

Floor vegetation and soil of acidified *Picea abies* forests in the Giant Mountains (Central Europe)

Bylinná vegetace a půdní prostředí acidifikovaných horských smrčín Krkonoš

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Dedicated to František Procházka on the occasion of his 60th birthday

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In autochthonous montane Norway spruce forest of the Giant Mts (Krkonoše Mts) exposed to the airborne acidification, four representative communities identified as *Athyrio alpestris-Piceetum typicum*, *Calamagrostio villosae-Piceetum typicum*, *Calamagrostio villosae-Piceetum fagetosum* and *Sphagno-Piceetum molinietosum* were analysed. Their plant cover, soil profiles and soil acidity were examined as a baseline study on six permanent plots, situated along the gradient of decreasing air deposition. Prevailing soil types were leptic, humic and gleyed podzols. In 1995, B2 horizons were found strongly acid (pH_{aq} between 4.3 and 3.9), and FH horizons were strongly to very strongly acid (pH_{aq} between 2.7 and 3.9). This soil acidity differed from that referred in the same region by Matuskiewicz 35 years ago. In plants, three kinds of long-term responses were distinguished. (1) Abundance of species with most roots in the uppermost horizon was related to the opening of the tree canopy in declining forests (increase of *Deschampsia flexuosa*, retreat of bryophytes *Polytrichum formosum*, *Sphagnum girgensohnii*, *Dicranum scoparium*). (2) Acidophilous forbs (*Homogyne alpina*, *Tridentalis europaea*, *Oxalis acetosella* and *Maianthemum bifolium*) with most roots in the strongly acidified FH horizon became less frequent. (3) In keystone species with root system reaching down to B horizon their reaction was not related linearly to the forest damage and/or soil acidity (e.g. expansion of *Calamagrostis villosa* partly due to its facultative endomycotrophy and/or both dieback and increase of *Vaccinium myrtillus*).

Keywords: Soil profile, soil acidity, phytosociological composition, spruce forest, Krkonoše Mts

Introduction

Decline of montane Norway spruce forests in Central Europe, evoked by acid deposition is accompanied by far-reaching disintegration of these ecosystems (Peřina et al. 1984, Krause 1989, Schulze et al. 1989, Kubíková 1991, Wieder et al. 1998). Biotic interactions and processes affected by the decreasing soil pH, release of toxic cations, shifts in nutrient cycling and resource availability are manifested in changes of floristic composition, population abundance, spreading of grasses and nitrophilous species (Falkengren-Grerup 1989, Pyšek 1992, Fiala 1996). The dynamics of forest decline may differ site by site according to the local loading by pollutants, and with respect to geologic and climatic predisposition, forest composition, physiognomy and management.

Relative sensitivity of ecosystems to acidic input varies within Europe. Apart from Fennoscandinavia, Scotland, Portugal and the Central Alps, the ranges of Bohemian Mas-

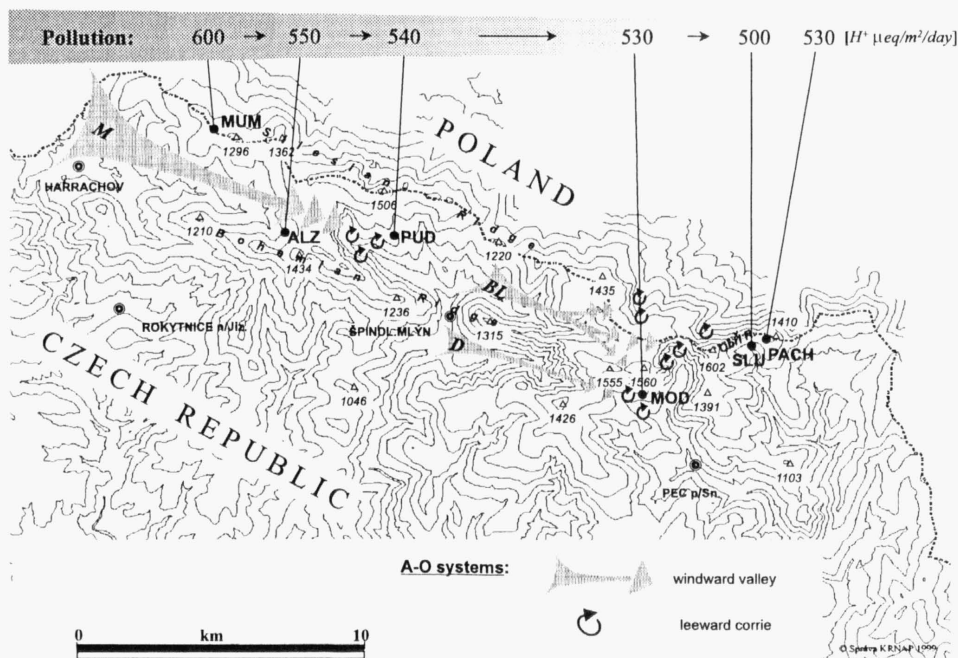


Fig. 1. – Location of the examined six plots in the Giant Mts., the Sudetes with regard to the A-O systems of Mumlava M, Bílé Labe BL and Dlouhý Důl D (Jeník 1961). Decreasing gradient of acidifying deposition (H^+ in throughfall between June 2 and November 4, 1994) is given according to Hošek & Kaufman (1995). Plots: MUM – Mumlavská Mt, ALZ – Alžbětinka, PUD – Pudlava, MOD – Modrý důl valley, SLU – Slunečné údolí valley, PACH – Pašerácký chodník.

sif belong to the highly sensitive regions with a low critical load (Kämäri et al. 1992). In the Giant Mts (Krkonoše/Karkonosze), the topmost range in Bohemian Massif, the critical load was assessed between 50 and 100 $\text{meq } H^+ \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Skořepová & Pokorný 1993). Due to their position eastwards the “Black Triangle”, a region with large coal-burning power plants in Germany, Poland and Bohemia, heavy acid deposition is documented in these mountains (Hošek & Kaufman 1995). In the 1980s, chemical composition of the air, rain-fall, snow and rime showed that the average daily concentration of SO_2 ranged between 13 and 20 $\mu\text{g}/\text{m}^3$ (Štursa 1988).

The flow of polluted air masses in slightly undulating relief of the Giant Mts with rounded heights and wide valleys is lined up by a series of anemo-orographic systems (A-O systems sensu Jeník 1961; Fig.1). Air currents, coming mainly from the west, are gathered by two parallel ridges (Bohemian and Silesian) stretched in the west-to-east direction and streamlined from the foothills up to the accelerating summit plateaux of the western and eastern Giant Mts. To the East, Southeast or Northeast of both these plateaux, increased deposition proceeds to cirques with leeward vortex of air masses polluted by aerosols and ash (Vacek 1981).

Montane spruce forests of the Giant Mts are spread from 900 up to the timberline ranging between 1250 and 1350 m, covering a characteristic montane catena of cambisols and podzols above and below 1100 m, respectively (Pelíšek 1966, Emmer 1996). Initial signs

of forest disturbance induced by acid rain were observed in 1976 (Tesař et al. 1982). In the mid-nineties, almost 80 % of the Norway spruce stands above 900 m a. s. l. disintegrated and their surviving trees showed prominent loss of needles (Vacek & Vašina 1991, Cudlín & Chmelíková 1995), reduced radial increment (Sander et al. 1995), suppressed fructification and viability of seeds (Vacek 1981), retreat of symbiotic ectomycorrhizal basidiomycetes (Cudlín et al. 1990) and large-scale infestation by insects, namely by the larch bud moth *Zeiraphera diniana* (Kalina, Skuhrový et al. 1985).

In spite of numerous observations that have been carried out into damaged trees of the declining Central European forests (see above) and into already deforested areas (Pyšek 1992, Fiala 1996), only marginal attention has been devoted to the non-tree component in these disintegrating ecosystems yet (Fabiszewski et al. 1993, Zolnierz et al. 1994). Thus this baseline study aims at recording of the phytosociological composition and soil acidity in declining autochthonous spruce forests of the Giant Mts under different acidifying deposition in the mid-nineties.

Material

Six autochthonous Norway spruce stands from the upper montane forest zone (above 1100 m a. s. l.) were examined on the plots 50 × 50 m² in size located on the NW-to-NE transect through the Giant Mts (Table 1). Pollution load of the plots was decreasing from the Northwest to the Northeast, acid deposition onto the plots was partly modified by their position within the A-O systems (Fig. 1).

Table 1. – Basic characteristics of the examined Norway spruce stands including their geographic situation, mean age of spruce trees, original density of trees and coefficient of tree damage in 1994 (i. e. product of proportion of dead trees by percentage of complete defoliation derived from data by Vosátka et al. 1995).

Plot	Mumlavská Mt.	Alžbětinka	Pudlava	Modrý důl	Slunečné údolí	Pašerácký chodníček
Latitude	50°49'	50°46'	50°45'20"	50°44'	50°45'	50°45'
Longitude	15°08'	15°11'30"	15°13'30"	15°22'	15°25'30"	15°26'
Age (yrs)	180	200	102	140	154	145
Density (m ⁻²)	0.051	0.063	0.071	0.064	0.08	0.126
Damage	0.86	0.3	0.31	0.14	0.2	0.26

On granites of the western Giant Mts, three plots were chosen on both the windward and leeward slopes of the Mumlava A-O system (Fig. 1). On the westernmost summit of the Silesian ridge, the plot Mumlavská Mt (MUM) was selected in the most polluted part of the Giant Mts where the flow of air currents is gathered into the Mumlava A-O system. Seasonal rainfall is the highest among the examined sites, its 5-months total reached about 580 mm (Hošek & Kaufman 1995, Chmelíková, personal communication). Situated above a steep ravine on the NW-facing slope of Bohemian ridge, the plot Alžbětinka (ALZ) was exposed to the accelerating windward part of the Mumlava A-O system. In the past, it was maintained by stripped clearcutting and drainage. In the leeward part of the Mumlava A-O system, the autochthonous spruce stand Pudlava (PUD) was examined on

the SSE boulder slope of the Labský důl valley. Seasonal rainfall of the 5-months total about 450 mm was least among the examined plots, together with the Slunečné údolí valley.

On mica schists in the eastern Giant Mts the other three plots were placed in leeward positions. The plot Modrý důl (MOD) on the south-facing slope of the Studniční Mt (1560 m a. s. l.) was partly effected by the Bílé Labe and Dlouhý důl A-O systems (Fig. 1). Behind the Sněžka Mt (1602 m a. s. l.), the plots Slunečné údolí valley (SLU) and Pašerácký chodníček (PACH) were located on the south-facing slope beneath the Obří hřbet ridge, the former in its bottom part, the latter 50 m a. s. l. higher.

Methods

Soil investigation and analyses

On the six plots, 18 soil profiles were excavated in 1992 and 1993. General morphological characteristics and classification of these soils were performed according to the Morphogenetic Soil Classification System of Czechoslovakia (Němeček et al. 1990), the nomenclature of humus forms and horizons followed taxonomic classification by Green et al. (1993).

Between May and October 1995, soil solution was sampled twice a month on 10 sites. After vacuum extraction by Superquartz lysimeters (Prenart Equipment ApS, Frederiksberg, Denmark) from the surface organic FH and A horizons pH was measured electrochemically. Soil pH of E, B1 and B2 horizons was determined electrochemically in a 1: 5 m/v soil-water suspension; ten measurements were carried for each horizon on the plot. Discussed pH-values by Zlatník (1925) and Matuskiewicz & Matuskiewicz (1960) were measured colorimetrically. However, both colorimetric and electrometric measurements were found comparable (Falkengren-Grerup 1989).

Diversity and pattern of floor vegetation

Between 13 and 16 September 1995, phytosociological relevés were sampled within the 50 × 50 m plots separately for each main facies (= a homogeneous patch of herb vegetation). Community relevés were assessed by combining the species abundance in the relevés made in a given facies and of facies proportion in the plot. Proportion of the plot covered by the given facies was taken into account. Total sampling area of a community relevé is given in Table 3. Abundance of populations was assessed according to Braun-Blanquet's semiquantitative scale (e. g. Mueller-Dombois & Ellenberg 1974, Moravec et al. 1994), bryophyte species were recorded only if covering more than 10 %. Area covered by dominant populations was assessed from the vegetation maps at the scale 1: 20, taken in downslope belts 30 by 50 m with an inner subgrid of 2.5 m between 12 and 29 August 1994. In syntaxonomic identification of the examined plant communities, classification by Jirásek (1995) and nomenclature by Moravec (1983), for plant names Neuhauslová & Kolbek (1982) were followed. Variability among the facies from different stands/plots was evaluated by means of DECORANA ordination (Hill 1979) after ordinal transformation of the relevé data according to van der Maarel (1979). As a measure of species richness the number of species was used, statistical evaluation among facies was carried out using ANOVA and Duncan's multiple test were used (Table 3).

Differences in composition of the examined phytocoenoses were inferred from the comparison with descriptions given by Jirásek (1995), Vacek (1984: central Giant Mts, southern slopes of the Labský důl valley), Sofron (1981: western Bohemia), Mikyška (1972: Orlické hory Mts), Sýkora (1971: Jizerské hory Mts), Matuskiewicz & Matuskiewicz (1960: northern slopes of Giant Mts), Müller (1936: Jizerské hory Mts) and Zlatník (1925: western and central Giant Mts). The comparison was based on the assumption that for an autochthonous mature successional stage, so called climax community, the sampling and description of the association by phytosociological methods of Zurich-Montpellier school are representative for a given region (Mueller-Dombois & Ellenberg 1974). The comparative relevé in Table 3 was chosen after evaluation of several relevés of the given association according to two reasons: (i) its record was taken as near as possible to the studied plot and (ii) its phytosociological combination was most similar to that in the plot. According to Lepš & Hadincová (1992) subjective errors may appear in phytosociological sampling of rare and/or sparse species (cover degree r or +) due to overlooking and/or differing assessments of their cover degree. This implies that in the phytosociological comparisons only cover degrees of more abundant populations should be included. Our comparison does not measure a change caused by the acid rain, though it may refer to the differences in plant communities under long-term exposure to different acid deposition.

Results

Relevés from the examined plant communities in the Giant Mts belonged to four associations/subassociations. According to evaluation by DECORANA, the facies from plots Mumlavská Mt., Alžbětinka and Modrý důl plots were ordinated separately (except for those with *Deschampsia flexuosa*, *Vaccinium myrtillus* and *Polytrichum formosum*). The clusters correspond to the associations distinguished as *Sphagno-Piceetum molinietosum* (Sýkora 1971) Jirásek 1995, *Athyrio alpestris-Piceetum typicum* Hartmann 1959 and *Calamagrostio villosae-Piceetum fagetosum* (Mikyška 1972) Jirásek 1995 (Fig. 2). Ordination space of the former association was related to the presence of *Molinia coerulea*, and absence of bryophytes (low values on the 1st axis). Contrasting ordination for the relevés from Modrý důl, a representative for the *Calamagrostio villosae-Piceetum fagetosum*, was marked by frequent bryophytes (high 1st values). Ordination of facies belonging to the *Athyrio alpestris-Piceetum typicum* corresponded to the occurrence of species from wet minerotrophic sites and alpine grasslands (high 2nd values), like *Nardus stricta*, *Potentilla erecta*, *Carex pallescens*, *Juncus filiformis*, *Deschampsia cespitosa*. Common ordination space of relevés from Pudlava and the Slunečné údolí valley suggested their syntaxonomic similarity within the *Calamagrostio villosae-Piceetum typicum* Hartmann in Hartmann and Jahn 1967. Central ordination of their facies relevés coincided with the mesic character of the association in the Giant Mts. The relevés from Pašerácký chodníček showed similar ordination to the *Calamagrostio villosae-Piceetum typicum*, on the one hand, and the influence of near treeline, on the other hand; because of its incompleteness and transient composition the stand was classified separately as the *Calamagrostio villosae-Piceetum typicum* var. *avenellosum*.

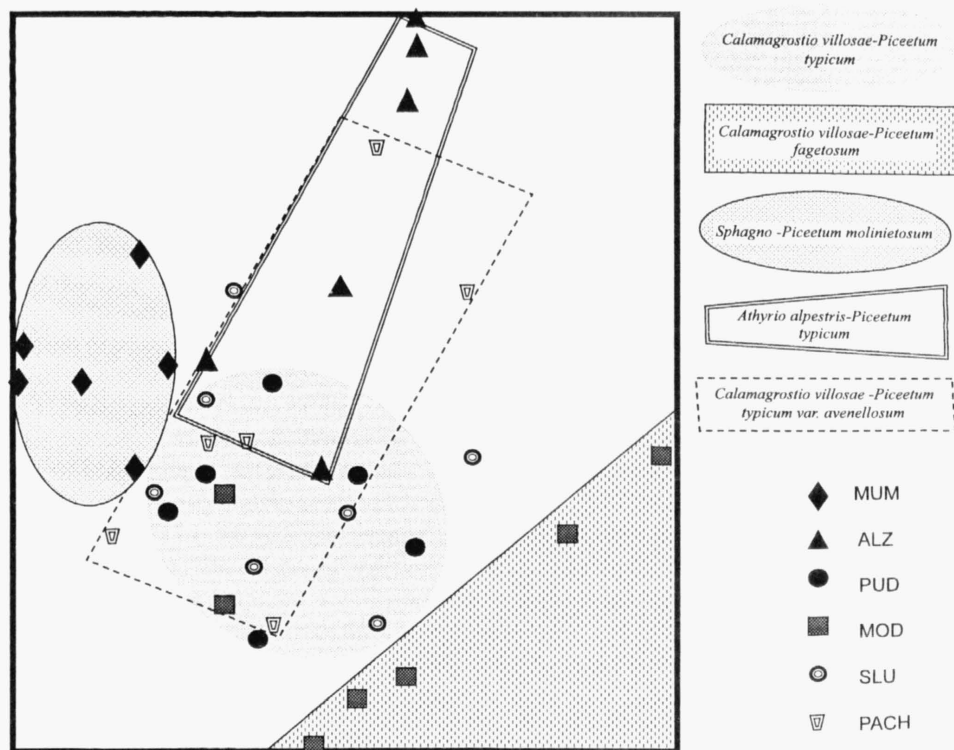


Fig. 2. – Identification of four phytosociological associations in the examined Norway spruce forests in the Giant Mts based on the DECORANA ordination of relevés sampled in the distinct facies on the six plots: MUM – Mumlavská Mt, ALZ – Alžbětinka, PUD – Pudlava, MOD – Modrý důl valley, SLU – Slunečné údolí valley, PACH – Pašerácký chodníček.

Mumlavská Mt: *Sphagno-Piceetum molinietosum*

In this plot, belonging to the most disintegrated forests in the Giant Mts, only 11 trees remained alive in the mid-nineties after ten years of perceptible decline; these 7 % of hardly surviving trees had lost 90 % of their foliage already. Before degradation, the stand belonged to wet spruce forests on the worse drained flat summit, marked by undulating surface with uprooted remnants. The latest remnants of trees with canopy persisted on better drained slopes slightly inclined to the south and southwest.

Soil characteristics: Gleyed and humic podzols prevailed on the compact coarse-grained granite. Gleys and pseudogleys with black placic horizons on impermeable massive granite were more frequent here than in the other plots. Shallow organosols, not deeper than 0.70 m, appeared sparsely. In the course of season groundwater table was fluctuating in a wide range from soil surface to mineral bedrock; in organosols, humus horizons remained water-saturated for most of the year except for long dry periods when water level sank down to the bedrock.

Humus forms in podzols and related soil types were represented mostly by humimors and hydromors with outstanding H horizons. Thickness of the combined F+H horizons ranged between 0.08 and 0.14 m, albic horizon was poorly developed (between 0.04 and 0.09 m). Stony B horizon with about 35 % coarse fragments reached down to 0.90 m, gravel fragments in the depth of 0.40 m were cemented by amorphous material. Soils in the plot were strongly acid (mean pH in FH and B2 horizons reached 3.4 and 4.3, respectively). Horizon A was most acid in the profile, horizon B2 in this plot belonged to the least acid one among the examined plots (Table 2).

Vegetation pattern: Phytosociological composition of the plot in the mid-nineties was most similar to the *Sphagno-Piceetum* subass. *moliniotosum* (Sýkora 1971) Jirásek 1995. Total number of recorded species was lowest among the examined plots; seven facies marked by low species diversity have been distinguished in the community (Table 3).

Extensive predominance of grasses was a conspicuous physiognomic feature, namely that of the omnipresent *Deschampsia flexuosa*. Dense stands of *Calamagrostis villosa* accompanied by abundant *Galium saxatile* covered 33.4 % of the plot on slightly inclined sites. Gleys and organosols of the flat summit were covered by the grass *Molinia caerulea* (7.8 % of the plot), wet microsites were occupied by hygrophilous *Eriophorum vaginatum*, *Carex canescens* and *Juncus filiformis*. On the transition between the facies with *Molinia* and *Calamagrostis*, *Vaccinium myrtillus* occupied 11.2 % of the plot on the driest stony sites.

Comparison with the 25-year-old description given by Sýkora (1971) suggested the following differences in phytosociological composition: (i) higher abundance of grasses, namely of *Deschampsia flexuosa* and *Molinia caerulea*, (ii) less bryophytes (namely *Polytrichum commune*, *P. formosum*, *Sphagnum girgensohnii*) and dicots (*Trientalis europaea*, *Homogyne alpina* and *Vaccinium myrtillus*), and (iii) lower occurrence of *Eriophorum vaginatum*. Abundance of *Dicranum scoparium*, *Dryopteris dilatata*, *Lycopodium annotinum* and *Vaccinium vitis-idaea* in the descriptions was too low to provide a reliable evidence about any change (Table 3).

Table 2. – Distribution of acidity in soil profiles of the examined plots. Maximum and minimum pH-values are given sampled in 1995.

Plot Horizon	Mumlavská Mt	Alžbětinka	Pudlava	Modrý důl	Slunečné údolí	Pašerácký chodníček
FH	3.0–3.9	3.2–3.5	2.8–3.3	3.4–3.8	2.7–4.1	3.3–3.7
A	2.9–3.6	2.8–3.4	3.3–3.7	3.5–4.0	2.7–4.3	3.3–3.6
E	3.4–3.6	3.1–3.5	3.3–3.9	3.7–4.2	3.1–3.8	3.4–3.6
B1	3.8–4.0	3.7–4.2	3.7–4.0	4.1–4.4	3.8–4.0	3.8–4.0
B2	4.3–4.4	4.0–4.3	4.1–4.2	4.2–4.6	4.0–4.1	3.9–4.1

Alžbětinka: *Athyrio alpestris*-*Piceetum typicum*

Declining forest with 41 % of partly disturbed trees (defoliated from 50 %) in mid-nineties, belonged to the highly productive autochthonous spruce stands of the Giant Mts in the past. The plot was marked by a favourable drainage regime that resulted, together with stripped cutting, in a high microsite diversification.

Soil characteristics: Colluvial deposits of porphyric granite were covered by well drained podzols and leptic podzols. Other soil types were rare, gleyed podzols arose along drainage ditches and lithosols on the top of few large stones. The humimor horizons F and H reached a thickness between 0.08 and 0.14 m; albic horizon was well developed in the thickness between 0.08 and 0.16 m. Very deep B horizon with mean stone content of 40 % reached down to 1.60 m on depth. Underground water table was not detected. Soils were very strongly acid (pH in FH and B2 horizons reached 3.2 and 4.2, respectively); horizon A was most acid in the profile.

Vegetation pattern: The community belonged to the *Athyrio alpestris*-*Piceetum typicum* Hartmann et Jahn 1967, an association of well-aerated, nutrient richer habitats near the upper treeline. Despite prominent disturbance of trees, floristic composition was the richest of the examined plots showing 8 facies with the highest species diversity (Table 3).

Most of the plot was covered by expansive stands of *Deschampsia flexuosa*; in 1994 its population occupied 74.8 % of the plot, except for the damp sites and proximity of tree trunks. A mosaic of *Athyrium distentifolium* (two thirds) and *Calamagrostis villosa* (one third) covered 60 % of the area. Hygrophilous species *Sphagnum fallax*, *Juncus filiformis*, *Carex canescens*, or rare *Molinia caerulea* occupied damp sites in gaps. In small openings, species of alpine grasslands, *Anthoxanthum alpinum* and *Nardus stricta*, were established. Vegetation-free spots persisting beneath dense canopy were sparse (2.8 %).

The difference against composition from 1968 and 1977/1978 sampled in the neighbouring Jizerské hory Mts (Sýkora 1971) and Labský důl valley (Vacek 1984), respectively, was marked by (i) higher occurrence of *Deschampsia flexuosa* that occupied originally less than 5 %, (ii) increased abundance of *Calamagrostis villosa* and *Vaccinium myrtillus*, (iii) higher frequency of alpine-grassland species, and (iv) lower abundance of *Athyrium distentifolium* and *Polytrichum formosum* (Table 3).

Pudlava: *Calamagrostio villosae*-*Piceetum typicum* on granite

In the mid-nineties, the plot displayed a progressive decline of the forest. Only 46 % of trees survived and their crowns were injured by 58 % defoliation. The plot was noted by a high spatial variability of moisture. Small dish-like depressions in lower parts of the slope were soaked by underground water. In newly arising gaps with numerous boulders, intensive desiccation of the thin soil profile suppressed establishment of plants, on large boulders the soil profile was even missing.

Soil characteristics: On the colluvium of mid-coarse grained granite the development of podzols prevailed, mainly that of gleyed podzol and humic podzol. The deposits were favourable for intensive lateral movement of underground water. Common humus form was humimor, on waterlogged sites transiting to hydromor. Thickness of the combined F and H horizons ranged between 0.07 and 0.15 m and that of albic horizon between 0.06 and 0.14 m. Underground water table was maintained at about 0.4 m below

surface for most of the season. Soil in the plot was strongly acid, mean pH in FH and B2 horizons reached 3.0 and 4.1, respectively (Table 2).

Vegetation pattern: Floristic composition of the community, recognized as *Calamagrostio villosae-Piceetum typicum* Hartmann in Hartmann and Jahn 1967, was not rich. Seven facies were identified in this community with a low species diversity (Table 3) which was similar to that in the Mumlavská Mt, Slunečné údolí valley and Pašerácký chodníček.

In the mid-nineties, the half-flowering dominant *Calamagrostis villosa* accompanied by abundant *Gentiana asclepiadea* occupied 62.2 % of the area. Bare ground, covering 17 %, was most common on plots in the western Giant Mts. With its 12.5 % of cover, *Deschampsia flexuosa* was marked by the lowest occurrence among the examined plots. Sites sheltered beneath the dense canopy were occupied by mosses, mainly by *Polytrichum formosum*; on wet sites with gleyed podzols *Sphagnum fallax* appeared. *Vaccinium myrtillus* was sparse (7 %) and covered the driest sites on boulders and beneath closed spruce canopy.

Comparison of the present phytosociological composition with that recorded in 1978 on the opposing slope of the Labský důl valley by Vacek (1984) suggests (i) lower present occurrence of bryophytes and ferns (*Polytrichum formosum*, *Dicranum scoparium*, *Dryopteris dilatata*) and (ii) higher abundance of *Deschampsia flexuosa* (Table 3).

Modrý důl: *Calamagrostio villosae-Piceetum fagetosum*

In the mid-nineties, this stand belonged to the best preserved upper montane forests in the Giant Mts, with 59 % of the surviving trees with crowns that lost 35 % of foliage. The plot was situated on a steep slope (Table 1) with two oblongate depressions along little rills occupied by vegetation of damp sites. Between the rills a well-drained convex relief was covered by huge remnants of decaying fallen trees and stumps that prevented soil erosion.

Soil characteristics: Humic and leptic podzols developed on a deep colluvium of mica schists. Soil profiles were very well drained, movement of lateral groundwater was recorded only after snow-melt and/or during rainy periods. In podzols, the thickness of humimor F and H horizons ranged between 0.04 and 0.10 m and that of albic horizon between 0.02 and 0.07 m. Horizon B, with mean stone content of 45 %, reached down to 1.4 m. The soil was least acid among the examined plots, with mean pH reaching 3.7 and 4.4 in FH and B2 horizons, respectively (Table 2).

Vegetation pattern: The community was classified as *Calamagrostio villosae-Piceetum fagetosum* (Mikyška 1972) Jirásek 1995. It was marked by occurrence of numerous shade-tolerant ferns (see the next paragraph) and several species of nutrient-richer sites (like *Calamagrostis arundinacea*, *Prenanthes purpurea*, *Streptopus amplexifolius*). Vegetation diversity accounted both for the high total number of recorded species and for site differentiation: ten species-rich facies were distinguished (most among the examined plots). Mean species diversity of facies did not differ significantly from that in the Slunečné údolí valley (Table 3).

Bare ground covered 37 % of the plot, i. e. most among the examined plots. Grasses occupied 47 % of the surface, of which (i) two thirds belonged to a mixture of loose *Deschampsia flexuosa* with sole tussocks of *Polytrichum formosum* and little shrubs of *Vaccinium myrtillus*, and (ii) a quarter to *Calamagrostis villosa*. Other accompanying spe-

cies *Calamagrostis arundinacea*, *Luzula pilosa*, *Senecio nemorensis*, *Prenanthes purpurea*, *Hypericum maculatum*, *Maianthemum bifolium*, *Oxalis acetosella* and *Streptopus amplexifolius* occupied less than 2 %. *Blechnum spicant*, *Athyrium distentifolium*, *Dryopteris dilatata* and *Phegopteris connectilis* were frequent ferns. In damp sites along rills, hygrophilous species were spread, such as *Deschampsia cespitosa*, *Sphagnum squarrosum* and *S. girgensohnii*.

For a convenient comparison, phytosociological data were exploited coming from the Orlické hory Mts, a near range in the Middle Sudetes (Mikyška 1972). No old satisfactory description of this association was found for the Giant Mts, and thus only a rough regional comparison could be done with a mixed beech stand sampled in the western Giant Mts by Zlatník (1925). Only mild differences were detected in the composition of community, namely lower appearance of the acidophilous forbs *Homogyne alpina* and *Maianthemum bifolium* (Table 3).

Slunečné údolí valley: *Calamagrostio villosae-Piceetum typicum* on mica schists

In the mid-nineties, this spruce stand represented a relatively healthy forest in the Giant Mts. In comparison to the Modrý důl plot, the percentage of surviving trees was lower (45 %) and the degree of defoliation was similar (36 %). The plot verged sharply to the valley bottom of the Jelení potok brook, only the uppermost parts were less inclined. Several soaks were active in the lower part of the plot, scree and stony fields of the middle part were covered by shallow soil profile.

Soil characteristics: Humic and leptic podzols prevailed on the strongly weathered colluvium of mica schist, cambisols developed on sites with higher accumulation of fine particles. Deep stony accumulations of schists were noted by lateral movement of underground water, percolation was active only after snowmelt or heavy rains.

In podzols, the thickness in humimor horizons F and H ranged between 0.06 and 0.19 m, and that of less developed albic horizon between 0.09 and 0.17 m. The B horizon reached 1.9 m in depth and contained 80 % of stones in average. Soil pH in B2 horizon was very acid (mean: 4.0) in FH horizon the soil was very strongly acid, in comparison to other plots its mean value was medium (3.3). The acidity of FH and A horizons over the plot was most variable among the examined plots (Table 2).

Vegetation pattern: The association belonged to *Calamagrostio villosae-Piceetum typicum* Hartmann in Hartmann & Jahn 1967. Floristic composition was not rich, nine facies were recognized with medium species diversity that did not differ significantly from Pudlava, Mumlavská Mt and Modrý důl valley (Table 3).

Bare ground covered 19.2 %, grasses covered more than 60 % of the plot. *Calamagrostis villosa* took over 40.7 % of the area. In the shade, *Deschampsia flexuosa* has extended on 21.8 % and was accompanied by *Polytrichum formosum*. Similar area (20.7 %) was occupied by *Vaccinium myrtillus*, here with the most abundant population among the study plots. *Sphagnum squarrosum* and *Deschampsia cespitosa* were established on damp sites.

Present composition was compared to that reported by Zlatník (1925) in the near Obří důl valley, the phytosociological composition of which corresponded to the later descriptions of the association given by Vacek (1984) and Matuskiewicz & Matuskiewicz (1960). In Zlatník's relevés (i) more bryophytes and dicots were recorded, namely *Dicranum scoparium*, *Trientalis europaea* and *Vaccinium myrtillus*, (ii) while *Calamagrostis villosa* was less abundant (Table 3).

[illegible]

<i>Nardus stricta</i>	.	.	.	.	.	r	.	.	.	.	.	.	.	+	.	.
<i>Rumex alpestris</i>	.	.	.	.	.	r	.	.	.	.	.	.	.	+	r	.
<i>Stellaria nemorum</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
<i>Veratrum lobelianum</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.
<i>Plagiothecium undulatum</i>	.	.	.	1	.	.	+	.	.	.	.	1	.	+	.	.
<i>Potentilla erecta</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
<i>Carex stelullata</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
<i>Poa nemoralis</i>	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.
<i>Senecio nemorensis</i>	.	+	r	.	.	.	.	.	.	.	.	.	.	.	r	.
<i>Oxalis acetosella</i>	+	3	r	.	.	.	.	.	.	.	.	1	+	r	.	.
<i>Maianthemum bifolium</i>	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Polygonatum verticillatum</i>	+	1-2	r	.	.	.	.	.	.	.	.	+	.	.	.	.
<i>Streptopus amplexifolius</i>	.	1-2	+	.	.	.	.	.	.	.	.	.	+	.	.	.
<i>Phegopteris connectilis</i>	+	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.
<i>Blechnum spicant</i>	2	.	r	.	+	.	.	+	.	.	.	+	.	.	.	.
<i>Prenanthes purpurea</i>	+	.	r	.	.	.	.	.	.	.	.	+	.	.	.	.
<i>Hieracium murorum</i>	+	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Calamagrostis arundinacea</i>	.	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.
<i>Hypericum maculatum</i>	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Dryopteris</i> sp. div.	1-2	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.
<i>Huperzia selago</i>	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Polytrichum commune</i>	1	.	.	.	.	.	1	.	.	.	.	.	.	.	2	r
<i>Vaccinium vitis-idaea</i>	+	.	.	2	.	.	.	+	.	.	.	.	.	.	+	.
<i>Lycopodium annotinum</i>	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	+
<i>Athyrium filix-femina</i>	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	r
<i>Polygonum bistorta</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Other bryophytes	.	1	.	1	+	.	+	.	.	.	.	2	1	.	.	.

Pašerácký chodníček: *Calamagrostio villosae-Piceetum typicum* var. *avenellosum*

A mosaic of densely clustered trees surrounded by extensive openings was established on a well-drained mild slope. In the mid-nineties, 45 % of trees survived injured by 47 % defoliation of crowns.

Soil characteristics: Soil profile of the plot was less developed, exposed stony accumulations of schists were covered mostly by shallow leptic and gleyed podzols, in a small area cambisols appeared. Lateral movement of underground water was frequent during the whole season. Slanted lower parts of the plot covered by shallow soil profile and numerous soaks were noted for frequent proofing and tree falls.

In podzols, the thickness of combined humimor F and H horizons ranged between 0.09 and 0.12 m and that of the albic horizon between 0.08 and 0.09 m. In the B horizon, reaching 0.75 m deep, mean content of stones was 75 %. In the FH horizon, mean pH-value of 3.5 suggested very acid soil environment. However, according to bottom limit, the measured acidity was not so low (Table 2). Among the examined plots, B2 horizon with mean pH 4.0 represented the acidmost environments, together with the Slunečné údolí valley.

Vegetation pattern: The vegetation belonged to *Deschampsia flexuosae-Piceetum* Hadač et al. 1969 which was later classified as *Calamagrostio villosae-Piceetum typicum* var. *avenellosum* (Hadač et al. 1969) Jirásek 1995. This later classification coincided with our ordination by DECORANA (Fig. 2) where most of the facies relevés from this plot were projected into the space for the *Calamagrostio villosae-Piceetum* (Pudlava and Slunečné údolí valley). Number of species was only slightly higher than in the other *Calamagrostio villosae-Piceetum* associations, however, 7 facies were distinguished with low species richness, similar to that of the Mumlavská Mt and Pudlava (Table 3).

Physiognomy of the association was predetermined by *Deschampsia flexuosa*, most abundant among the plots in eastern Giant Mts, as frequent as in Alžbětinka. Its carpets with *Polytrichum formosum* covered 67.2 % of the area. In well-drained openings, looser stands of *Calamagrostis villosa* were established on 33.4 % of the plot. Other unshaded microsites were marked by establishment of the species from alpine grasslands (*Nardus stricta*, *Anthoxanthum alpinum*). On sites sheltered by tree canopy, *Luzula pilosa* appeared. Stands of *Deschampsia cespitosa* surrounded wet flushes. Bare ground covered 15.2 % of the area on shaded sites.

Original description of the association comes from the remote Bohemian Forest (Sofron 1981). For comparison, the phytosociological material from the Jizerské hory Mts was exploited, sampled by Zlatník (1925: 25b) in lower montane spruce forest and by Müller (1936). Our plot near the treeline comprised species of the alpine grasslands (*Nardus stricta*, *Anthoxanthum alpinum*, *Rumex alpestris*) and of open wet flushes (*Sphagnum fallax*, *Carex canescens*, *Juncus filiformis*). Comparison of the abundance suggested that the stands in Pašerácký chodníček differed obviously by lower occurrence of acidophilous forbs *Homogyne alpina* and *Trientalis europaea*.

Table 4. – Soil acidity pH_{aq} in the respective horizons of the three associations identical to those in the plots (ALZ – Alžbětinka, PUD – Pudlava, SLU – Slunečné údolí valley, MOD – Modrý důl valley) as sampled in 1924 near Mumlavský waterfall in the western Giant Mts¹ (Zlatník 1925), in 1959 in the Obří důl Valley, eastern Giant Mts² [Matuskiewicz & Matuskiewicz 1960, given as 'minimum (mean) maximum' value, n = number of measurements] and in the mid 1980s by Vacek (³ 1987: V bažinkách, ⁴ 1990: Strmá stráň).

association	horizon	1924	1959	mid 1980s
<i>Athyrio alpestris-</i>	FH	4.2	–	3.3 ⁴
<i>-Piceetum typicum</i>	A	–	4.3 (4.5) 4.8 (n = 22)	3.6 ⁴
(ALZ)	E	5.2	–	3.7 ⁴
	B	4.9	4.5 (4.8) 5.3 (n = 10)	4.1 ⁴
<i>Calamagrostio villosae-</i>	FH	5.0	–	3.1 ⁴
<i>-Piceetum typicum</i>	A	–	4.3 (4.4) 4.5 (n = 11)	3.3 ⁴
(PUD, SLU)	E	4.4 ²	–	3.6 ⁴
	B	4.3 ²	4.5 (4.7) 5.0 (n = 5)	3.6–3.8 ⁴
<i>Calamagrostio villosae-</i>	FH	5.5		3.6 ³
<i>-Piceetum fagetosum</i>	A	–		–
(MOD)	E	–		4.1 ³
	B	4.8 ¹		4.3–4.5 ³

Discussion

Soil acidity

The identified forest communities were related to the soil types observed on the studied plots. In all soil profiles, actual pH-values decreased from subsoil to topsoil horizons, humus horizons showed strongly and very strongly acid reaction, B horizons showed medium acidity. In the respective horizons, pH-values corresponded to the given plant association, e.g. the highest and the lowest pH-values of B horizon were observed in the *Calamagrostio villosae-Piceetum fagetosum* (MOD) and *Calamagrostio villosae-Piceetum typicum* (PUD, SLU), respectively, regardless bedrock and acid deposition. On mineral ground, *Calamagrostio villosae-Piceetum typicum* represented the most acid spruce forest. These observations corresponded to the assessment of Vacek (1987, 1990) and differed partly from the past records by Matuskiewicz & Matuskiewicz (1960) and Zlatník (1925) also who observed the lowest soil acidity in the *Calamagrostio villosae-Piceetum typicum*, but higher pH was in *Calamagrostio villosae-Piceetum fagetosum*, and the highest values in *Athyrio alpestris-Piceetum typicum*. In the last association, pH of A horizon measured by Matuskiewicz & Matuskiewicz (1960) ranged between 4.3 and 4.8 (Table 4), and we assessed similar amplitude but shifted down by 1.5 pH-unit (Table 2). This indicates that the aluminium buffer range near pH 4.2 was reached, which might have slowed down further dropping of acidity (Ulrich 1991). In the most polluted *Sphagno-Piceetum molinietosum* (MUM) its relatively higher soil pH-values probably accounted for the change in decomposition rate of organic horizon that increased in the disintegrating forest due to broad fluctuations of its ground water level and higher temperature in the unshaded ground.

Since the late 1950s, continuous pedological assessments have been carried out by the forestry enterprise Lesprojekt (Materna & Lochman 1988). Certain highly tentative interpretations of their measurements were proposed by Emmer (1996) who concluded that in the Giant Mts an abrupt decrease of pH occurred during 1960s. Since then only slight changes were detected. Also Podrázský (1996) evaluating soil acidity in 35 sites marked by signs of former acidification, mentioned their tendency to restoration since 1983. Similar trends of abrupt acidification followed by restoration were confirmed also in the near Orlické hory Mts (Vacek et al. 1994). To ascribe the decrease in pH measured in different periods and different areas to the effect of acid rain is questionable (Markewitz et al. 1998, Likens et al. 1996). Soil properties in ecosystems are altered spontaneously over long time periods, and, moreover, acid precipitation is only one factor of a complex of sources of acidity in forest ecosystems (Ulrich 1986, Markewitz et al. 1998). Nevertheless, the comparison of measurements from a certain kind of communities done at different time may suggest important information about long-term change in the landscape.

The variability of an ample pH data set sampled by Matuskiewicz & Matuskiewicz (1960) in well-defined soil profiles of the northern Giant Mts may be considered as representative of soil acidity of different types of Norway spruce forests in this region. As stated above, our measurements carried out throughout the 1995 season are overlapping with the range of pH-values from 1959 only marginally. In opposite, the few pH-values gained by Zlatník (1925) in 1924 did not differ from those in 1959 (Table 4). Therefore we suggest that pH in the B horizons of the studied Norway spruce associations decreased. This coin-

cides with the conclusion of Emmer (1996) and also with generally observed trends in Central European coniferous forests (Klimo & Kulhavý 1985, Nilsson 1986 sec. Ulrich 1991).

Plant cover

The compared differences in phytosociological composition under higher acid deposition were more pronounced. The abundance of *Deschampsia flexuosa* was higher on more polluted plots, regardless of the community type. Also lower occurrence of bryophytes was found more often on more polluted plots. This coincides with observations in the Polish Giant Mts where Fabiszewski et al. (1993), analyzing herb layer in three associations of *Piceetum hercynicum* (comparable with *Calamagrostio villosae-Piceetum typicum*, *Sphagno-Piceetum molinietosum* and *Athyrio alpestris-Piceetum typicum*), concluded that the abundances of *Deschampsia flexuosa* and *Polytrichum formosum* were significantly (positively and negatively, respectively) correlated with the degree of canopy damage.

In declining forests the retreat of *Vaccinium myrtillus* (and *V. vitis-idaea*) is often mentioned (Kubiková 1989, Zolnierz et al. 1994). In the latter study this retreat was related to the spreading of grasses (namely of *Calamagrostis villosa*) which does not coincide with our observations. The abundance of blueberry was either (i) decreasing like in *Calamagrostio villosae-Piceetum typicum* and/or *Sphagno-Piceetum molinietosum*, or (ii) stable like in *Athyrio alpestris-Piceetum*, or (iii) even increasing as mentioned by Vacek et al. (1996). According to our comparisons, spread of *Calamagrostis villosa* proceeds independently of *Vaccinium myrtillus*. The detailed research of *Calamagrostis villosa* showed that its expansion is related to its facultative endomycotrophic dependence on *Deschampsia flexuosa* (Soukupová et al. 1998, Vosátka & Dodd 1998).

In contrast to Zolnierz et al. (1994) who mentioned an increase of *Galium saxatile*, *Athyrium distentifolium* and *Oxalis acetosella* (and also of *Chamerion angustifolium* and *Rubus idaeus* occurring in lower altitudes than our plots) we refer to the decline in *Athyrium distentifolium* and *Oxalis acetosella*. Unfortunately, no records are given for acidophilous forbs *Maianthemum bifolium*, *Trientalis europaea* and *Homogyne alpina*. Our comparisons suggest little changes in their occurrence, which coincides with the results of Falkengren-Grerup (1989) from the acidified beech forests in southern Scandinavia where topsoil pH changed from the median value 5.2 to 4.4 over the period of 40 to 60 years. Vascular plants responded in four ways – some of them shifted ecological amplitude towards the lower pH (e. g. *Stellaria holostea*), other increased abundance at lower pH (e. g. *Oxalis acetosella*, *Maianthemum bifolium*), still other increased abundance regardless soil acidity (e. g. *Poa nemoralis*) and the last group responded regardless, soil acidity (*Deschampsia flexuosa*). The above author predicted that spreading of successful acid-tolerant species might be only temporary as most of the examined species were sparse or missing from acid environments. Soil acidity in Giant Mts in the mid-nineties was much lower than that observed in southern Scandinavian forests where ecological optimum of acidophilous dicots ranging between 4.5 and 5.0 pH was ascertained. With further decrease of pH their populations might be reduced and this was confirmed by our observations. We did not find *Homogyne alpina*, *Oxalis acetosella*, *Trientalis europaea* and *Maianthemum bifolium* on sites where pH of the FH horizon was lower than 3.3, 3.5, 3.1 and 3.8, respectively. For instance, *Homogyne alpina*, the highly constant species of Nor-

way spruce forests (Matuskiewicz & Matuskiewicz 1960, Jirásek 1995), was not recorded in two of our plots at all (MUM, PACH) and in MOD its abundance was low.

Three groups of herb species of the declining upper montane spruce forests could be distinguished with regard to the long-term response to airborne acidification: (1) Acid-tolerant species with shallow roots that occupy the uppermost organic horizon where soil acidification is hindered by income of buffering substances from dead plant material. This is namely *Deschampsia flexuosa* that uses available nutrients and increased irradiation, and its spread is not hampered by very acid environment. Simultaneously, unfavourable microclimate and competitive abilities of the spreading grasses suppress bryophytes that are able to exploit only the uppermost organic horizon L. (2) Perennial acidophilous species with deeper roots reaching down to the most acidified horizon FH (or just below it) that obviously retreat due to drastic decrease of pH. (3) The last group is represented by species with root system reaching deep down to the B horizon, such as *Calamagrostis villosa* and *Vaccinium myrtillus*. The response of these keystone species that require enough nutrients for their development is rather complicated, often intermediated by interspecific relationships.

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Souhrn

Imisně podmíněný rozpad středoevropských horských smrčín souvisí s komplexní degradací těchto ekosystémů. V Krkonoších s kritickou zátěží jednou z nejnižších v Evropě, vystavených blízkému sousedství emisních zdrojů Černého trojúhelníka, je odumírání smrkových porostů pozorováno od roku 1976. Zatímco k problematice poškození dřevin i vegetačním imisním poměrům na rozsáhlých imisních holinách se vztahovala řada studií, ovlivnění nestromových komponent v rozpadajících se lesích bylo doposud sledováno jen okrajově. Právě jim, jmenovitě aciditě půdních profilů a fytoocenologickému složení degradujících autochtonních horských smrčín, je věnována tato studie, jejímž hlavním cílem je podat výchozí popis stavu k roku 1995 na šesti trvalých plochách (Mumlavská hora MUM, Alžbětinka ALZ, Pudlava PUD, Modrý důl MOD, Slunečné údolí SLU a Pašerácký chodníček PACH) umístěných v nadmořské výšce cca 1200 m na gradientu kyselá depozice klesajícím v pohorí od severozápadu k severovýchodu (obr.1).

Na podkladě ordinace fytoocenologických snímků odebraných v r. 1995 odděleně pro jednotlivé homogenní úseky bylinného podrostu (facie) byly porosty trvalých ploch zařazeny do čtyř asociací (obr. 2): *Athyrio alpestris-Piceetum typicum* (ALZ), *Calamagrostio villosae-Piceetum fagetosum* (MOD), *Sphagno-Piceetum molinietosum* (MUM) a *Calamagrostio villosae-Piceetum typicum* (PUD, SLU), tato včetně var. *avenelletosum* (PACH, dříve *Deschampsio flexuosae-Piceetum*). Asociacím odpovídalo i zastoupení půdních typů, reprezentovaných nejčastěji podzoly humusovými (PUD, SLU, MOD, MUM), oglejenými (MUM, ALZ, PACH, PUD) a kryptopodzoly (ALZ, PACH, SLU, MOD), případně kambisoly (SLU, PACH) a lithosoly (ALZ, PUD); výjimečně se vyskytovaly gleje, psedogleje a ojediněle organosoly (MUM). Půdní acidita v B2 horizontech dosahovala reakce velmi kyselé (pH_{aq} v rozmezí 4,3 až 3,9), u FH horizontů pak velmi až velmi silně kyselé (pH_{aq} v rozmezí 2,7 až 3,9). Zjištěný soubor hodnot půdní kyselosti jednotlivých půdních horizontů v příslušných společenstvech se odlišoval od souboru pořízeného Matuskiewiczovými v obdobných společenstvech Krkonoš před 35 lety (Matuskiewicz & Matuskiewicz 1960). Při srovnání recentních fytoocenologických snímků se staršími (tab. 3) byly rozdíly ve složení společenstev vyšší při jejich vyšší exponovanosti vůči imisím. U druhů je možno rozlišit tři skupiny reakcí: (1) Druhy povrchově kořenící svou abundancí reagovaly na otevírání rozpadajícího se stromového

patra (rozmístání *Deschampsia flexuosa*, ústup mechorostů *Polytrichum formosum*, *Sphagnum girgensohnii*, *Dicranum scoparium*); (2) Dvouděložné acidofilní byliny kořenující převážně v silně acidifikovaném FH horizontu svou přítomností zřejmě snížily (*Maianthemum bifolium* je uváděno ve snímcích, kde pH v horizontu FH nebylo nižší než 3,8, *Oxalis acetosella* ne níže než 3,5, *Homogyne alpina* do 3,3 a *Trientalis europaea* do 3,1); (3) U druhů s kořenovým systémem dosahujícím do B horizontu není jejich reakce zpravidla přímo závislá na poškození lesa nebo změně půdní acidity, nejčastěji jde o klíčové druhy společenstev podrostu se zprostředkovanými biotickými interakcemi (např. šíření *Calamagrostis villosa* souvisí částečně s fakultativní endomykotrofní závislostí na metličce křivolaké, u populací *Vaccinium myrtillus* nemusí docházet pouze k ústupu).

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