5%) in beech stands and 22–38% (average 33.2%) in mixed spruce-beech stands in the period of observation.

Tab. XII shows the types of transition matrices for the separate localities. It was not possible to identify any typical sequence of transition matrices. The initial period could be described by matrices of types A and C, types C and D were typical of the intermediate period, and heterogeneity increased in the last years (e.g. types H and F were additional ones). The beginning of



5. Graph of the main sequences of the transition matrix types by *Picea abies*. Types in grey fields have a frequent repetition

IX. Dynamics of foliage of the spruce stands (average values in per cent; totally defoliated trees are included)

| Permanent plot | Number of trees | Year  |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
|----------------|-----------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|                |                 | 1976  | 1977  | 1978  | 1979  | 1980  | 1981  | 1982  | 1983  | 1984  | 1985  | 1986  | 1987  | 1988  | 1989  | 1990  | 1991  | 1992  | 1993  | 1994  | 1995  | 1996  | 1997  |
| 3              | 65              |       |       |       |       |       | 72.00 | 68.15 |       |       | 60.58 | 51.81 | 45.14 | 47.40 | 47.50 | 45.00 | 42.10 | 46.38 | 42.90 | 45.15 | 43.62 | 43.48 | 41.66 |
| 4              | 69              |       |       |       |       |       | 78.70 | 76.16 |       |       | 65.00 | 57.92 | 50.00 | 53.44 | 58.60 | 53.12 | 49.27 | 56.04 | 58.44 | 63.02 | 59.48 | 56.87 | 57.29 |
| 5              | 48              |       |       |       |       |       | 82.19 | 78.44 |       |       | 57.42 | 51.63 | 47.65 | 42.35 | 48.60 | 47.50 | 46.59 | 46.14 | 50.87 | 48.26 | 47.95 | 50.19 | 50.30 |
| 10             | 132             |       |       |       |       |       | 71.67 | 69.77 |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| 11             | 74              | 80.67 | 80.67 | 80.67 | 79.59 | 77.50 | 58.58 | 53.85 | 51.42 | 48.38 | 44.93 | 40.07 | 36.82 | 30.88 | 36.15 | 31.22 | 29.86 | 29.26 | 31.55 | 30.41 | 29.46 | 35.47 | 31.28 |
| 12             | 77              | 82.92 | 82.92 | 82.92 | 82.14 | 80.84 | 68.23 | 64.48 | 64.87 | 60.78 | 57.27 | 47.29 | 44.35 | 38.12 | 41.69 | 36.75 | 34.42 | 33.72 | 34.36 | 30.26 | 31.04 | 27.59 | 25.78 |
| 13             | 84              | 85.06 | 85.54 | 85.71 | 84.88 | 84.64 | 78.69 | 73.39 | 73.39 | 70.65 | 67.62 | 61.49 | 59.76 | 57.76 | 64.52 | 59.40 | 53.45 | 56.01 | 58.33 | 62.08 | 64.58 | 62.76 | 60.77 |
| 14             | 60              | 85.42 | 85.92 | 86.17 | 86.08 | 86.08 | 80.50 | 80.67 | 77.75 | 70.50 | 67.67 | 62.25 | 61.83 | 56.33 | 63.92 | 58.25 | 53.17 | 50.92 | 53.92 | 58.92 | 52.17 | 43.92 | 39.08 |
| 15             | 61              | 85.65 | 85.65 | 85.90 | 84.26 | 83.93 | 76.31 | 75.16 | 60.98 | 56.56 | 54.67 | 46.80 | 44.59 | 35.16 | 31.17 | 28.36 | 26.48 | 26.39 | 10.66 | 2.79  | 2.29  | 1.32  | 0.73  |
| 16             | 187             |       |       |       |       |       | 79.01 | 75.59 | 69.12 | 61.87 | 53.58 | 50.96 | 53.77 | 50.16 | 56.00 | 53.26 | 51.98 | 45.99 | 43.66 | 39.41 | 24.70 | 16.31 |       |
| 17             | 240             |       |       |       |       |       | 83.46 | 75.29 | 68.88 | 58.29 | 50.21 | 46.08 | 44.33 |       |       |       |       |       |       |       |       |       |       |
| 18             | 69              |       |       |       |       |       | 75.87 | 69.42 | 62.17 | 52.32 | 47.68 | 44.64 | 42.32 | 38.12 | 44.50 | 39.49 | 34.71 | 35.07 | 32.68 | 31.52 | 31.30 | 4.63  | 3.11  |
| 19             | 155             |       |       |       |       |       | 77.13 | 74.19 | 69.68 | 64.23 | 61.77 | 54.84 | 50.58 | 48.71 | 55.40 | 51.19 | 49.10 | 52.10 | 48.32 | 54.03 | 54.48 | 54.55 | 55.10 |
| 20             | 121             |       |       |       |       |       | 76.98 | 74.26 | 70.17 | 63.43 | 61.94 | 55.70 | 52.69 | 47.98 | 49.30 | 47.73 | 46.61 | 51.74 | 45.94 | 50.61 | 49.42 | 47.77 | 40.95 |
| 21             | 140             |       |       |       |       |       | 70.14 | 71.43 | 67.71 | 63.86 | 62.29 | 56.07 | 57.36 | 49.89 | 58.10 | 57.96 | 57.64 | 52.46 | 57.04 | 58.64 | 57.57 | 59.86 | 59.39 |
| 22             | 145             |       |       |       |       |       | 79.31 | 76.90 | 73.34 | 68.45 | 66.66 | 59.72 | 56.38 | 53.41 | 61.10 | 60.03 | 56.59 | 56.69 | 54.72 | 57.97 | 60.27 | 58.86 | 62.58 |
| 23             | 199             |       |       |       |       |       | 71.93 | 68.72 | 64.60 | 58.42 | 54.45 | 46.01 | 43.89 | 37.96 | 42.80 | 42.39 | 42.51 | 42.11 | 40.23 | 47.49 | 46.63 | 48.92 |       |
| 24             | 132             |       |       |       |       |       | 80.77 | 79.66 | 76.10 | 72.95 | 72.23 | 65.34 | 64.09 | 60.08 | 66.40 | 66.78 | 67.12 | 63.67 | 62.50 | 64.09 | 65.30 | 64.34 | 64.81 |
| 25             | 106             |       |       |       |       |       | 80.66 | 78.35 | 74.43 | 70.57 | 67.92 | 60.99 | 55.57 | 53.58 | 58.40 | 64.15 | 57.92 | 55.52 | 45.55 | 56.42 | 59.67 | 19.57 | 3.20  |
| 26             | 136             |       |       |       |       |       | 66.07 | 55.70 | 41.54 |       |       |       |       |       |       |       |       |       |       |       |       |       |       |

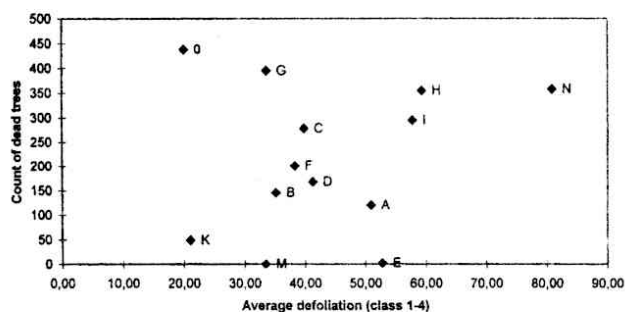


X. Sequence of the transition matrix types of defoliation for Norway spruce

| Permanent plot: | 01 | 02 | 04 | 05 | 06 | 07 | 08 | 09 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
|-----------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| 76:             |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 77:             |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 78:             |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 79:             |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 80:             | A  | E  |    |    |    | E  | N  | H  |    | E  | H  | C  | E  | H  |    |    |    |    |    |    |    |    |    |
| 81:             | E  | E  |    |    | E  | E  | F  | F  | F  | E  | F  | C  | F  | F  | C  | C  | C  | C  | F  | C  | F  | A  | C  |
| 82:             | F  | A  | A  | A  | A  | A  | A  | A  | F  | F  | F  | F  | F  | F  | C  | C  | C  | C  | H  | F  | C  | C  | F  |
| 83:             | A  | G  | C  | A  | G  | A  | B  | C  | F  | C  | F  | F  | G  | F  | C  | C  | C  | C  | C  | A  | E  | C  | A  |
| 84:             | B  | A  | B  | B  | I  | B  | B  | C  | C  | B  | C  | F  | F  | A  | C  | I  | B  | F  | B  | C  | F  | F  | F  |
| 85:             | B  | G  | C  | C  | G  | B  | F  | B  | A  | B  | C  | A  | A  | G  | B  | B  | B  | C  | B  | C  | F  | A  | A  |
| 86:             | B  | B  | B  | B  | B  | B  | N  | B  | B  | B  | B  | B  | B  | B  | B  | B  | B  | B  | B  | C  | A  | B  | B  |
| 87:             | H  | G  | B  | B  | B  | B  | M  | B  | D  | B  | B  | B  | A  | C  | B  | D  | B  | B  | B  | C  | I  | C  | B  |
| 88:             | C  | B  | C  | B  | B  | B  | M  | C  | B  | B  | B  | B  | B  | B  | B  | M  | B  | B  | B  | L  | B  | B  | B  |
| 89:             | G  | B  | B  | B  | L  | B  | N  | B  | B  | B  | B  | G  | B  | B  | B  | B  | B  | B  | B  | B  | B  | B  | B  |
| 90:             | O  | B  | B  | B  | B  | B  | M  | B  | B  | B  | B  | B  | B  | C  | C  | B  | B  | B  | B  | B  | B  | A  | B  |
| 91:             | D  | B  | B  | B  | G  | B  | C  | C  | B  | C  | C  | B  | B  | B  | B  | C  | B  | B  | C  | B  | B  | B  | C  |
| 92:             | D  | B  | C  | B  | B  | B  | C  | B  | B  | B  | B  | B  | B  | O  | B  | B  | C  | B  | B  | B  | C  | B  | B  |
| 93:             | D  | A  | B  | B  | B  | B  | B  | B  | C  | C  | C  | B  | B  | O  | A  | C  | B  | B  | B  | B  | B  | B  | B  |
| 94:             | B  | A  | C  | B  | B  | B  | B  | B  | B  | B  | C  | K  | B  | O  | G  | B  | A  | B  | B  | B  | A  | B  | B  |
| 95:             | B  | E  | B  | B  | B  | A  | B  | G  | B  | B  | G  | B  | B  | M  | G  | O  | B  | B  | B  | C  | B  | H  | O  |
| 96:             | B  | E  | C  | B  | B  | E  | B  | B  | B  | B  | B  | B  | B  | G  | O  | B  | H  | C  | A  | B  | B  | K  | O  |

Statistical evaluation of the difference between the matrix type sequence in the single plots and common (average) sequence during 1981/1982 to 1996/1997 ( $f = 15$ ,  $\chi^2[95\%] = 24.996$ ;  $\chi^2(A) - \text{reference set of all plots}$ ,  $\chi^2(B) - \text{reference set of all plots without the comparative plot}$ )

|      |             |             |     |       |       |     |       |       |
|------|-------------|-------------|-----|-------|-------|-----|-------|-------|
| TVP: | $\chi^2(A)$ | $\chi^2(B)$ | 21: | 17.80 | 30.70 | 25: | 13.23 | 16.65 |
| 01:  | 37.74       | 57.56       | 16: | 20.27 | 8.35  | 14: | 11.25 | 15.00 |
| 15:  | 35.70       | 51.59       | 13: | 16.42 | 22.76 | 12: | 9.51  | 11.82 |
| 08:  | 31.45       | 45.36       | 19: | 14.54 | 22.66 | 09: | 8.38  | 10.50 |
| 24:  | 27.47       | 42.86       | 22: | 14.57 | 22.09 | 04: | 5.50  | 6.37  |
| 23:  | 25.26       | 40.38       | 02: | 17.29 | 21.46 | 05: | 5.04  | 6.11  |
| 06:  | 23.11       | 34.55       | 07: | 14.98 | 20.19 | 20: | 4.53  | 5.29  |
| 18:  | 23.21       | 33.74       | 10: | 12.86 | 17.08 | 11: | 3.79  | 4.43  |



6. Evaluation of the transition matrix types by spruce according to a simulation model (ten year period of the change of initial stand using average transition matrix of the respective type). Initial stand consists of 100 trees of each defoliation classes 0 to 4

the period of observation was characterised by continuous deterioration of stand health (Fig. 8). There was a change in this trend in 1986–1987 (see the changes in average defoliation and frequency of the types of transition matrices), when deterioration slowed down or on the contrary, the health state of beech stands started improving. The improvement was interrupted in some years with increasing defoliation or dieback of other trees.

With respect to the effect of transition matrices of the separate types on a ten-year development model of forest stand (with 100 individuals in each class of defoliation 0 to 4 at the beginning of modelled period; see Fig. 9) types A to I were divided into the following groups:

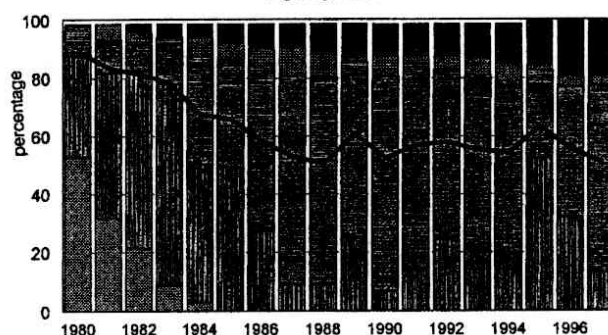
- improvement or stabilisation of stand state – types H, D, or C (applying to maintenance of stand state);
- deterioration of stand state (increasing defoliation or tree diebacks) – types F, E, B, A, I.

It is possible to distinguish three groups of plots (PRP designated by **bold** digits represent stands in which no statistically significantly different sequence of the types of transition matrices was determined in comparison with the whole set of remaining PRP):

- Stands with low defoliation, without any continual several-year period of health state deterioration – PRP **2, 29** (mixed spruce-beech stands).

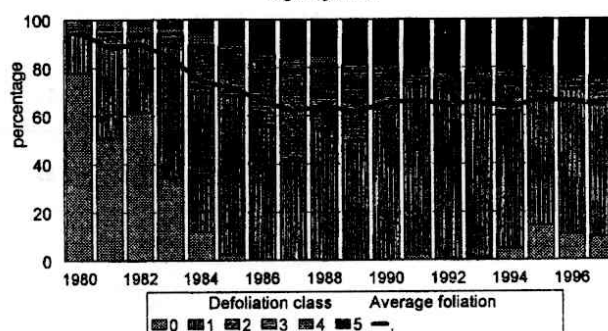
## PRP 27

*Fagus sylvatica*



## PRP 31

*Fagus sylvatica*

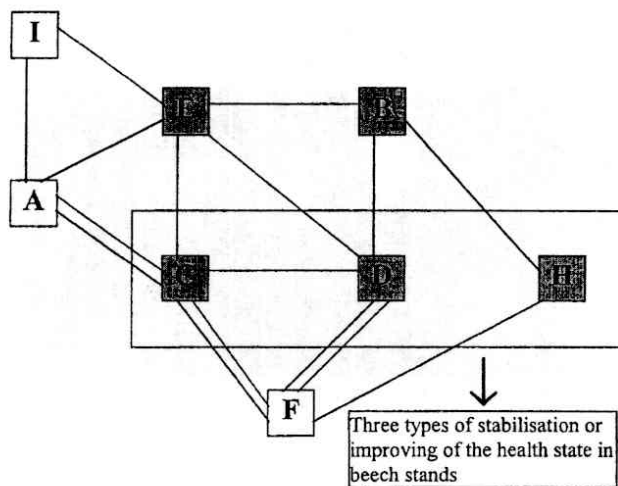


7. Trend of average foliation and particular defoliation class of beech on plots 27 and 31

- Stands with continuous deterioration of health state (increasing defoliation and tree diebacks) – PRP 6, 7, 8, 9 (mixed spruce-beech stands); maximum average defoliation was about 35% in the whole period of observation, maximally 30% of trees died.
- Stands with great damage and a continual several-year period of health state deterioration – PRP **1, 31, 32** (mixed stands) and **27, 28, 30** (beech stands); maximum average defoliation was about 35–45% in the whole period of observation, lower percentage was exceptional (PRP 30), 17–23% of trees died within 17 years, sometimes diebacks were concentrated in a single period (36% of trees died on PRP 1 within a year).

XI. Dynamics of foliage of the beech stands (average values in per cent; totally defoliated trees are included)

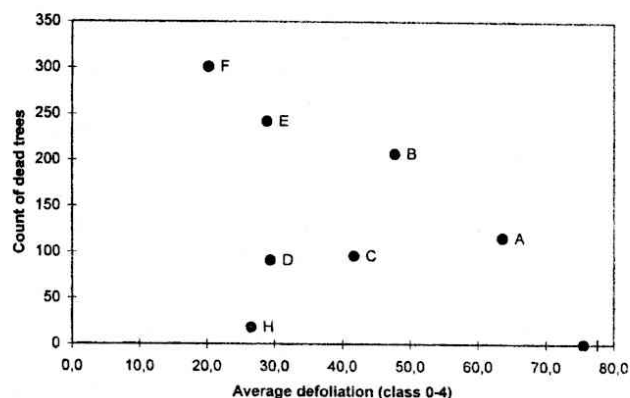
| Permanent plot | Number of trees | Year  |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
|----------------|-----------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|                |                 | 1980  | 1981  | 1982  | 1983  | 1984  | 1985  | 1986  | 1987  | 1988  | 1989  | 1990  | 1991  | 1992  | 1993  | 1994  | 1995  | 1996  | 1997  |
| 27             | 275             | 89.26 | 83.45 | 81.34 | 78.51 | 67.48 | 65.90 | 58.30 | 52.90 | 50.44 | 60.88 | 52.35 | 56.85 | 57.78 | 55.25 | 54.18 | 63.36 | 55.68 | 51.03 |
| 28             | 137             | 95.11 | 90.83 | 89.01 | 84.27 | 72.41 | 71.57 | 66.28 | 63.94 | 64.93 | 69.12 | 63.58 | 68.61 | 69.05 | 67.55 | 60.66 | 69.05 | 61.81 | 57.63 |
| 29             | 69              | 99.45 | 94.91 | 96.27 | 90.00 | 84.64 | 83.64 | 80.18 | 79.10 | 80.18 | 80.91 | 80.55 | 80.09 | 81.48 | 80.27 | 86.72 | 79.73 | 72.94 | 75.18 |
| 30             | 82              | 94.39 | 89.02 | 89.70 | 84.57 | 75.49 | 73.84 | 71.40 | 70.43 | 67.56 | 69.45 | 71.71 | 69.94 | 68.78 | 67.44 | 72.01 | 67.16 | 73.29 | 69.88 |
| 31             | 85              | 94.76 | 88.41 | 89.94 | 84.18 | 74.47 | 71.65 | 66.18 | 61.82 | 64.06 | 61.47 | 65.24 | 66.41 | 64.59 | 65.53 | 63.47 | 66.76 | 65.94 | 64.06 |
| 32             | 105             | 92.14 | 84.81 | 85.44 | 79.03 | 68.50 | 68.01 | 62.38 | 61.02 | 63.88 | 66.36 | 69.46 | 67.77 | 63.16 | 64.71 | 65.44 | 65.44 | 63.60 | 58.91 |



8. Graph of the main sequences of the transition matrix types by *Fagus sylvatica*. Types in grey fields have a frequent repetition

### Mixed stands

Tab. XIII shows foliage dynamics of spruce-beech stands, and it is plotted in Fig. 10 using an example of PRP 2. The average regional foliage of spruce-beech stands was 86.0% in spruce and 95.3% in beech in



9. Evaluation of the transition matrix types by beech according to a simulation model (ten year period of the change of initial stand using average transition matrix of the respective type). Initial stand consists of 100 trees of each defoliation classes 0 to 4

1980, and only 47.3 and 63.4% in 1997, i.e. an average annual increase in defoliation of 2.3% in spruce and 1.9% in beech. In the period of great damage (1981–1988), average foliage ranged between 50.5% and 81.4% in spruce and 68.2% and 89.5% in beech, i.e. an average annual increase in defoliation was 4.1% in

XII. Sequence of the transition matrix types of defoliation for beech

| Permanent plot | 01 | 02 | 06 | 07 | 08 | 09 | 27 | 28 | 29 | 30 | 31 | 32 |
|----------------|----|----|----|----|----|----|----|----|----|----|----|----|
| 80:            | A  | C  | C  | C  | A  | C  | B  | A  | C  | B  | A  | B  |
| 81:            | B  | C  | C  | C  | F  | C  | B  | H  | C  | E  | E  | C  |
| 82:            | B  | C  | C  | C  | C  | C  | E  | B  | C  | E  | A  | B  |
| 83:            | B  | C  | F  | F  | C  | C  | E  | E  | C  | E  | I  | E  |
| 84:            | E  | C  | C  | C  | E  | H  | B  | B  | C  | C  | E  | B  |
| 85:            | C  | C  | C  | C  | E  | B  | D  | B  | C  | C  | C  | B  |
| 86:            | C  | C  | D  | D  | C  | B  | D  | D  | D  | D  | D  | D  |
| 87:            | D  | C  | D  | D  | D  | D  | D  | D  | D  | D  | D  | D  |
| 88:            | F  | A  | E  | F  | D  | E  | D  | D  | D  | D  | D  | D  |
| 89:            | C  | C  | E  | C  | A  | D  | D  | D  | D  | E  | E  | D  |
| 90:            | F  | F  | D  | E  | D  | D  | D  | D  | D  | C  | A  | D  |
| 91:            | D  | D  | C  | D  | F  | F  | D  | B  | D  | C  | E  | D  |
| 92:            | D  | C  | B  | E  | D  | D  | D  | B  | D  | H  | D  | E  |
| 93:            | C  | C  | D  | D  | D  | D  | D  | E  | H  | H  | C  | B  |
| 94:            | C  | C  | F  | F  | D  | D  | D  | H  | F  | H  | C  | B  |
| 95:            | D  | C  | H  | C  | D  | H  | D  | E  | C  | F  | F  | E  |
| 96:            | C  | C  | B  | C  | D  | C  | D  | D  | A  | A  | C  | C  |

Statistical evaluation of the difference between the matrix type sequence in the single plots and common (average) sequence during 1981/1982 to 1996/1997 ( $f = 16$ ,  $\chi^2[95\%] = 24.296$ ;  $\chi^2(A)$  – reference set of all plots,  $\chi^2(B)$  – reference set of all plots without the comparative plot)

| Permanent plot: | $\chi^2(A)$ | $\chi^2(B)$ |
|-----------------|-------------|-------------|
| 31:             | 20.30       | 38.04       |
| 09:             | 18.34       | 31.62       |
| 30:             | 19.83       | 31.01       |
| 08:             | 17.54       | 30.22       |
| 06:             | 17.09       | 27.88       |
| 28:             | 15.78       | 24.74       |

| Permanent plot: | $\chi^2(A)$ | $\chi^2(B)$ |
|-----------------|-------------|-------------|
| 01:             | 14.99       | 22.38       |
| 02:             | 8.93        | 20.95       |
| 07:             | 11.30       | 18.03       |
| 29:             | 9.31        | 15.12       |
| 32:             | 8.57        | 11.80       |
| 27:             | 6.83        | 9.97        |

spruce and 3.1% in beech. If damage caused by bark beetle were excluded, average annual defoliation would be 3.0% in spruce, and excluding damage caused by beech scale and wood-destroying fungi, it would be 2.1% in beech. 1981, 1984, 1986 and 1987 were the years with critical environmental pollution stress, when a reduction in foliage was massive in spruce (by 4.7–7.9%) as well as in beech (by 3.4–8.0%). In the years of damage abatement (1989–1997) average foliage ranged from 47.3 to 50.4% in spruce and from 63.4 to 70.7% in beech, i.e. an average annual increase in spruce defoliation was 0.4% and in beech defoliation 0.9% (it would be 0.2 and 0.4%, respectively, if the effects of biotic pests were excluded). The effect of biotic pests was very harmful on PRP 1 (bark beetle attack to spruce-trees and attacks of beech scale and wood-destroying fungi to beech-trees) – see Váček (1995).

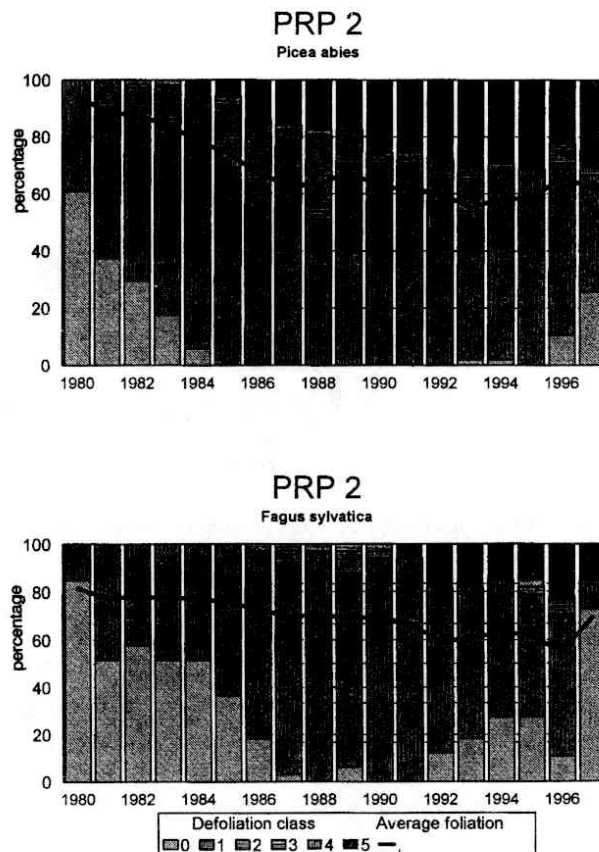
#### General comments on defoliation trends

Six plots with mixed stands were used to compare damage of two main species under identical conditions (cf. Váček, 1989b). Such a low number of plots is not obviously sufficient for this purpose. In general, no substantial differences were observed between the species growing in mixed stand or in pure stand. Therefore the above evaluation by transition matrices was made with respect to tree species not to the group of plots.

There was a decrease in standard deviation of defoliation (STD) in *Picea abies* on the separate plots. Low STD values can be insignificant if the number of trees is small. The zero STD values cannot be taken as actually zero ones because defoliation variability within a classification class and variability neglected due to classification error should be taken into account. Only a homogeneous group of resistant individuals will survive stress impacts. First, STD will increase to ca. 20%, then it will decrease. The stand appears to have a chance of survival when STD decreases to 5–10% and the number of living trees is sufficiently high at the same time. A similar mechanism of decrease in standard deviation of defoliation was observed on some plots with beech. It was more difficult to be discerned because the level of stress to this species was likely relatively lower (higher tolerance of the species).

Damage to *Sorbus aucuparia* was evaluated on two plots (PRP 27 and 29) to obtain additional data. Processes of damage seem to be similar to those in beech.

With regard to the management practices, damage to individual trees or a decrease in their foliage were investigated in relation to tree classes as it can be very important for evaluation of changes in stand structure (Váček, Lepš, 1995). The degree of defoliation can be considered as a criterion of impacts of external factors: crucial importance is ascribed to air pollutants



10. Trend of average foliage and particular defoliation class of spruce and beech on plot 2

in an air-pollution area while a tree class describes growth constitution resulting from natural development of trees in the framework of cenotic relationships in forest stand (Váček, 1987b).

In the period of the first signs of damage (1976–1980), i.e. in forest stands almost free of damage with declining tree class, average foliage is mostly reduced, probably as a result of diminishing light intensity. This relation is most explicit at differentiated age structure, and it is better perceptible in spruce than in beech. This state is disturbed as a result of pollutant impacts in the period of great damage (1981–1988), and foliage in tree classes assumes the values conditioned by a large complex of external and internal factors. The degree of defoliation is related to tree class but the closeness of this relation is associated with the degree of stand damage. Not only subdominant and co-dominant trees but also dominant trees suffer from defoliation with an increasing intensity of pollutant impacts (cf. Váček, 1986b).

Dominant spruce-trees had lower foliage than co-dominant ones on PRP 3, 11, 12, 21 and 23 with great pollution stress as early as in 1984. A similar situation was observed in spruce-trees of spruce-beech stands with pollution stress (PRP 6). This relatively small difference substantially increased as a result of growing pollution stress over the years of observation.



XIII. Dynamics of foliage of the mixed stands (average values in per cent; total defoliated trees are included)

| Permanent plot and species (sm – Norway spruce, bk – beech) | Number of trees | Year  |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
|---|-----------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|   |                 | 1980  | 1981  | 1982  | 1983  | 1984  | 1985  | 1986  | 1987  | 1988  | 1989  | 1990  | 1991  | 1992  | 1993  | 1994  | 1995  | 1996  | 1997  |
| 1 sm  | 31              | 84.19 | 77.74 | 79.03 | 77.10 | 73.87 | 69.35 | 63.39 | 50.65 | 50.48 | 36.45 | 17.42 | 17.50 | 15.32 | 16.09 | 17.26 | 13.71 | 12.71 | 10.96 |
| 1 bk  | 47              | 91.60 | 84.79 | 83.94 | 82.77 | 77.45 | 76.38 | 72.45 | 64.79 | 69.15 | 67.23 | 63.87 | 38.15 | 29.36 | 36.74 | 35.85 | 40.00 | 40.43 | 39.26 |
| 2 sm  | 51              | 94.11 | 88.63 | 87.45 | 84.12 | 78.53 | 74.12 | 67.06 | 63.04 | 63.33 | 67.65 | 62.55 | 61.67 | 60.10 | 55.10 | 58.33 | 58.34 | 58.63 | 61.76 |
| 2 bk  | 33              | 97.73 | 92.73 | 93.64 | 92.73 | 92.73 | 90.45 | 87.12 | 83.64 | 84.39 | 82.87 | 83.18 | 79.85 | 71.36 | 72.27 | 76.21 | 73.64 | 78.03 | 83.03 |
| 6 sm  | 51              | 93.43 | 91.08 | 86.47 | 78.82 | 62.55 | 57.25 | 43.33 | 38.53 | 40.78 | 35.49 | 33.53 | 36.90 | 35.20 | 33.50 | 32.70 | 37.50 | 38.70 | 37.40 |
| 6 bk  | 158             | 95.54 | 90.60 | 89.40 | 86.46 | 77.22 | 73.20 | 68.99 | 58.26 | 60.63 | 57.75 | 58.38 | 61.51 | 61.32 | 57.23 | 54.87 | 59.94 | 59.21 | 50.31 |
| 7 sm  | 30              | 96.50 | 95.50 | 90.67 | 82.50 | 74.67 | 72.67 | 65.17 | 65.17 | 70.33 | 69.83 | 69.17 | 67.00 | 69.67 | 69.67 | 69.17 | 74.17 | 73.18 | 72.83 |
| 7 bk  | 215             | 94.98 | 90.30 | 88.72 | 86.81 | 81.88 | 79.00 | 74.51 | 65.49 | 75.84 | 76.23 | 73.88 | 72.58 | 74.05 | 67.56 | 71.98 | 76.70 | 76.49 | 73.79 |
| 8 sm  | 9               | 58.33 | 53.89 | 48.89 | 51.11 | 51.11 | 48.33 | 46.11 | 31.67 | 31.67 | 36.67 | 29.47 | 38.33 | 45.56 | 34.44 | 38.89 | 47.78 | 45.56 | 42.77 |
| 8 bk  | 97              | 96.24 | 91.86 | 92.01 | 85.72 | 77.11 | 77.53 | 75.52 | 68.56 | 66.91 | 69.69 | 64.02 | 65.21 | 65.67 | 62.89 | 61.65 | 68.25 | 71.50 | 71.75 |
| 9 sm  | 57              | 89.74 | 81.49 | 76.84 | 73.07 | 66.75 | 67.11 | 65.26 | 53.85 | 56.93 | 56.32 | 52.11 | 55.53 | 57.37 | 54.56 | 53.77 | 60.08 | 56.75 | 57.11 |
| 9 bk  | 57              | 95.88 | 86.84 | 84.82 | 84.04 | 78.95 | 80.79 | 78.42 | 68.51 | 65.09 | 70.35 | 64.91 | 65.51 | 62.63 | 59.04 | 59.83 | 64.12 | 70.61 | 62.28 |

The level of vegetation changes was expressed by indexes calculated as a sum of variances of ordination scores for one to four first axes of DCA (calculated for herb layer). The level of stand damage at a locality was expressed as a proportion of trees of a given species that died in 1985–1997, or as maximum determined average defoliation of trees of a given species (in case more than 75% of trees died, maximum defoliation equalled 100%). Relations between these variables were tested by indexes of linear correlation (Tab. XIV).

Data show that the degree of damage can be influenced by the level of change in herb layer structure in the ecosystem; such a result was expected. But the character of this effect was very surprising – changes in herb layer were smaller at greater stand damage. There were relatively small changes in vegetation even in the case of the plots with totally destroyed tree layers (cf. Vacek et al., 1996c). This fact should be analysed in greater detail to avoid its misinterpretation. It is necessary to take into account the following facts and assumptions:

1. Forest stand without cultural treatments that does not suffer any damage increases its density in the process of growth, and this can be a cause of great changes in herbaceous vegetation.
2. It is evident that the herbaceous vegetation of spruce stands that suffered relatively severe damage is similar to clear-cut vegetation after the tree layer was destroyed by decline or felling.
3. Mechanisms leading to damage of the woody component of an ecosystem rarely act as factors of herbaceous vegetation succession.
4. It is to assume that mountainous forest ecosystems are continually disturbed by natural factors; a slightly open character of tree layer is maintained in this way.

The analyses were also aimed at a relation between the level of change in vegetation (in this case expressed as a shift of the plot in DCA four-dimensional space at the beginning of the period of observation and at its end) and height above sea level. The relation was statistically insignificant in general, but a trend of diminishing level of change in vegetation was observed with increasing height above sea level. This trend was least perceptible in beech and mixed stands ( $r = -0.328$ ) while in spruce stands (group of plots designated by Pi) the relation was significant at a 5% level ( $r = -0.539$ ).

A similar attempt to describe the relation between vegetation damage and change was made for moss layer. All results were statistically insignificant, but there was a trend of increase in the level of change in moss layer in forest stands with greater damage (with respect to variability calculated on the basis of the first four or three ordination axes), especially in spruce stands. The trend was more perceptible if the proportion of dead trees was confronted with maximum defoliation

(maximum calculated value of correlation coefficient for spruce stands was  $r = 0.34$ ).

## CONCLUSION

Three typical periods were distinguished with respect to the dynamics of health state of the stands (mainly defoliation) during years 1976–1995. Moderate changes in foliage were determined in the period of the first signs of damage (1976–1980) (average annual increase in defoliation in spruce stands was 0.4%). A perceptible increase in defoliation occurred in the period of great damage (1981–1989) (3.0–4.4% per annum in spruce and 3.1–3.4% per annum in beech). Stabilisation or improvement of stand state were observed in the period of damage abatement (1987–1997) in those stands that were not attacked by pests, mainly by bark beetle.

Average defoliation was increasing in the period of the first signs of damage as the tree class was declining. This relationship was fully disturbed as a result of pollution stress in the period of great damage, and not only subdominant and co-dominant trees were affected by defoliation but also dominant ones. When stand damage is evaluated, it is to be aware of the fact that pollution stress is regularly accompanied by higher sensitivity to some biotic and abiotic factors, and this is explicitly reflected in accelerated (even many times) dynamics of damage and in subsequent stand destruction. The highest tolerance was observed in beech stands, spruce-beech stands showed lower tolerance, and spruce stands were the least tolerant of all.

Trends of stand health can be described by transition matrices. If permanent observation of stand defoliation is used to define up-to-date transition matrices, it is possible to estimate further trends of forest ecosystems quite exactly on the basis of a constructed model. Transition matrices can also be used to identify developmental stages of stand damage and regeneration. The knowledge will be applied to plan forest management measures in forest stands.

XIV. Linear correlation coefficients for variables of change in the herb layer (sum of variances of ordination score for the first one to four DCA axes) and degree of the tree layer damage. All values are not significant except those designated by \* ( $\alpha \leq 5\%$ ) and \*\*\* ( $\alpha \leq 0.5\%$ )

| Sum of variance of the DCA axes                | Maximal defoliation (%) | Share of dead trees (%) |
|--|-------------------------|-------------------------|
| <i>Picea abies</i>                             |                         |                         |
| [1]  | +0.1110                 | +0.1157                 |
| [1]+[2]  | -0.3362                 | -0.1534                 |
| [1]+[2]+[3]                                    | -0.3084                 | -0.1287                 |
| [1]+[2]+[3]+[4]                                | -0.2862                 | -0.1581                 |
| <i>Fagus sylvatica</i> (mixed stands included) |                         |                         |
| [1]  | -0.7572***              | -0.2904                 |
| [1]+[2]  | -0.7517***              | -0.2446                 |
| [1]+[2]+[3]                                    | -0.6612*                | -0.3521                 |
| [1]+[2]+[3]+[4]                                | -0.5346                 | -0.4213                 |

The evidence of forest ecosystem destruction and regeneration based on tree component or stand health evaluation within 21 years was complemented by data on the dynamics of herb and moss layers. The analyses provided information acquired by the study of ground vegetation as an indicator responding to changes in light conditions in the process of defoliation and natural development of stand, limiting the potential of regeneration. The cyclical character of some species that influence, and even prevent in many cases, natural or artificial regeneration (e.g. grass communities with dominance of *Calamagrostis villosa* and high ferns *Athyrium distentifolium*) was confirmed. Reforestation should not be undertaken in the peak developmental stages of these communities. On the other hand, it is worth waiting for about 3–5 years before dominance and sociability are reduced, i.e. until more favourable conditions for reforestation are created. This will largely decrease a risk of reforestation failure as a result of weeds and bracken.

It is to state at the very end of the paper that regeneration targets and methods should be based not only on relative tolerance of tree species in the types of stands but also on their ecological valence, ground layer state and economic possibilities while respecting the present functional importance of the site.

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## STAV LESNÍCH POROSTŮ NA VÝZKUMNÝCH PLOCHÁCH V KRKONOŠÍCH V LETECH 1976–1997

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Podle dynamiky zdravotního stavu, zejména pak defoliace, byla v průběhu sledovaných let 1976–1997 vylišena tři charakteristická období. V období prvních příznaků poškození (léta 1976–1980) došlo k nepatrné dynamice olistění (průměrné roční zvýšení defoliace ve smrkových porostech 0,4 %). V období silného poškození (léta 1981–1989) byl zaznamenán výrazný vzrůst defoliace (3,0–4,4 % ročně u smrku a 3,1–3,4 % ročně u buku). V období ústupu poškození (léta 1989–1997) naopak došlo ke stabilizaci až zlepšení stavu ve sledovaných porostech, které nebyly napadeny škůdci, zejména kůrovcem.

V období prvních příznaků poškození s ustupující stromovou třídou vzrůstala průměrná defoliace. Vlivem imisí v období silného poškození byl tento vztah zcela porušen a defoliace postihovala nejen podúrovňové a úrovňové stromy, ale i jedince nadúrovňové. Při posuzování poškození porostů je nutné brát v úvahu to, že imisní stres je zpravidla provázen zvýšenou citlivostí vůči některým biotickým a abiotickým činitelům, což se mnohdy výrazně (až několikanásobně) projevuje v urychlení dynamiky poškození a následné destrukci porostů. Největší toleranci projevily bukové, nižší smrkobukové a nejnižší smrkové porosty.



Vývoj zdravotního stavu porostů lze dobře popsat pomocí přechodových matic. Při využití permanentního sledování defoliace porostů pro definici aktuálních přechodových matic lze pomocí vytvořeného modelu poměrně přesně odhadnout další vývoj sledovaných lesních ekosystémů. Přechodové matice je možné užít i pro rozlišení vývojových etap poškození a regenerace porostů. Tyto poznatky jsou pak základem pro plánování hospodářsko-úpravnických opatření v porostech.

Poznatky o postupu destrukce i regenerace lesního ekosystému podle hodnocení stromové složky, resp. zdravotního stavu porostů v průběhu 21 let doplňovaly údaje o dynamice bylinného a mechového patra. Z těchto analýz vyplynula i řada poznatků limitujících možnosti obnovy, vyplývajících ze sledování přízemní vegetace jako indikátoru reagujícího na změnu světelných poměrů v průběhu defoliace a přirozeného vývoje

porostu. Bylo zjištěno, že u řady druhů, které ovlivňují a mnohdy až znemožňují přirozenou či umělou obnovu (např. travní společenstva s dominancí *Calamagrostis villosa* a vysokých kapradin *Athyrium distentifolium*), dochází k výrazné cykličnosti. Realizovat obnovu není vhodné zejména v kulminační fázi rozvoje těchto společenstev. Naopak se vyplatí počkat asi 3–5 let, než dojde ke snížení jejich dominance a sociability, tj. k vytvoření podmínek pro obnovu mnohem příznivějších. Značně se tím sníží riziko obnovního neúspěchu daného vlivem buřeně.

V závěru lze konstatovat, že při volbě obnovních cílů a postupů je nutné vycházet nejen z relativní tolerance dřevin v jednotlivých typech porostů, ale i z jejich ekologické valence, stavu přízemního patra a hospodářských možností při respektování současného funkčního významu stanoviště.

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