Silva Gabreta	vol. 9	p. 81–104	Vimperk, 2003

Climax spruce forests in the Bohemian Forest

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Abstract
The high diversity conditioned by high habitat variation has been confirmed in spruce forests of the Bohemian Forest. All spruce forest associations analysed in the Czech Republic have been found in this area. In this paper, attention is paid to climax spruce forests, mainly the *Calamagrostio villosae-Piceetum* and *Athyrio alpestris-Piceetum*, further also the *Anastrepto-Piceetum* and *Dryopterido dilatatae-Piceetum*, their phytosociology, ecology, distribution and variability. From the ordination diagram, the relations of the individual spruce-forest syntaxa to soil texture and acidity can be seen.

Key words: vegetation diversity, phytosociology, variability, synecology, distribution, Bohemian Forest, SW Bohemia

Introduction

The first synthetical studies on syntaxonomy and synecology of climax and waterlogged spruce forests of the Czech Republic were published by Sofron (1981), Jirásek (1996), and Jirásek in Husová et al. (2002). However, the studies synthesizing the material from the whole Czech Republic did not sufficiently evaluate the spruce-forests diversity from the Bohemian Forest. Kučera (1978–1990, 1991), Nesvadbová et al. (1994), Sofron (1981, 1985), Sofron & Šandová (1972), Sofron & Štěpán (1971) studied spruce forests in some parts of the Bohemian Forest.

The intensive phytosociological research of the spruce forests in the Bohemian Forest began since 1999. Studies on waterlogged spruce forests, the *Sphagno-Piceetum* (Tüxen 1937) Hartmann 1953, the *Bazzanio-Piceetum* Braun-Blanquet & Sissingh in Braun-Blanquet, Sissingh & Vlieger 1939 and the *Soldanello-Piceetum* Braun-Blanquet, Sissingh & Vlieger 1939 have been published (Neuhäuslová & Eltsova 2001, 2002a, b), as well as the Map of potential natural vegetation of the Šumava NP with its explanatory text (Neuhäuslová 2001). In this contribution, attention is paid to climax spruce forests, above all the most frequent *Calamagrostio villosae-Piceetum* Hartmann in Hartmann & Jahn 1967 and the *Athyrio alpestris-Piceetum* (Hartmann 1959) Hartmann & Jahn 1967 with their lower syntaxa, further to the *Anastrepto-Piceetum* Stöcker 1967 and the *Dryopterido dilatatae-Piceetum* Sýkora ex Sofron 1981.

In the framework of the project of the Grant Agency of the Czech Republic Nr. 206/99/1416 attention was paid to diversity and dynamics of vegetation and soil biota in spruce-forests ecosystems not only in the Šumava National Park, but also in the whole area of the Bohemian Forest.

Basic characteristics of the studied area

The Bohemian Forest is a mountain system lying on the southwestern border of the Czech Republic. The geological substrate is formed mostly by Moldanubicum rocks with prevailing paragneisses and migmatites, and Moldanubicum pluton represented by several broader granite massifs.

Data on the long-term averages of temperature and precipitation in various parts of this mountain system vary markedly (Sofron et al. in Neuhäuslová 2001). Thus, the mean annual temperatures reach approx. 6°C at 700 m a.s.l., at the altitude of ca. 1300 m only 1.3°C. Maximum amplitude between the highest and lowest temperature recorded in the Bohemian Forest was almost 76°C. In the 50-years average, the annual precipitation achieved 797 $mm.yr^{-1}$ in the village Nová Pec (735 m a.s.l.), and, in the 30-years average even 1486–1552 $mm.yr^{-1}$ near Březník (1167 m a.s.l.). However, extreme values in some years exceeded 2000 $mm.yr^{-1}$. The soils at higher altitudes correspond to podsols or spodo-dystric cambisols, less frequently rankers, histosols or lithosols.

In 1991, nature- and landscape protection on the Czech side of the Bohemian Forest resulted in the declaration of the Šumava National Park. However, some parts of the Bohemian Forest have been protected earlier (see Zatloukal in Neuhäuslová 2001). In 1963, the Šumava Protected Landscape Area has been declared. In 1990, the Bohemian Forest (=Šumava Mts.) became a member of the world system of UNESCO Biosphere Reserves.

Methodology

Phytosociological relevés were recorded according to the principles of the Braun-Blanquet approach (Braun-Blanquet 1964, Moravec 1994). For the dominance and abundance estimation the 7-grade scale (Braun-Blanquet 1964) was used. Relevés were collected mainly in the field by the first author, partly with J. Sofron or J. Jirásek, and also published data or manuscripts from the Bohemian Forest have been used, above all Sofron (1981), Sofron & Štěpán (1971), Vorel (1968). The data set was stored using the database program TURBO(VEG) (Hennekens 1996, Hennekens & Schaminee 2001) and analysed by the program TWINSPAN (Hill 1979). The final display of the relevés was performed subjectively, being based mainly on the results of TWINSPAN synthesis and field experience.

Detrended corresponce analysis (DCA) in the program package CANOCO for Windows (ter Braak & Šmilauer 1998) was used for presentation of variation among the communities. The rare species occurring in less than 3 relevés were excluded from the analysis.

The nomenclature of higher plants follows Ehrendorfer (1973), that of bryophytes Frahm & Frey (1992) and the names of lichens are after Poelt (1969). The names of syntaxa have been used according to Moravec (1995).

Basic characteristics of the spruce-forest syntaxa

A. *Calamagrostio villosae-Piceetum* Hartmann in Hartmann & Jahn 1967 (Tables 1–3)
(Synonymum: *Soldanello-Piceetum* sensu Sofron & Štěpán 1971 p. max. p.)

Diagnostic species combination: Tree- and shrub layer (T, S): *Picea abies*, field layer (F): *Avenella flexuosa*, *Calamagrostis villosa*, *Dryopteris dilatata*, *Luzula sylvatica*, *Picea abies*, ground layer (G): *Dicranum scoparium*, *Polytrichum formosum*.
Structure, species composition: This community is formed of three- to four-layered spruce stands with weakly closed shrub layer, and mostly a dense field layer dominated by grasses or

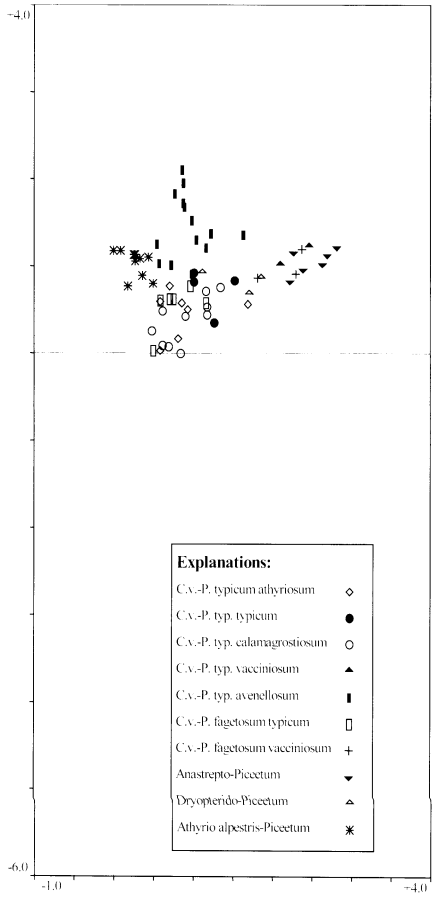

Fig. 1. Ordination diagram (DCA) of the communities.

other graminoids (*Avenella flexuosa*, *Calamagrostis villosa*, *Luzula sylvatica*) or dwarf-shrubs (*Vaccinium myrtillus*). Acidophilous species of spruce- or spruce-beech forests are frequent. Rarely, *Oxalis acetosella* belongs to subdominant species. The forest regeneration is very weak in spruce plantations, in near-natural forests a little better, but a high stocking rate of red deer has been reducing very markedly the regeneration of broadleaved trees and fir. Also the ground layer is well developed, very rich in species, formed by mosses, liverworts and Sphagna, and lichens. *Polytrichum formosum* and *Dicranum scoparium* are the most frequent mosses. Liverworts occur mostly with very low dominance. *Sphagnum girgensohnii* is frequent, but its cover is usually low.

Ecology: Climax forests at the highest altitudes of the Šumava National Park and Protected Landscape Area, mostly over 1200 (1250) m a.s.l., on the tops of mountain ridges and isolated hills and in the upper part of slopes. At inversion levels, these stands cover the border zone of frost basins and valleys with accumulated cold air. The climate is characterized by a very short (up to short), cold (up to moderately cold), moist up to very moist summer, with the mean annual temperature 2–4°C, January isotherm –3°C to –7°C and long-lasting snow cover, lying 140–180 days per year (Quitt 1971).

The soils correspond mostly to humus podsols or iron-humus podsols, developing on mica-schists, paragneisses or granitoids. They are sandy-loamy, loamy-sandy to sandy (in deeper horizons), with an admixture of scree or stones. In analyzed soil samples, the $pH_{(KCl)}$ values were very low (2.8–3.6) in higher horizons, deeper they achieved values of ca. 3.3–4.0. From exchangeable cations, Ca^{2+} varied between 1.4–5.3 meq/100 g dried soil in the A_1 horizon (exceptionally >8 meq/100 g dried soil, influence of soil liming). The exchangeable Al^{3+} achieved ca. 3–17 meq/100 g dried soil. The saturation of sorption complex with bivalent cations (Ca^{2+} and Mg^{2+}) was very low (1.6–6 meq), the C:N ratio ranges between 17–22 (see Table 6). In the analysed soil samples a marked accumulation of Al^{3+} or, less frequently, H^+ ions is to be observed, above all in soils of the typical subassociation (Table 6, analyses 1–3) and the *Vaccinium myrtillus*-Variant of the *Calamagrostio villosae-Piceetum fagetosum* (Table 6, analyses 4–5).

Variability: In this association, two subassociations can be distinguished – the typical subassociation (*Calamagrostio villosae-Piceetum typicum* with 5 variants), and the subassociation with beech (*Calamagrostio villosae-Piceetum fagetosum* with two variants).

1. *Calamagrostio villosae-Piceetum typicum* Hartmann in Hartmann & Jahn 1967 (Tables 1 and 2)

Less frequent subassociation of the ass. *Calamagrostio villosae-Piceetum* in the Bohemian Forest (Neuhäuslová 1998, 2001) with prevailing *Picea abies* in the mostly monospecific tree layer and sporadically developed shrub layer. Besides *Sorbus aucuparia*, the proportion of other species in these two layers is sporadic. In the field layer, grasses (*Avenella flexuosa*, *Calamagrostis villosa*), dwarf shrubs (*Vaccinium myrtillus*), less frequently *Luzula sylvatica* with *Athyrium distentifolium* prevail. The cover of the ground layer achieves mostly 20–60%.

This unit represents the ecological optimum of the *Calamagrostio villosae-Piceetum*, occurring on moist to fresh nutrient-poor podsol soils rich in scree and stones at the altitudes about 1250–1300 m a.s.l. and higher. The climate is cold, with 160–180 frost days.year^{-1} and the mean January temperature between –6°C up to –7°C.

On the basis of differences in the floristic composition and/or dominants, the following variants can be distinguished: a) var. with *Athyrium distentifolium*, b) typical variant, c) var. with *Calamagrostis villosa*, d) var. with *Vaccinium myrtillus* and e) var. with *Avenella flexu-*

osa. The sequence of the individual variants in Tables 1 and 2 corresponds to the diminishing soil moisture.

a) *Calamagrostio villosae-Piceetum typicum* var. *athyriosum* Jirásek 1996 (Table 1, rel. 1–7)

This variant representing a link with the *Athyrio alpestris-Piceetum* and covering moderately concave relief forms with long-lasting snow cover is characterized by the dominance of *Calamagrostis villosa* or *Vaccinium myrtillus*, partly with codominance of *Luzula sylvatica*, *Oxalis acetosella* or *Athyrium distentifolium*. Sometimes, *Luzula sylvatica* dominates the field layer. This syntaxon is differentiated by the more or less regular occurrence of hygrophilous species *Athyrium distentifolium*, *Oxalis acetosella* (sometimes with high cover) and *Soldanella montana*, rarely *Streptopus amplexifolius*, *Prenanthes purpurea* or *Cicerbita alpina* and *Polygonatum verticillatum*. From the bryophytes, *Lophozia ventricosa* and *Plagiothecium undulatum* differ this variant from the following ones. The soils are well aerated, their humification and moisture are favourable, the water content the highest among the subunits of the typical subassociation. Stands of this variant cover mostly shady levels above 1270 m a.s.l. At inversion levels of cold mountain valleys, they occur at lower altitudes, below 1150 m a.s.l. (e.g. Table 1, rel. 2).

b) *Calamagrostio villosae-Piceetum typicum* var. *typicum* Jirásek 1996 (Table 1, rel. 8–11)

For this variant, absence of differential species is characteristic. In the field layer, species form a mosaic without any marked dominance of one taxon only. Together with *Calamagrostis villosa*, the species *Avenella flexuosa*, *Dryopteris dilatata*, *Lycopodium annotinum* and/or *Vaccinium myrtillus* belong to the most frequent. *Polytrichum formosum*, sometimes together with *Dicranum scoparium*, prevails in the species-rich ground layer.

In the Bohemian Forest, this variant is relatively rare. It was found on convex, mostly moderate slopes, at higher levels of the mountain border ridge or in the sub-top areas of isolated mounts. The habitat conditions represent the ecological optimum of the whole subassociation.

c) *Calamagrostio villosae-Piceetum typicum* var. *calamagrostiosum villosae* Jirásek 1996 (Table 1, rel. 12–21)
(Syn.: *Soldanello-Piceetum* var. with *Calamagrostis villosa* sensu Sofron & Štěpán 1971, see also *Picea-Calamagrostis villosa* soc. Hilitzer 1929)

This variant is characterized by a marked dominance of *Calamagrostis villosa* with a subdominance of *Avenella flexuosa*, and with a low proportion of dwarf-shrubs (*Vaccinium myrtillus*, absence of *Vaccinium vitis-idaea*). The species of moist soils *Blechnum spicant* (differential species), *Luzula sylvatica*, *Lycopodium annotinum*, *Soldanella montana* are relatively frequent. Besides *Dicranum scoparium* and *Polytrichum formosum*, species *Dicranodontium denudatum*, *Sphagnum girgensohnii*, *Barbilophozia lycopodioides*, *Rhytidiadelphus loreus*, *Lepidozia reptans* occur frequently in the ground layer, indicating favourable water regime of these podsol soils with a weaker decomposition of organic material. However, in comparison with the both foregoing variants, some hygrophilous bryophytes are less frequent (*Sphagnum girgensohnii*, *Polytrichum commune*) and the soil moisture is lower.

This variant belongs to the frequent syntaxa of the climax spruce forests in the Šumava National Park and the whole area of the Bohemian Forest. However, in the last few years, a certain shift to the dominants changes in the field layer to the benefit of *Avenella flexuosa* can be found (Wild et al. 2003).

Variant	*athyriosum*								*typicum*					*calamagrostiosum villosae*											*vaccinisum*		
Relevés, nr.	1	2	3	4	5	6	7	%	8	9	10	11	%	12	13	14	15	16	17	18	19	20	21	%	22	23	%
Number of species	24	23	26	21	26	24	22		27	15	16	14		23	17	37	33	11	24	25	18	33	18		21	13	
T																											
Picea abies	4	4	3	3	4	4	3	100	4	3	3	4	100	4	5	5	4	4	4	4	4	3	4	100	3	4	100
Sorbus aucuparia								0				+	25					1						10	2		50
S																											
Picea abies	1	1		+		+		57	+	1	+		75		1	+	1		+	+		1	1	70			0
Sorbus aucuparia				r			r	29					0			+						r	+	30			0
F Diff. *Calamagrostio villosae-Piceetum typicum athyriosum*																											
Athyrium distentifolium	+	2	+	+	+	+	2	100					0											0			0
Diff. *Calamagrostio villosae-Piceetum typicum calamagrostiosum villosae*																											
Blechnum spicant								0					0		+	+	r					+		40			0
Diff. *Calamagrostio villosae-Piceetum typicum vacciniosum*																											
Vaccinium myrtillus			3	+	r	+		57	r	2	+		75				1				+	r	2	2	50	4	4	100
Vaccinium vitis-idaea								0					0											0		1	50
a)																											
Calamagrostis villosa	4	2	4	3	1	4	3	100	2	2	2	2	100	5	5	4	5	5	3	3	3	3	3	100	2	1	100
Luzula sylvatica	2	2	2	2	4	2	2	100	1	1	1	1	100	2	1	1	2	1	2	1	+	2	1	100	1		50
Homogyne alpina	+	1			+	+	+	71		+			25			1	+			+		+	1	50	1		50
Soldanella montana		+	+	+	1		+	71					0	+	1	+	+							40	+		50
Lycopodium annotinum	2		2	1		1		57	+	2			50		2		1		2	+	2	+		60			0
Streptopus amplexifolius			+	+	+		+	57					0		r	+								20			0
Trientalis europaea		+	1				1	43			+		25		+	+	r	+					r	50	1		50
b)																											
Avenella flexuosa	3	1	2	2	1	2	2	100	+	1	2	2	100	+	3	+	+	2	2	2	2	2	2	100	2	2	100
Dryopteris dilatata	+	1	2	2	1	1	1	100	+	2	2	2	100	1	1	+	r	1	+	1	2	2	1	100	1	+	100
Oxalis acetosella	+	1	1	1	2	1	r	100	r	1	1	2	100	+	1	+	+	1	+				1	+	80	+		50
Maianthemum bifolium	r		r			+		43			+		25	+	1	1	+	+						50	1		50
Galium saxatile			+	1	1			43					0											0			0
c)																											
Prenanthes purpurea					+		r	29					0											0			0
Phegopteris polypodioides			1					14					0											0			0
Polygonatum verticillatum					+			14					0	+	+								r	30			0
d)																											
Rubus idaeus			r			r		29					0											0			0
Carex pilulifera						r		14					0			r								10			0
Melampyrum sylvaticum								0					0									+		10		+	50
e)																											
Picea abies		1	+	1	+		+	71	+	1		1	75	+	+	+	r		1	+	+	+	2	90	r	+	100
Sorbus aucuparia	r			1	+		1	57	+	+		r	75				r	+		+		+		40		+	50
G																											
Dicranum scoparium	2	2	+	1	2	2	1	100	2	1	1	2	100	+	1	1	1	1	2	2		1	2	90	2	2	100

Polytrichum formosum	3	2	1	2	2	2	2	100	3	2	1	1	100	2	2	2	2	1	3	2	1	1	2	100	2	2	100
Lophozia ventricosa	r	.	+	+	+	+	+	86	.	.	.	.	0	.	.	+	.	.	.	+	.	r	.	.	30	.	.	0
Polytrichum commune	1	1	2	.	.	+	1	71	+	2	.	r	75	.	.	1	+	.	.	.	.	.	.	20	.	.	0
Barbilophozia lycopodioides	+	2	.	.	+	+	.	57	+	.	+	+	75	+	.	+	+	.	+	+	+	+	+	80	.	+	50
Dicranodontium denudatum	.	1	+	+	+	.	.	57	+	+	.	.	50	r	.	+	+	.	+	+	1	+	+	80	.	.	0
Plagiothecium undulatum	1	+	.	.	.	+	.	43	.	.	.	.	0	+	.	.	.	.	.	.	.	1	.	20	.	.	0
Lepidozia reptans	+	.	.	+	.	.	.	43	+	.	.	.	25	.	.	+	+	.	+	.	.	+	.	40	.	.	0
Tetraphis pellucida	r	.	.	+	.	.	+	43	r	.	.	.	25	.	.	+	r	.	+	.	.	+	+	50	.	.	0
Rhytidiadelphus loreus	r	3	.	.	.	.	.	29	+	.	1	r	75	r	.	+	1	.	+	1	.	+	+	70	1	.	50
Cladonia digitata	+	.	.	.	.	.	+	29	+	.	r	.	50	.	.	+	+	.	+	.	+	r	.	50	.	.	0
Ptilidium ciliare	+	.	.	.	.	.	+	29	.	.	.	.	0	.	.	.	.	.	.	+	.	+	.	20	.	.	0
Calypogeia integristipula	.	+	.	.	.	+	.	29	.	.	.	.	0	.	.	.	.	.	.	.	.	r	.	10	.	.	0
Sphagnum quinquefarium	.	.	1	+	.	.	.	29	.	.	.	.	0	.	.	.	.	.	.	.	.	1	.	10	.	.	0
Cephalozia bicuspidata	.	.	+	.	.	.	+	29	.	.	.	.	0	.	.	.	.	.	.	.	.	.	.	0	.	.	0
Bazzania trilobata	+	.	.	.	.	.	.	14	+	.	.	r	50	+	.	1	+	.	.	+	.	.	.	40	.	.	0
Cephalozia lunulifolia	.	+	.	.	.	.	.	14	+	.	.	.	25	.	.	r	.	.	.	.	.	.	.	10	.	.	0
Barbilophozia attenuata	.	+	.	.	.	.	.	14	.	.	.	.	0	.	.	.	.	.	+	.	.	.	.	10	.	.	0
Plagiothecium laetum	.	.	+	.	.	.	.	14	.	.	.	.	0	.	.	.	.	.	.	+	+	+	.	30	+	+	100
Pleurozium schreberi	.	.	.	.	+	.	.	14	.	.	.	.	0	r	.	.	.	.	+	.	.	r	.	30	1	.	50
Cladonia coniocraea	.	.	.	.	.	+	.	14	.	.	.	.	0	.	.	.	.	.	.	.	+	r	.	20	.	.	0
Calypogeia sp.	.	.	.	.	.	+	.	14	r	.	r	.	50	.	.	r	.	.	.	.	.	.	.	10	.	.	0
Cladonia fimbriata	.	.	.	.	.	+	.	14	+	.	.	.	25	.	.	+	.	.	.	.	.	.	+	20	.	.	0
Calypogeia azurea	.	.	.	.	.	.	+	14	r	.	.	.	25	+	.	+	.	.	.	.	.	.	.	20	.	.	0
Anastrepta orcadensis	.	.	.	.	.	.	.	0	+	.	.	.	25	.	.	r	.	.	+	.	+	+	.	40	.	.	0
Cladonia gracilis	.	.	.	.	.	.	.	0	+	.	.	.	25	.	.	.	.	.	.	.	.	.	.	0	.	.	0
Cladonia chlorophaea	.	.	.	.	.	.	.	0	+	.	.	.	25	.	.	+	+	.	.	.	+	.	.	30	.	.	0
Cladonia phyllophora	.	.	.	.	.	.	.	0	+	.	.	.	25	.	.	r	+	.	.	.	.	.	.	20	.	.	0
Mylia taylorii	.	.	.	.	.	.	.	0	r	.	.	.	25	.	.	.	+	.	.	.	.	.	.	10	.	.	0
Ptilidium pulcherrimum	.	.	.	.	.	.	.	0	.	.	.	.	0	r	.	+	r	.	+	+	.	.	.	50	.	.	0
Barbilophozia floerkei	.	.	.	.	.	.	.	0	.	.	.	.	0	.	+	.	.	.	+	+	+	+	.	50	+	.	50
Plagiothecium sp.	.	.	.	.	.	.	.	0	.	.	.	.	0	+	.	r	.	.	+	.	.	.	.	30	.	.	0
Cladonia rangiferina	.	.	.	.	.	.	.	0	.	.	.	.	0	.	.	.	+	.	+	.	.	.	.	20	.	.	0
Dicranum fuscescens	.	.	.	.	.	.	.	0	.	.	.	.	0	.	.	.	.	.	.	.	+	+	.	20	.	.	0
Lophocolea heterophylla	.	.	.	.	.	.	.	0	.	.	.	.	0	.	.	.	.	.	.	+	.	.	.	10	.	+	50

Species in one relevé only: F: *Acer pseudoplatanus* (3:r), *Carex canescens* (14:r), *Cicerbita alpina* (5:+), *Gentiana pannonica* (7:+), *Hupezia selago* (2:+), *Listera cordata* (15:r), *Persicaria bistorta* (22:+), *Solidago virgaurea* (20:r), *Senecio hercynicus* (5:r), G: *Brachythecium reflexum* (18:+), *Calypogeia muelleriana* (12:+), *Cephaloziella rubella* (14:+), *Chiloscyphus polyanthos* (18:+), *Cladonia squamosa* (14:+), *Cladonia uncinalis* (22:+), *Cladonia pyxidata* (17:+), *Dicranella heteromalla* (12:r), *Dicranum polysetum* (12:+), *Hylocomium splendens* (18:+), *Icmadophila ericetorum* (19:+), *Lophocolea bidentata* (20:r), *Marchantia polymorpha* (15:+).

Explanations: T – tree layer; S – shrub layer; F – field layer; G – ground layer; Diff. – differential species; a) diagnostic species of the class *Vaccinio-Piceetea* and lower syntaxa; b) acidophilous forest species of a large phytosociological and ecological amplitude; c) diagnostic species of the class *Querco-Fagetea*; d) other species; e) juvenile trees.

Localities in Table 1. *Calamagrostio-Piceetum typicum*

Calamagrostio-Piceetum typicum athyriosum

1. Prášily, Jelení skok, 400 m^2, 1270 m a.s.l., E, 5°, T 65%, S 5%, F 100%, G 45%, Vorel 1968, Table 1, rel.13/42P, 1963.
2. Ptačí Vrchy Hills, 400 m^2, 1140 m a.s.l., NNW, 7°, T 60%, S 5%, F 80%, G 20%, Neuhäuslová 15/1999.
3. Špičník Mt., above of road turning, 400 m^2, 1260 m a.s.l., NW, 5°, T 35%, S 0%, F 90%, G 15%, Neuhäuslová 29/1999.
4. Ca. 400 m E from the Pytlácký Roh locality, above of new road, 400 m^2, 1290 m a.s.l., NW, 10°, T 40%, S 1%, F 80%, G 20%, Neuhäuslová 26/1999.
5. Boubín Mt., near the top, above the spring, 400 m^2, 1280 m a.s.l., SE, 15°, T 60%, S 0%, F 85%, G 15%, Neuhäuslová & Jirásek 102/1999.
6. Poledník Mt., moderate convex slope, 1280 m a.s.l., ESE, 3°, T 70%, S 3%, F 95%, G 50%, Vorel 1968, Table 1, rel. 14/12P, 1962.
7. Blatný Vrch Hill, ca. 2,5 km WSW from Březník, 1350 m a.s.l, 400 m^2, ENE, 25°, T 40%, S 1%, F 75%, G 10%, Neuhäuslová 25/1999.

Calamagrostio-Piceetum typicum, typical var.

8. Near the top of Oblík Mt., 1230 m a.s.l., 400 m^2, E, 20°, T 80%, S 3%, F 50%, G 25%, Vorel 1968, Table 1, rel. 25/9Sr.
9. 1.5 km W from the top of Černá Hora Mt., SSW from Kvilda, 200 m^2, 1260 m a.s.l., NW, 5°, T 40%, S 5%, F 40%, G 50%, Neuhäuslová & Jirásek, 111/1999.
10. Stráž Mt., top-near level, 400 m^2, 1302 m a. s. l., SE, 2°, T 50%, S 2%, F 60%, G 15%, Neuhäuslová & Jirásek 82/2000.
11. Černá Hora Mt., top area, 400 m^2, 1315 m a.s.l., ENE, 2°, T 60%, S 0%, F 25%, G 20%, Neuhäuslová H/2001.

Calamagrostio-Piceetum typicum calamagrostiosum villosae

12. Prášily, sub-top area of Ždanidla Mt., 400 m^2, 1245 m a.s.l., N, 5°, T 75%, F 100%, S 0%, G 20%, Vorel 1968, Table 1, rel. 18/20P.
13. Luzný Mt., 1 km S from the top, 300 m^2, 1200 m a.s.l., W, 3°, T 75%, S 0%, F 85%, G 20%, Sofron 1981, Table 1, rel. 11.
14. Srní, Vydra, moderate slope above the spring area of the Tmavý Potok Stream, 400 m^2, 1220 m a.s.l., S, 2°, T 70%, S 5%, F 95%, G 40%, Vorel 1968, Table 1, rel. 19/36Sr.
15. Srní, Jezerní Hřbet Ridge, 400 m^2, 1220 m a.s.l., SSE, 3°, T 65%, S 5%, F 95%, G 45%, Vorel 1968, Table 1, rel. 20/3Sr.
16. Královský Hvozd Ridge, between Svaroh and Jezerní Hora Mounts, 400 m^2, 1320 m a.s.l., SW, 10°, T 75%, S 0%, F 80%, G 5%, Sofron 1981, Table 1, rel. 7.
17. Srní, Oblík Mt., 400 m^2, 1175 m a.s.l., NNW, 20°, T 60%, S 3%, F 90%, G 50%, Vorel 1968, Table 2, rel. 16/6Sr.
18. Jezernice Mt., 4.5 km SW from Srní, 400 m^2, 1260 m a.s.l., E, 3°, T 55%, S 1%, F 45%, G 50%, Neuhäuslová & Sofron 72/2000.
19. Jezerní Mt., under Rozvodí location, 400 m^2, 1280 m a.s.l., SE, 25°, T 55%, S 0%, F 45%, G 15%, Neuhäuslová & Sofron 15/2000.
20. Černá Hora Mt., 400 m^2, 1235 m a.s.l., NE, 35°, T 50%, S 3%, F 55%, G 40%, Neuhäuslová 22/2000.
21. Studená Hora Mt., 400 m^2, 1250 m a.s.l., W, 5°, T 70%, S 5%, F 85%, G 30%, Neuhäuslová 1998.

Calamagrostio-Piceetum typicum vaccinosum

22. Luzný Mt., near the state border, 225 m^2, 1200 m a.s.l., S, 3°, T 55%, S 0%, F 75%, G 30%, Sofron 1981, rel. 35.
23. Studená Hora Mt., 400 m^2, 1335 m a. s. l., T 65%, S 0%, F 95%, G 35%, Neuhäuslová 1998.

d) *Calamagrostio villosae-Piceetum typicum* var. *vacciniosum myrtilli* var. nova Neuhäuslová hoc loco (Table 1, rel. 22–23)
(Syn.: *Myrtillo-Piceetum* sensu Sofron 1981 p.p., *Vaccinio myrtilli-Piceetum* Sofron 1993, *Soldanello-Piceetum* var. with *Vaccinium myrtillus* sensu Sofron & Štěpán 1971 p.p., *Calamagrostio villosae-Piceetum vaccinietosum* Jirásek 1996 p. max. p., see also *Picea-Vaccinium myrtillus* soc. Hilitzer 1929 p.p.)

Nomenclatural type: Sofron (1981): Table 3, rel. 32. Holotypus.
Differential species: *Vaccinium myrtillus*, *V. vitis-idaea*.
This species-poorer variant is characterized by prevailing *Vaccinium myrtillus*, sporadically occurring *Vaccinium vitis-idaea* in the field layer, and dominant *Polytrichum formosum* or *Dicranum scoparium* in the ground layer. Hygrophilous and more nutrient-demanding species in the field and ground layers decrease (e g. *Luzula sylvatica*, *Homogyne alpina*, *Soldanella montana*, *Lycopodium annotinum*, *Polytrichum commune*, *Lepidozia reptans*, *Tetraphis pellucida*, *Bazzania trilobata* etc.). It was found on fresh, stone-rich podsol soils of shady slopes of the mountain ridge and in corries of glacial lakes.

e) *Calamagrostio villosae-Piceetum typicum* var. *avenellosum* Jirásek 1996 (Table 2, rel. 1–14)
(Syn.: *Deschampsio flexuosae-Piceetum* sensu Sofron 1981 non Hadač et al. 1969, *Soldanello-Piceetum* var. with *Deschampsia flexuosa* sensu Sofron & Štěpán 1971, see also *Picea-Deschampsia flexuosa* soc. Hilitzer 1929)

For this species-poor variant, the dominance of *Avenella flexuosa*, frequently with subdominant *Calamagrostis villosa*, is typical. The hygrophilous species of moist soils (e.g. *Athyrium distentifolium*, *Soldanella montana*, *Homogyne alpina*, *Trientalis europaea*, *Lycopodium annotinum*, *Streptopus amplexifolius*) are less frequent, with lower cover degree. Also the occurrence of *Vaccinium myrtillus* is rare. In comparison with the foregoing variants, marked differences can be seen in the cover of bryophytes (see Tables 1 and 2). The species *Sphagnum girgensohnii*, *Polytrichum commune*, *Barbilophozia lycopodioides*, but also *Rhytidiadelphus loreus* occur with relatively low frequency only.

The low number of hygrophilous species indicates less favourable water regime. The podsol soils of these forest stands are poorer in nutrients than those of the foregoing variant, very strongly acidic and drier. The shift from the *Calamagrostis villosa*-dominated stands to those dominated by low-pH tolerant and low-nutrient tolerant *Avenella flexuosa* has been observed by the studies on spruce-forests changes in the Šumava National Park (Bohemian Forest) since the 1970s, too (Neuhäuslová & Wild 2000, Wild et al. 2003).

2. *Calamagrostio villosae-Piceetum fagetosum* (Mikyška 1972) Jirásek 1996 (Table 3, rel. 1–10)

This unit represents a link between the typical climax spruce forests of the *Calamagrostio villosae-Piceetum typicum* and mountain spruce-beech forests of the *Calamagrostio villosae-Fagetum*. Besides the spruce, *Abies alba* and *Fagus sylvatica* occur sporadically in the tree layer.

However, in comparison with the spruce-beech forests of the *Calamagrostio villosae-Fagetum* Mikyška 1972, the beech achieves here the lower tree layer only, while its growth in the spruce-beech forests is very good. Natural or near-natural stands of this subassociation are very rare at present, above all in the central, border-near part of the Šumava National Park and

Table 2. *Calamagrostio villosae-Piceetum typicum* var. *avenellosum.*

Relevés, nr.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	%
Number of species	**7**	**9**	**9**	**10**	**13**	**25**	**10**	**24**	**22**	**27**	**16**	**11**	**17**	**13**	
T															
Picea abies	4	3	3	4	5	4	4	4	4	4	4	3	3	4	**100**
S															
Picea abies	.	.	1	.	.	1	1	.	1	1	.	.	.	.	**36**
Sorbus aucuparia	.	+	.	.	.	r	.	.	.	.	.	.	.	.	**14**
F Diff															
Avenella flexuosa	5	4	5	5	4	4	3	3	3	3	3	3	3	3	**100**
a)															
Calamagrostis villosa	+	2	2	1	2	2	2	2	+	2	2	3	3	3	**100**
Luzula sylvatica	.	+	1	.	1	1	2	1	r	+	1	2	2	2	**86**
Trientalis europaea	.	.	.	.	.	+	+	+	.	.	+	.	.	1	**36**
Lycopodium annotinum	1	.	.	.	.	+	.	.	+	+	.	.	.	.	**29**
Athyrium distentifolium	.	+	+	.	.	.	+	.	.	.	.	+	.	.	**29**
Homogyne alpina	.	.	.	.	+	.	.	.	.	+	2	.	.	.	**21**
Huperzia selago	.	.	.	.	.	r	.	.	+	r	.	.	.	.	**21**
Blechnum spicant	.	.	.	.	.	r	.	.	r	.	.	.	.	.	**14**
b)															
Dryopteris dilatata	1	+	2	2	1	+	1	2	.	+	1	1	1	2	**93**
Oxalis acetosella	.	+	+	2	+	.	.	.	.	+	1	r	2	2	**64**
Vaccinium myrtillus	.	.	.	1	.	+	.	.	.	r	3	.	.	.	**29**
Galium saxatile	.	.	1	.	.	.	.	.	.	.	.	.	1	.	**14**
c)															
Picea abies	+	+	+	+	r	+	+	+	+	+	r	r	r	+	**100**
Sorbus aucuparia	+	.	.	1	.	+	.	r	.	r	+	.	r	.	**50**
G															
Polytrichum formosum	1	2	+	1	1	1	1	1	1	2	+	2	1	2	**100**
Dicranum scoparium	.	1	.	.	1	1	1	+	2	1	2	1	1	2	**79**
Dicranodontium denudatum	.	.	.	+	.	+	.	+	+	1	+	1	.	.	**43**
Barbilophozia floerkei	.	.	.	.	+	+	.	+	.	+	+	.	.	.	**36**
Cladonia digitata	.	.	.	.	+	.	.	r	+	+	.	.	.	+	**36**
Tetraphis pellucida	.	.	.	.	.	+	.	+	.	+	.	.	+	+	**36**
Lophozia ventricosa	.	.	.	.	+	.	.	+	.	+	+	.	.	.	**29**
Lepidozia reptans	.	.	.	.	.	+	.	+	+	+	.	.	.	.	**29**
Rhytidiadelphus loreus	.	.	.	.	.	1	.	+	.	.	.	.	.	2	**21**
Sphagnum girgensohnii	.	.	.	.	.	1	.	.	1	1	.	.	.	.	**21**
Barbilophozia lycopodioides	.	.	.	.	.	.	.	+	+	.	.	.	+	.	**21**
Plagiothecium undulatum	.	.	.	.	.	1	.	+	.	.	.	.	.	.	**14**
Bazzania trilobata	.	.	.	.	.	+	.	.	.	+	.	.	.	.	**14**
Cladonia furcata	.	.	.	.	.	+	.	.	.	+	.	.	.	.	**14**
Orthodicranum montanum	.	.	.	.	.	.	+	+	.	.	.	.	.	.	**14**
Ptilidium ciliare	.	.	.	.	.	.	.	+	+	.	.	.	.	.	**14**

Table 2. continues

Relevés, nr.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	%
Number of species	7	9	9	10	13	25	10	24	22	27	16	11	17	13	
Cladonia gracilis									+	+					14
Cladonia coniocraea									+	+					14
Polytrichum commune									1		+				14
Plagiothecium laetum									r					+	14
Dicranella heteromalla												1	+		14

Species in one relevé only: F: *Taraxacum* sect. *Ruderalia* (4:r), *Carex pilulifera* (6:+), *Stellaria alsine* (13:+), G: *Calypogeia integristipula* (13:+), *C. neesiana* (8:r), *Cephalozia leucantha* (10:+), *Cetraria islandica* (9:+), *Cladonia fimbriata* (10:+), *C. phyllophora* (6:+), *C. rangiferina* (9:1), *Dibaeis baeomyces* (9:r), *Dicranum fuscescens* (8:+), *Hypnum cupressiforme* (13:+), *Lophocolea bidentata* (13:+), *L. heterophylla* (8:+), *Mylia taylorii* (10:+), *Plagiothecium* sp. (5:+), *Rhytidiadelphus triquetrus* (6:+), *Sphagnum capillifolium* (8:+).

Localities in Table 2. *Calamagrostio villosae-Piceetum typicum var. avenellosum*

1. Královský hvozd Ridge, 600 m S from the Pták point, 1200 m a.s.l., 1600 m², N, 25°, T 70%, S 0%, F 95%, G 2%, Sofron 1981, rel. 29.
2. Between Trojmezná and Třístoličník Mounts, 1345 m a.s.l., 400 m², W, 2°, T 45%, S 1%, F 85%, G 30%, Neuhäuslová 17/1999.
3. Ostrý Hill, near the state border, N from the top, 1220 m a.s.l., 400 m², NE, 7°, T 45%, S 3%, F 95%, G 1%, Neuhäuslová & Sofron 52/1999.
4. Svaroh Hill, 1260 m a.s.l., 400 m², NE, 2°, T 65%, S 0%, F 90%, G 3%, Neuhäuslová 58/1999.
5. Stožec Hill, 1340 m a.s.l., 400 m², NNE, 1°, T 80%, S 0%, F 80%, G 7%, Vorel 1968, Table 1, rel. 23/51St.
6. Prášily, Jezerní Hřbet Ridge, 1240 m a.s.l., 400 m², N, 2°, T 75%, S 5%, F 95%, G 15%, Vorel 1968, Table 1, rel. 21/3P.
7. Between Trojmezná and Třístoličník Mounts, 1320 m a.s.l., 400 m², W, 2°, T 70%, S 2%, F 90%, G 7%, Neuhäuslová 18/1999.
8. Poledník Mt., ca. 100 m SE from the top, 1314 m a.s.l., 400 m², SE, 2°, T 50%, S 0%, F 60%, G 5%, Neuhäuslová & Sofron 9/2000.
9. Prášily, point 1238.6 of the Jezerní Hřbet Ridge, 1225 m a.s.l., 400 m², NW, 15°, T 70%, S 1%, F 75%, G 30%, Vorel 1968, Table, rel. 4/4P.
10. Prášily, the ridge of Poledník Mt., 1233 m a.s.l., 400 m², SSE, 3°, T 75%, S 50%, F 90%, G 20%, Vorel 1968, Table 1, rel. 24/2P.
11. Trojmezná Mt., sub-top area, 1350 m a.s.l., 400 m², W, 3°, T 55%, S 0%, F 90%, G 15%, Neuhäuslová 16/1999.
12. Between Třístoličník Mt. and nameless hill in direction to Trojmezná Mt., 100 m², 1320 m a.s.l., SW, 3°, T 40%, S 0%, F 95%, G 15%, Neuhäuslová & Jirásek 94/1999.
13. Boubín Mt., sub-top area, 100 m², 1350 m a.s.l., N, 10°, T 40%, S 0%, F 95%, G 5%, Neuhäuslová & Jirásek 99/1999.
14. Stráž Mt., sub-top area, 400 m², 1302 m a.s.l., SE, 2°, T 50%, S 0%, F 60%, G 30%, Neuhäuslová 83/2000.

Protected Landscape Area. However, the potential natural distribution of this syntaxon is more extensive than that of the foregoing *Calamagrostio villosae-Piceetum typicum*, not only in the National Park, but in the area of the whole Bohemian Forest (see Neuhäuslová 2001). Natural stands are mostly replaced by spruce plantations. The recent distribution of the natural or near-natural stands of this subassociation is rather reduced not only due to forest management (spruce plantations) but also due to high number of red deer, which browses a big part of beech and fir seedlings. Besides the occurrence of beech and fir in all layers, the species *Dryopteris filix-mas*, *Gymnocarpium dryopteris*, *Hieracium murorum*, *Luzula pilosa*, *Phe-*

Table 3. *Calamagrostio villosae-Piceetum fagetosum.*

Variant	*typicum*								*vacciniosum*			
Relevés, nr.	1	2	3	4	5	6	7	%	8	9	10	%
Number of species	22	15	26	35	30	22	23		15	11	23	
S												
Picea abies	5	4	3	3	4	3	4	**100**	3	3	3	**100**
Fagus sylvatica	+	+	.	r	.	.	.	**43**	.	.	(+)	**33**
T												
Sorbus aucuparia	.	+	+	r	2	+	.	**86**	1	+	+	**100**
Picea abies	+	.	r	2	1	+	+	**86**	1	+	.	**67**
Fagus sylvatica	2	(r)	.	r	.	.	.	**43**	.	.	.	**0**
F Diff. Variant												
Vaccinium myrtillus	+	r	r	2	2	1	+	**100**	4	4	3	**100**
Vaccinium vitis-idaea	.	.	.	.	.	.	.	**0**	+	.	1	**67**
a)												
Calamagrostis villosa	3	5	2	3	2	4	4	**100**	2	2	2	**100**
Luzula sylvatica	2	1	2	3	1	2	2	**100**	.	.	2	**33**
Lycopodium annotinum	2	1	1	+	2	+	2	**100**	.	.	+	**33**
Trientalis europaea	.	.	r	2	1	+	+	**71**	.	.	+	**33**
Homogyne alpina	+	.	r	1	+	.	+	**71**	.	.	1	**33**
Soldanella montana	+	.	.	1	.	.	+	**43**	.	.	.	**0**
b)												
Dryopteris dilatata	1	1	2	2	2	1	1	**100**	1	2	1	**100**
Avenella flexuosa	2	1	2	2	1	2	3	**100**	2	.	2	**67**
Oxalis acetosella	+	+	1	2	2	3	2	**100**	.	+	.	**33**
Galium saxatile	.	.	2	+	.	+	r	**57**	.	.	.	**0**
Maianthemum bifolium	+	.	1	+	.	1	.	**57**	.	.	.	**0**
c)												
Luzula pilosa	.	.	1	+	r	.	+	**57**	.	.	.	**0**
Prenanthes purpurea	+	.	.	.	r	.	+	**43**	.	.	.	**0**
Gymnocarpium dryopteris	.	.	.	r	.	.	r	**29**	.	.	.	**0**
d)												
Epilobium angustifolium	r	.	.	.	r	+	.	**43**	.	.	.	**0**
e)												
Sorbus aucuparia	+	+	+	+	1	+	+	**100**	r	.	.	**33**
Picea abies	+	r	+	+	.	+	1	**86**	+	+	1	**100**
Fagus sylvatica	+	.	r	.	.	r	.	**43**	.	.	.	**0**
Abies alba	.	.	.	.	.	.	.	**0**	r	r	.	**67**
G												
Dicranum scoparium	1	1	2	1	+	2	1	**100**	2	1	1	**100**
Polytrichum formosum	1	1	r	1	+	1	2	**100**	1	3	2	**100**
Rhytidiadelphus loreus	+	.	1	1	+	.	.	**57**	.	.	2	**33**
Lepidozia reptans	+	.	+	+	r	.	.	**57**	.	.	.	**0**
Lophozia ventricosa	.	.	+	+	r	+	.	**57**	+	.	+	**67**

Table 3. continues

Variant	*typicum*								*vacciniosum*			
Relevés, nr.	1	2	3	4	5	6	7	%	8	9	10	%
Number of species	22	15	26	35	30	22	23		15	11	23	
Barbilophozia lycopodioides	.	.	+	+	+	+	.	57	.	+	.	33
Plagiothecium laetum	.	.	+	+	+	.	1	57	.	.	.	0
Ptilidium ciliare	.	.	+	+	.	+	.	43	.	.	.	0
Tetraphis pellucida	.	.	.	+	r	+	.	43	.	.	.	0
Sphagnum girgensohnii	.	.	.	+	+	.	1	43	.	.	+	33
Lophocolea heterophylla	.	.	+	+	.	.	.	29	.	.	.	0
Bazzania trilobata	+	.	.	+	.	.	.	29	.	.	1	33
Anastrepta orcadensis	.	.	.	.	+	.	+	29	.	.	.	0
Sphagnum capillifolium	.	1	.	.	.	.	.	14	+	.	1	33
Dicranodontium denudatum	.	.	+	.	.	.	.	14	1	.	+	67
Orthodicranum montanum	.	.	+	+	.	.	.	29	.	.	.	0
Cephalozia bicuspidata	.	.	.	+	.	.	.	14	.	.	+	33
Barbilophozia floerkei	.	.	.	.	.	+	.	14	.	.	.	0
Pleurozium schreberi	.	.	.	.	.	.	1	14	1	+	.	67

Species in one relevé only: T: *Abies alba* (2:1), *Sorbus aucuparia* (8:1), S: *Abies alba* (2:+), F: *Athyrium filix-femina* (4:1), *Dryopteris filix-mas* (5:r), *Hieracium murorum* (6:r), *Phegopteris connectilis* (7:+), *Rubus idaeus* (4:+), *Senecio nemorensis* agg. (4:+), *Streptopus amplexifolius* (10:r), G: *Blepharostoma trichophyllum* (10:+), *Brachythecium reflexum* (5:r), *Calypogeia azurea* (4:r), *Lophocolea bidentata* (5:r), *Hylocomium splendens* (8:+), *Plagiochila porelloides* (2:1), *Plagiothecium undulatum* (5:1), *Pohlia nutans* (5:r), *Polytrichum commune* (4:+), *Ptilidium pulcherrimum* (2:r), *Sphagnum palustre* (5:1).

Localities in Table 3.

Calamagrostio villosae-Piceetum fagetosum var. *typicum*

1. Prášily, Revier Poledník 111f, Vorel 1968, Table 2, rel. 8/16P.
2. NE slope of Ostrý Mt., 400 m², 1170 m a.s.l, NE, 20°, T 60%, S 3%, F 80%, G 10%, Soefron 1981, p. 22, rel. 2.
3. Near the gamekeeper's lodge of Roklanská Hájenka, 400 m², 1205 m a.s.l., plane, T 40%, S 1%, F 70%, G 15%, Neuhäuslová 3/2001.
4. Studená Hora Mt., S from the road from Březník, 400 m², 1255 m a.s.l., SSW, 8°, T 40%, S 10%, F 90%, G 7%, Neuhäuslová 4/1999.
5. Černá Hora Mt., ca. 100 m N from the rest point by the springs of the Vltava River, 400 m², 1190 m a.s.l., E, 7°–10°, T 55%, S 7%, F 75%, G 10%, Neuhäuslová 23/2000.
6. Studená Hora Mt., S from the road to the gamekeeper's lodge of Roklanská Hájenka, 400 m², 1200 m a.s.l., NNW, 5°, T 35%, S 2%, F 85%, G 10%, Neuhäuslová 2001.
7. Studená Hora Mt., W from the Široká Cesta road, 400 m², 1190 m a.s.l., W, 10°, T 60%, S 2%, F 70%, G 35%, Neuhäuslová 119/1999.

Calamagrostio villosae-Piceetum fagetosum var. *vacciniosum*

8. Královský Hvozd Ridge, Ostrý Mt., 200 m², 1200 m a.s.l, NE, 2°, T 35%, S 5%, F 90%, G 10%, Neuhäuslová & Sofron 53/1999.
9. 250 m from the top of Hraničník Mt., 400 m², 1250 m a.s.l, N, 25°, T 40%, S 5%, F 70%, G 30%, Neuhäuslová & Buryová 14/1999.
10. Březník, ca. 1 km NW from Malá Mokrůvka Mt., 400 m², 1240 m a.s.l., NW, 7°, T 50%, S 3%, F 85%, G 30%, Neuhäuslova 1998.

gopteris connectilis, *Polygonatum verticillatum*, *Prenanthes purpurea* and *Senecio nemorensis* agg. differ this syntaxon from the typical subassociation.

For the stands of the *Calamagrostio-Piceetum fagetosum*, isolated hills and shady slopes of mountain ridges at climatically more favourable levels between ca. 1200–1250 m a.s.l. are typical, on sunny slopes achieving ca. 1300 m a.s.l. On places of climatic inversions these stands can be found at lower levels about 1150 m a.s.l. The number or frost days/year varies between 140–160, the mean January temperature achieves –3°C up to –5°C (see Quitt 1971). The soils are very strongly acidic podsols with low saturation with bivalent cations (see Table 6, analyses 4 and 5).

The very well developed, near-natural stands of this subassociation occur in the southeastern part of the Šumava National Park, in the area of the Smrčina and Třístoličník Ridges, and in the Poledník Ridge in the northwestern part of the Park.

In this subassociation, two variants can be distinguished: typical variant and var. with *Vaccinium myrtillus*.

a) *Calamagrostio villosae-Piceetum fagetosum* var. *typicum* Jirásek 1996 (Table 3, rel. 1–7)

The characteristics of the typical variant correspond to those of the subassociation, with its optimal habitat conditions. This variant has been recorded on the Trojmezná Hora and Poledník Ridges, Smrčina and Hraničník Mounts.

b) *Calamagrostio villosae-Piceetum fagetosum* var. *vacciniosum* Jirásek 1996 (Table 3, rel. 8–10)
(Syn.: *Calamagrostio villosae-Piceetum vaccinietosum* Jirásek 1996 p.p., *Fago-Picetum myrtilletosum* Reinhold 1979 p.p.)

Differential species: *Vaccinium myrtillus*, *V. vitis-idaea*.
For this variant, prevailing *Vaccinium myrtillus* and the occurrence of *Vaccinium vitis-idaea* in the species-poor field layer, as well as the absence or only rare occurrence of hygrophilous spruce-forest species (*Homogyne alpina*, *Luzula sylvatica*, *Lycopodium annotinum*, *Oxalis acetosella*, *Soldanella montana*, *Trientalis europaea*, *Fagion*-species, as well as hygrophilous bryophytes, see Table 3) are typical. Comparing with the foregoing variant, the dominance of *Dicranodontium denudatum* and *Pleurozium schreberi* increased markedly. For the soils of this variant, very low pH-values and less favourable water regime than in soils of the typical variant are characteristic.

B. *Anastrepto-Piceetum* Stöcker 1967 (Table 4, rel. 1–5)

Diagnostic species combination: T–F: *Picea abies*, F: *Avenella flexuosa*, *Calamagrostis villosa*, *Dryopteris dilatata*, *Vaccinium myrtillus* (dom.), *Vaccinium vitis-idaea*, G: *Anastrepta orcadensis*, *Dicranum scoparium*, *Lophozia ventricosa*, *Mylia taylorii*, *Plagiothecium laetum*, *Polytrichum formosum*, species of the genus *Barbilophozia*, *Tetraphis pellucida* (see also Jirásek 1996, Jirásek in Husová et al. 2002, Stöcker 1968).
Structure, species composition: Species-poor spruce-dominated stands with admixture of *Sorbus aucuparia*, with prevailing *Vaccinium myrtillus*, frequent *V. vitis-idaea* and with a species-rich ground layer with prevailing *Polytrichum formosum*, *Dicranum scoparium* and frequent above mentioned liverworts. The relevé Nr. 5 in Table 4 seems to represent the transitional type to the following association.
Ecology: Spruce forests in the upper part of the spruce belt, on weakly stabilized screes or boulder ranker soils of steep slopes. The climate is very cold, with long-lasting snow cover.

High soil and air moisture and shady habitats are frequent (Jirásek 1996, Jirásek in Husová et al. 2002). The soils are very strongly acidic (pH_{KCl} <3.0).
Distribution: Typical, mostly small area covering community in corries of the Plešné, Černé and Čertovo Lakes (Sofron – pers. comm., Jirásek 1996, Jirásek in Husová et al. 2002), and at top levels of ridges or isolated high mounts, in some places in complex with the *Dryopterido dilatatae-Piceetum*.

C. *Dryopterido dilatatae-Piceetum* Sýkora ex Sofron 1981 (Table 4, rel. 6–8)
(See also *Picea-Nephrodium austriacum* soc. Hilitzer 1929)

Diagnostic species combination: Diff. F: *Dryopteris dilatata* (dom.). Species with higher constancy: T–F: *Picea abies*, F: *Avenella flexuosa*, *Calamagrostis villosa*, *Dryopteris dilatata*, *Luzula sylvatica*, *Vaccinium myrtillus*, G: *Bazzania trilobata*, *Dicranum scoparium*, *Lepidozia reptans*, *Polytrichum formosum*, *Ptilidium ciliare*.
Structure, species composition: *Three-layered spruce stands with admixed Sorbus aucuparia*, with prevailing *Dryopteris dilatata* in the field layer, and well developed ground layer with prevailing *Dicranum scoparium* or *Polytrichum formosum*, on moister sites with *Bazzania trilobata* or further liverworts, mosses or lichens (*Cladonia* species). The boreal or mountain liverworts typical for foregoing association are mostly entirely missing (Table 4, Ass. diff. species).
Distribution: The relevés were recorded in the central part of the Šumava National Park, in the Šumavské Pláně Plateau (Stráž Mt., Neuhäuslová & Sofron in Neuhäuslová 2001: 122, and on Ždanidla Mt., Vorel 1968) and in the Boubínsko-Stožecká Hornatina highlands.
Ecology: Association of (lower to) medium to higher levels (or isolated higher summits) in the mountain spruce belt on scree (to boulder) ranker soils, on steep slopes (15–25/45°) of various orientation. It represents blocked subclimax successional stage, leading to the *Calamagrostio villosae-Piceetum* (Jirásek 1996, Jirásek in Husová et al. 2002).

D. *Athyrio alpestris-Piceetum* (Hartmann 1959) Hartmann & Jahn 1967 (Table 5, rel. 1–13)
(Syn.: *Soldanello-Piceetum* var. with *Athyrium alpestre* and *Oxalis acetosella* sensu Sofron & Štěpán 1971, see also *Picea-Athyrium alpestre* soc. Hilitzer 1929)

Diagnostic species combination: Diff. T–F: *Fagus sylvatica*, F: *Athyrium distentifolium*, *Prenanthes purpurea*, *Silene dioica*, *Stellaria nemorum*. Species with higher constancy: T–F: *Picea abies*, F: *Athyrium distentifolium*, *Calamagrostis villosa*, *Dryopteris dilatata*, *Homogyne alpina*, *Luzula sylvatica*, *Oxalis acetosella*, *Soldanella montana*, *Sorbus aucuparia*, *Trientalis europaea*, *Vaccinium myrtillus*, G: *Dicranum scoparium*, *Polytrichum formosum*.
Structure, species composition: Three- to four-layered, well growing stands dominated by spruce, with a weak occurrence of *Acer pseudoplatanus* and *Fagus sylvatica* or *Sorbus aucuparia* in the tree-, shrub- and field layers. The field layer is dominated by ca. 120–150 cm high tufts of *Athyrium distentifolium*, species of moist soils (e.g. *Luzula sylvatica*, *Oxalis acetosella*, *Prenanthes purpurea*, *Silene dioica*, *Stellaria nemorum*) occur frequently. Almost regularly, *Oxalis acetosella* forms groups in the centre of *Athyrium distentifolium* tufts. In comparison with the foregoing associations, the cover of spruce-forest species is lower, however, the herbs and ferns of the order *Fagetalia* are relatively frequent (*Petasites albus*, *Phegopteris connectilis*, *Prenanthes purpurea*, *Polygonatum verticillatum*). The regeneration of *Picea abies* and *Sorbus aucuparia* is good. The ground layer is relatively rich in species, however, its cover is mostly low.

Table 4. *Anastrepto-Piceetum* and *Dryopterido dil.-Piceetum.*

Assotiation	***Anastrepto-Piceetum***						***Dryopt.-Piceetum***			
Relevés, nr.	**1**	**2**	**3**	**4**	**5**	**%**	**6**	**7**	**8**	**%**
Number of species	**18**	**27**	**17**	**17**	**20**		**18**	**15**	**15**	
T										
Picea abies	3	4	3	4	4	**100**	3	3	3	**100**
Sorbus aucuparia	.	.	.	.	r	**20**	r	.	.	**33**
S										
Picea abies	.	+	+	.	1	**60**	.	1	2	**67**
Sorbus aucuparia	.	+	+	2	.	**60**	.	r	.	**33**
F										
Diff. *Anastrepto-Piceetum*										
F *Vaccinium vitis-idaea*	+	+	.	.	1	**60**	.	.	.	**0**
G *Barbilophozia lycopodioides*	.	+	+	+	.	**60**	.	.	.	**0**
G *Lophozia ventricosa*	.	+	+	.	+	**60**	.	.	.	**0**
G *Tetraphis pellucida*	.	+	+	.	+	**60**	.	.	.	**0**
G *Mylia taylorii*	1	+	.	.	.	**40**	.	.	.	**0**
G *Anastrepta orcadensis*	.	.	.	+	+	**40**	.	.	.	**0**
Diff. *Dryopterido dilatatae-Piceetum*										
Dryopteris dilatata	2	+	2	1	r	**100**	3	3	2	**100**
a)										
Calamagrostis villosa	1	.	+	2	+	**80**	2	.	+	**67**
Luzula sylvatica	.	r	r	1	.	**60**	+	1	+	**100**
b)										
Vaccinium myrtillus	5	5	4	4	2	**100**	1	+	1	**100**
Avenella flexuosa	+	+	.	2	+	**80**	2	1	1	**100**
Oxalis acetosella	1	r	1	.	.	**60**	2	.	.	**33**
c)										
Picea abies	.	+	1	+	+	**80**	+	r	1	**100**
Sorbus aucuparia	.	+	.	1	.	**40**	.	.	+	**33**
e)										
Rubus idaeus	.	r	.	.	.	**20**	.	.	+	**33**
G										
Dicranum scoparium	2	2	1	2	3	**100**	2	2	3	**100**
Polytrichum formosum	2	2	3	+	2	**100**	1	4	2	**100**
Plagiothecium laetum	1	.	+	+	r	**80**	.	.	.	**0**
Rhytidiadelphus loreus	2	+	+	.	.	**60**	.	.	.	**0**
Dicranodontium denudatum	.	+	+	1	.	**60**	.	+	.	**33**
Pleurozium schreberi	.	+	+	.	.	**40**	.	.	+	**33**
Cladonia gracilis	.	+	.	.	+	**40**	.	+	.	**33**
Cladonia digitata	.	+	.	.	1	**40**	.	.	.	**0**
Barbilophozia attenuata	.	.	+	.	+	**70**	.	.	.	**0**
Dicranum fuscescens	.	.	.	+	+	**40**	+	.	.	**33**
Cetraria islandica	.	.	.	1	r	**40**	.	.	.	**0**

Table 4. continues

Assotiation	*Anastrepto-Piceetum*						*Dryopt.-Piceetum*			
Relevés, nr.	1	2	3	4	5	%	6	7	8	%
Number of species	18	27	17	17	20		18	15	15	
Bazania tricrenata	1	.	.	.	.	20	.	.	+	33
Cladonia fimbriata	.	+	.	.	.	20	.	+	.	33
Lepidozia reptans	.	.	.	.	+	20	+	+	+	100
Bazzania trilobata	.	.	.	.	+	20	r	+	.	67
Ptilidium ciliare	.	.	.	.	.	0	+	+	.	67

Species in one relevé only: F: *Athyrium distentifolium* (rel. 6:+), *A. filix-femina* (6:+), *Galium saxatile* (8:+), *Homogyne alpina* (4:+), *Huperzia selago* (1:+), *Luzula pilosa* (6:+), *Lycopodium annotinum* (6:+), *Melampyrum pratense* (4:+), G: *Barbilophozia floerkei* (2:+), *Calypogeia trichomanis* (7:+), *Cladonia pyxidata* (2:+), *Cladonia squamosa* (1:1), *Hypnum cupressiforme* (8:+), *Lophocolea heterophylla* (7:+), *Plagiochila porelloides* (1:+), *Plagiothecium* sp. (2:+), *P. undulatum* (1:1), *Pohlia nutans* (8:1), *Polytrichum juniperinum* (2:+), *Ptilidium pulcherrimum* (2:+), *Sphagnum capillifolium* (1:3), *S. girgensohnii* (2:1).

Localities in Table 4.

Anastrepto-Piceetum

1. Corrie of Čertovo Lake, 400m², 1170 m a.s.l., NE, 40°, T 30%, S 0%, F 90%, G 95%, Sofron 1981, rel. 40, Table 3.
2. Prášily, boulder-rich slope at the sub-top level of the Ždanidla Mt., 400 m², 1300 m a.s.l., S, 15°, T 75%, S 0%, F 80%, G 45%, Vorel 1968, Table 1, rel. 2/33P.
3. 100 m from the top of Hraničník Mt., 400 m², 1250 m a.s.l., N, 25°, T 40%, S 5%, F 70%, G 35%, Neuhäuslová 13/1999.
4. *Between Svarob and Jezerní Hora Mounts, 120 m², 1325 m a.s.l., NNE, 10°, T 70%, S 10%, F 90%, G 25%*, Neuhäuslová & Sofron 60/1999.
5. The Čertův Vrch Hill, 3.1 km SSE from Filipova Huť village, 400 m², 1235 m a.s.l., SSW, 20°, T 70%, S 5%, F 20%, G 65%, Neuhäuslová 66/2000.

Dryopterido dilatatae-Piceetum

6. The Stráž Mt., NW from Bučina village, sub-top level, 1290 m a.s.l., 400 m², SE, 15°, T 50%, S 0%, F 40%, G 30%, Neuhäuslová & Sofron, 82a/ 2000.
7. The Ždanidla Mt., scree at the sub-top level of the lower top, 400 m², 1305 m a.s.l., ENE, 5–15°, T 35%, S 0%, F 65%, G 70%, Vorel 1968, Table 1, rel. 3/34P.
8. Boubín Mt., near the forest castle, 150 m², 1200 m a.s.l., SE, 25°, T 30%, S 0%, F 40%, G 30%, Jirásek 1994 ms., 9, 8.

Some species of tall-herb communities which partly were not recorded in the individual relevés (*Cicerbita alpina, Veratrum album, Doronicum austriacum, Senecio hercynicus, Rumex alpestris*), occur in the stands of this association, too. On the contrary, *Avenella flexuosa*, frequent in the neighbouring stands of the *Calamagrostio villosae-Piceetum*, is rare.

Ecology: The *Athyrio alpestris-Piceetum* is a spruce forest of (supra-)montane levels, mostly above 1180 m a.s.l. (on shady, moist slopes of corries above 1160 m a.s.l.). It covers steep slopes [25–35(40)°] in concave relief forms, mostly of NE or E orientation. In the Bohemian Forest it grows frequently on the backwalls of the corries. For this vegetation unit, the cold levels with high humidity and soil moisture, long-lasting deep snow cover and frequent fogs are typical. The soils, saturated by water from many small brooks, correspond to gleyed oligotrophic cambisols, cambic gleys or gleyic podsols, sometimes with a higher admixture of gravel.

Distribution: Stands of the *Athyrium distentifolium*-rich spruce forests cover top-near levels of the southeastern part of the Šumava National Park in the Trojmezenská Hornatina highland (Smrčina, Hraničník, Plechý, Třístoličník Mounts), backwalls of the glacial corries of the

Table 5. *Athyrio alpestris-Piceetum.*

Subassociation	*typicum*										*athyrietosum fil.-fem.*				
Relevés, nr.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**%**	**10**	**11**	**12**	**13**	**%**
Number of species	**21**	**27**	**14**	**32**	**23**	**25**	**20**	**17**	**18**		**22**	**23**	**23**	**19**	
T															
Picea abies	4	3	3	3	3	2	3	3	4	**100**	3	3	3	4	**100**
Fagus sylvatica	.	.	.	.	(+)	+	(+)	(+)	.	**44**	.	.	.	.	**0**
Acer pseudoplatanus	.	.	.	.	.	.	.	.	.	**0**	1	.	.	.	**25**
S															
Picea abies	.	+	+	+	r	+	2	+	.	**78**	.	+	+	1	**75**
Sorbus aucuparia	.	.	r	+	.	.	1	+	.	**44**	.	.	r	+	**50**
Fagus sylvatica	.	.	.	.	.	+	.	+	.	**22**	.	+	.	.	**25**
Acer pseudoplatanus	.	.	.	.	.	.	.	.	.	.	.	.	.	+	**25**
F															
Diff. *Athyrio-Piceetum typicum*															
Athyrium distentifolium	4	4	4	4	4	3	3	3	4	**100**	3	3	4	4	**100**
Stellaria nemorum	+	.	+	1	.	.	+	.	+	**56**	2	r	.	.	**50**
Diff. *Athyrio-Piceetum athyrietosum filicis-feminae*															
Prenanthes purpurea	+	.	.	.	.	.	.	.	.	**11**	+	+	1	+	**100**
Acer pseudoplatanus	.	.	.	.	.	.	.	.	.	**0**	+	r	+	.	**75**
Athyrium filix- femina	.	.	.	.	.	.	.	.	.	**0**	1	.	+	.	**50**
a)															
Calamagrostis villosa	2	2	2	1	2	2	3	3	2	**100**	1	.	2	2	**75**
Luzula sylvatica	2	2	2	2	2	1	2	1	2	**100**	2	.	2	2	**75**
Trientalis europaea	+	1	2	+	+	.	r	2	+	**89**	.	2	1	1	**75**
Homogyne alpina	1	+	.	+	.	1	.	1	1	**67**	+	1	+	.	**75**
Soldanella montana	.	+	1	.	+	1	r	1	.	**67**	.	1	+	1	**75**
Streptopus amplexifolius	r	.	+	.	.	.	.	.	r	**33**	.	.	.	+	**25**
b)															
Dryopteris dilatata	1	+	2	2	1	1	1	1	1	**100**	1	1	1	r	**100**
Oxalis acetosella	2	2	2	1	2	.	2	2	3	**89**	3	2	3	2	**100**
Vaccinium myrtillus	+	+	2	+	2	.	1	2	.	**78**	.	2	+	.	**50**
Avenella flexuosa	2	2	.	.	.	+	.	+	2	**56**	.	+	1	.	**50**
Maianthemum bifolium	.	1	.	+	.	.	.	+	.	**33**	.	+	+	+	**75**
c)															
Silene dioica	.	+	.	r	.	.	.	.	.	**22**	.	.	.	.	**0**
Phegopteris connectilis	.	.	.	.	.	+	.	.	.	**11**	.	.	.	2	**25**
e)															
Picea abies	r	+	r	+	+	+	.	1	r	**89**	.	1	+	+	**75**
Sorbus aucuparia	.	r	.	+	+	+	r	r	r	**78**	+	r	.	.	**50**
Fagus sylvatica	.	.	.	+	.	+	.	+	.	**33**	.	.	.	r	**25**
G															
Rhizomnium punctatum	.	.	.	.	.	.	.	.	.	**0**	1	.	+	.	**50**
Polytrichum formosum	1	1	2	2	1	2	1	2	1	**100**	1	2	+	+	**100**
Dicranum scoparium	1	1	.	+	1	1	+	+	1	**89**	2	+	+	.	**75**
Dicranodontium denudatum	+	.	.	+	+	.	+	.	+	**56**	.	+	.	.	**25**
Lophocolea heterophylla	.	+	.	+	.	+	+	.	.	**44**	1	+	.	.	**50**
Polytrichum commune	1	.	.	+	.	1	.	.	1	**44**	.	.	.	+	**25**

Table 5. continues

Subassociation	*typicum*										*athyrietosum fil.-fem.*				
Relevés, nr.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**%**	**10**	**11**	**12**	**13**	**%**
Number of species	**21**	**27**	**14**	**32**	**23**	**25**	**20**	**17**	**18**		**22**	**23**	**23**	**19**	
Plagiothecium sp.	+	.	.	+	.	+	.	.	+	**44**	.	.	.	.	**0**
Sphagnum girgensohnii	1	.	.	.	.	1	.	.	1	**33**	.	.	.	+	**25**
Plagiothecium laetum	.	+	.	.	+	.	+	.	.	**33**	.	.	+	.	**25**
Lepidozia reptans	+	.	.	.	+	.	.	.	.	**22**	.	.	.	.	**0**
Barbilophozia lycopodioides	.	+	.	1	.	.	.	.	.	**22**	.	1	.	.	**25**
Plagiothecium undulatum	.	+	.	+	.	.	.	.	.	**22**	2	.	.	.	**25**
Plagiomnium affine	.	+	.	+	.	.	.	.	.	**22**	.	.	.	.	**0**
Dicranella heteromalla	.	+	.	.	+	.	.	.	.	**22**	1	.	.	.	**25**
Plygiothecium denticulatum	.	+	.	.	+	.	.	.	.	**22**	.	.	+	.	**25**
Orthodicranum montanum	.	r	.	.	+	.	.	.	.	**22**	.	.	+	.	**25**
Brachythecium reflexum	.	+	.	.	.	.	+	.	.	**22**	.	+	.	.	**25**
Pellia neesiana	.	.	.	+	.	+	.	.	.	**22**	.	.	.	.	**0**
Calypogeia azurea	.	.	.	r	.	+	.	.	.	**22**	.	.	.	.	**0**
Rhytidiadelphus loreus	.	.	.	r	.	+	.	.	.	**22**	.	.	.	+	**25**
Tetraphis pellucida	.	.	.	.	+	.	+	.	.	**22**	.	.	+	.	**25**

Species in one relevé only: F: *Blechnum spicant* (10:+), *Carex canescens* (4:r), *C. echinata* (6:r), *C. pilulifera* (4:r), *Deschampsia cespitosa* (6:1), *Equisetum sylvaticum* (6:+), *Galium saxatile* (5:+), *Lycopodium annotinum* (6:+), *Solidago virgaurea* (10:+), *Veratrum album* (3:+). G: *Barbilophozia attenuata* (5:+), *B. floerkei* (4:+), *Barbilophozia* sp. (8:1), *Brachythecium rivulare* (4:+), *B. starkei* (2:+), *Calypogeia mülleriana* (10:1), *Cladonia digitata* (1:+), *C. gracilis* (4:r), *C. furcata* (4:r), *Eurhynchium praelongum* (5:+), *Lophozia obtusa* (6:+), *Sphagnum russowii* (7:+), *S. teres* (10:1).

Localities in Table 5. *Athyrio alpestris-Piceetum*.

Subass.: *Athyrio alpestris-Piceetum typicum*

1. Stožec, Boubín Mt., 1300 m a.s.l., 400 m², NE, 20°, T 60%, S 0%, F 80%, G 10%, Vorel 1968, Table 1, rel. 6/43St.
2. Třístoličník Mt., sub-top level, 1340 m a.s.l., 400 m². E, 20°, T 35%, S 1%, F 95%, G 15%, Neuhäuslová 19/1999.
3. Nová Ves, Smrčina Mt., 1300 m a.s.l, 400 m², ENE, 7°, T 50%, S 3%, F 70%, G 15%, Neuhäuslová 11/1999.
4. Prášily, corrie under of Plesná Mt., 1275 m a.s.l., 400 m², NE, 35°, T 20%, S 3%, F 100%, G 20%, Vorel 1968, Table 1, rel. 5/35P.
5. Třístoličník Mt., 1190 m a.s.l., 400 m², NE, 10°, T 35%, S 1%, F 75%, G 10%, Neuhäuslová 20/1999.
6. Prášily, waterlogged slope N from the top of Ždanidla Mt., 1225 m a.s.l., 400 m², NNW, 10°, T 10%, S 10%, F 100%, G 20%, Vorel 1968, Table 1, rel. 7/40P.
7. Třístoličník Mt., 1180 m a.s.l., 100 m², NE, 15°, T 40%, S 10%, F 95%, G 7%, Neuhäuslová & Jirásek 93/1999.
8. Smrčina Mt., 1315 m a.s.l., 400 m², ENE, 10°, T 40%, S 3%, F 90%, G 5%, Neuhäuslová 122/1999.
9. Boubín Mt., top area, 1295 m a.s.l., 400 m², SW, 10°, T 50%, S 3%, F 90%, G 20%, Vorel 1962, 35St.

Subass.: *Athyrio alpestris-Piceetum athyrietosum filicis-feminae*

10. Corrie of Černé Lake, 1185 m a.s.l., 400 m², 40°, T 50%, S 0%, F 85%, G 50%, Sofron & Štěpán 1971, Table 1, rel. 16.
11. Nová Ves, Smrčina Mt., 1220 m a.s.l., 400 m², ENE, 15°, T 40%, S 10%, F 90%, G 15%, Neuhäuslová 1a/1999.
12. Třístoličník Mt., 1160 m a.s.l., 400 m², NNE, 10°, T 35%, S 7%, F 95%, G 15%, Neuhäuslová 19a/1999.
13. Železná Ruda, Vlčí Jámy ca. 6 km ESE from the town centre, 1100 m a.s.l., 250 m², N, 15°, T 60%, S 3%, F 95%, G 5%, Neuhäuslová & Sofron 35/2000.

Table 6. Soil analyses.

Calamagrostio villosae-Piceetum typicum, Poledník Mt., Table 1, rel. 6

Horizon	Depth (cm)	pH		Exchangeable ions in meq./100g dried soil				Saturation of sorpt. complex	C total %	N total %	C/N	Texture, ktg.				
		H_2O	KCl	Ca^{2+}	Mg^{2+}	Al^{3+}	H^+					IV	III	II	I	Ia
A_1	2–4	3.6	3.0	1.646	0.817	3.340	3.477	26.54	13.013	0.746	17.45	49.1	14.00	31.05	4.68	0.66
A_2	7–12	4.0	3.3	1.188	0.344	0.876	0.416	54.25	1.124	0.097	11.59	61.7	11.99	6.59	10.15	9.19
B_1	20–25	4.2	3.6	1.194	0.494	6.004	0.941	19.55	8.525	0.405	21.05	71.1	6.73	9.88	8.53	3.47
B_2C	30–40	4.3	3.9	1.192	0.445	4.043	0.236	27.67	8.209	0.258	31.85	72.1	2.82	20.81	3.43	0.56

Calamagrostio villosae-Piceetum typicum, Černá Hora Mt., Table 1, rel. 9

A_1	3–6	3.5	2.9	1.347	1.164	9.897	3.788	15.50	25.898	1.463	17.7	29.6	1.41	26.75	31.33	10.21
A_2	10–15	3.8	3.3	0.653	0.437	3.981	0.614	19.19	3.609	0.181	19.9	61.6	5.57	11.14	18.89	2.42
B_1	25–30	4.2	3.8	1.102	0.447	3.958	0.367	26.37	3.954	0.153	25.83	60.4	3.56	15.72	18.10	1.82

Calamagrostio villosae-Piceetum typicum, Studená Hora Mt., Table 1, rel. 23

A_L	8–15	3.5	2.8	5.324	1.138	4.673	4.760	40.69	21.185	0.955	22.17	25.9	1.33	35.64	30.08	6.30
A_2	16–20	3.7	3.1	1.919	0.583	3.421	2.044	31.40	7.431	0.390	19.08	57.0	3.66	23.65	12.56	2.71
B_1	21–26	3.8	3.5	2.246	0.673	17.228	0.615	14.06	7.410	0.392	18.91	48.0	6.92	33.49	10.09	0.99
B_2	27–35	4.4	4.0	1.950	0.571	2.994	0.469	42.13	4.615	0.167	27.59	67.7	2.49	26.91	2.16	0.42

Calamagrostio villosae-Piceetum fagetosum, Alpa Mt.

$A_1 + A_2$	7–12	3.6	3.1	1.757	0.799	5.400	2.867	23.62	16.647	0.795	20.95	61.9	4.46	26.21	5.41	1.64
B_2C	40–45	3.9	3.3	1.372	0.520	3.114	2.032	26.88	13.363	0.458	29.15	68.7	4.85	16.28	7.36	2.50

Calamagrostio villosae-Piceetum fagetosum, Hraničník Mt., Table 3, rel. 9

A_1	4–7	3.2	2.8	6.089	1.358	16.952	7.385	23.43	40.702	2.049	19.87	3.2	19.84	48.88	19.07	8.03
A_2	8–9	4.1	3.5	1.227	0.404	6.969	1.793	15.69	10.183	0.540	18.85	52.2	5.74	29.78	8.89	2.92
B_1	25–28	4.3	3.8	1.419	0.485	8.320	1.080	16.85	10.493	0.497	21.09	46.6	8.28	32.84	9.99	1.76
B_2	45–50	4.5	4.1	1.175	0.505	4.036	0.683	26.25	7.971	0.317	25.17	56.1	4.26	36.13	2.77	0.31

Plešné, Laka and Černé Lakes, spring sub-top areas of Poledník, Ždanidla, and Debrník Mounts in the northwestern part of the Bohemian Forest and on Boubín Mt. NW from Volary.

Variability: In the *Athyrio alpestris-Piceetum* of the Bohemian Forest, two subassociations can be distinguished: *Athyrio alpestris-Piceetum typicum* and *A. a.-P. athyrietosum filicis-feminae.*

1. *Athyrio alpestris-Piceetum typicum* Hartmann & Jahn 1967 (Table 5, rel. 1–9)

The typical subassociation without subass.-differential species is the most frequent unit of the *Athyrio alpestris-Piceetum.* It occupies colder, higher levels, mostly above ca. (1190) 1230 m a.s.l. In the Bohemian Forest, it is represented by its typical variant only, without any differential species.

This unit is relatively frequent in the Bohemian Forest. It has been recorded in various locations, from its northwestern summits (Ždanidla, Plesná, Poledník Mounts) to the southeastern border (Trojmezná Hora Ridge, Smrčina Mt., top-near levels), and Boubín Mt. (see also Vorel 1968), and above all in corries of the glacial lakes.

2. *Athyrio alpestris-Piceetum athyrietosum filicis-feminae* Jirásek 1996 (Table 5, rel. 10–13)

This subassociation is differentiated by the occurrence of *Acer pseudoplatanus* in all layers, and *Athyrium filix-femina* and *Prenanthes purpurea* in the field layer. In the ground layer, *Rhizomnium punctatum* seems to be linked with this unit, too.

The *Athyrio-Piceetum athyrietosum* occupies lower levels in the area of the association, mostly between ca. 1160–1230 m a.s.l. In the southeastern part of the National Park, this unit links with the stands of mountain sycamore-beech forests of the suballiance *Acerenion* Oberdorfer 1957 em. Husová in Moravec et al. 1982 (*Aceri-Fagetum* J. et M. Bartsch 1940) on stony soils. On (loamy-) sandy soils it links with mountain mixed spruce-beech forests of the *Calamagrostio villosae-Fagetum* Mikyška 1972.

It has been confirmed in the corrie of the Černé Lake, Třístoličník and Smrčina Mounts and Vlčí Jámy near Železná Ruda (here at relatively lower levels with snow accumulation along the episodical brook).

Discussion

In 1967, Stöcker (1967) described spruce forest with *Betula carpatica*, the *Anastrepto-Piceetum*, from the Hochharz Mts., Germany. In 1998, he studied this syntaxon in the Giant (=Krkonoše) Mts. He distinguished two subassociations, the *Anastrepto-Piceetum typicum* with two variants (typical variant, var. with *Hylocomium splendens*) and the *A.-P. oxalidetosum*. In 1996, Jirásek (1996) published a survey of spruce forest communities of the Czech Republic. There, he added many further relevés to this unit from the Hrubý Jeseník Mts. (Bednář & Pěnčíková 1985), Králický Sněžník Mts. (Krahulec 1979), Bohemian Forest (Sofron & Štěpán 1971) and Adršpašsko-Teplické Skály rocks (Sýkora & Hadač 1984).

According to the floristic composition, the *Anastrepto-Piceetum* is similar to the *Vaccinium myrtillus* variants of the *Calamagrostio villosae-Piceetum typicum* and *C.v.-P. fagetosum*, as well as to the *Dryopterido dilatatae-Piceetum*. In spite of it, it is possible to find marked differences not only in the floristic composition (Tables 1, 3, 4), but also in the ecology: in the *Vaccinium myrtillus* variants of the *Calamagrostio-Piceetum*, stones are mostly quite covered

by a continuous humus layer, while in the both further units, the boulder structure of soil profile is clearly visible and the upper soil layer is very thin and disconnected. The differences between the *Anastrepto-Piceetum* and *Dryopterido dilatatae-Piceetum* are given by the position in the spruce-forest belt: the *Anastrepto-Piceetum* is linked with upper, very cold levels of the slopes or inversion levels, for the *Dryopterido dilatatae-Piceetum*, the levels in the lower, less extreme part of the spruce-forest belt near the contact with mountain spruce-beech forests are typical (see also Jirásek 1996, Jirásek in Husová et al. 2002). In the *Vaccinium* variants of the *Calamagrostio villosae-Piceetum* as well as in the *Dryopterido dilatatae--Piceetum*, liverworts of high-mountain or boreal spruce forests typical for the *Anastrepto--Piceetum*, are missing. The differences can be seen in the tree growth, too (smaller trees in the *Anastrepto-Piceetum*).

Some authors do not distinguish the *Athyrio alpestris-Piceetum* as a separate association. Thus, e.g. Peterman & Seibert (1979) distinguished the "Fichten-Hochlagenwald" (*Soldanello-Piceetum barbilophozietosum*, Alpen-Frauenfarn Fazies), corresponding to the *Athyrio--Piceetum*. Into the unit "Fichten-Hochlagenwald" (*Soldanello-Piceetum barbilophozietosum*) all climax spruce forests of the Bohemian Forest have been included. However, the name is confusing, because in the original diagnosis by Braun-Blanquet et al. 1939 the *Soldanello--Piceetum* has been validly published for an other type of spruce forests (Neuhäuslová & Eltsova 2002b).

Ordination

The stands of the subassociations *Calamagrostio villosae-Piceetum typicum* and *C. v.-Piceetum fagetosum* are dispersed quite irregularly in the ordination space (Fig. 1). This relatively high level of heterogeneity can be explained probably as a result of very narrow relations between them linked with the forest management on the territory of the Bohemian Forest, where the majority of natural climax spruce and spruce-beech forests have been replaced by spruce plantations. On the contrary, the stands of the *Athyrio alpestris-Piceetum* as well as those of the *Anastrepto-Piceetum* are markedly separated from other relevés.

Within the subassociation *Calamagrostio villosae-Piceetum typicum* the higher level of specialisation belongs to the communities of the *Calamagrostio-Piceetum typicum* var. *avenellosum* representing very acidophilous and nutrient-poor variant. Relevés of the *Calamagrostio villosae-Piceetum typicum* var. *vacciniosum* and *Calamagrostio villosae–Piceetum fagetosum* var. *vacciniosum* are placed on the right side of ordination space and represent a link with the *Anastrepto-Piceetum*, which also occurs on fresh, scree- or boulder soils of shady slopes. Thus, according to position of relevés within the ordination space, the first axis can reflect soil texture and the second one acidity.

Acknowledgement. The authors thank the Grant Agency of the Czech Republic for the financial support of the project Nr. 206/99/1416. This study was supported by research project of the Institute of Botany of the Academy of Sciences of the Czech Republic, Nr. AVOZ6005908, too. Thanks are due to J. Jeník for his comments to this paper, J. Sofron and J. Jirásek for their help in the field, J. Vorel for permission to use his typological material, M. Albrechtová for carying out soil sample analyses, B. Buryová and H. Franklová, partly also M. Vondráček, helped by determination of bryophytes, and Z. Palice by determination of lichens.

References

Bartsch J. & Bartsch M., 1940: Vegetationskunde des Schwarzwaldes. *Pflanzensoziologie*, Jena, 4: 1–229.

Bednář V. & Penčíková M., 1985: Společenstva přirozených smrčin v povodí Merty v Hrubém Jeseníku [Communities of natural spruce forests in the valley of the Merta River in the Hrubý Jeseník Mts.]. *Acta Universitatis Palackyanae Olomucensis, Biol.*, 25: 47–64 (in Czech).

Braun-Blanquet J., 1964: *Pflanzensoziologie*. Springer Verlag, Wien & New York, 865 pp.

Braun-Blanquet J., Sissingh G. & Vlieger J., 1939: *Prodromus der Pflanzengesellschaften. Prodrome des Groupements végétaux. 6. Klasse der Vaccinio-Piceetea. (Nadelholz- und Vaccinienheiden-Verbände der eurosibirisch-nordamerikanischen Region).* In: Communications de la Station Internat. de Géobotanique Méditer. et Alpine 6: 1–123. Mari-Levit, Montpellier.

Ehrendorfer F. (ed.), 1973: *Liste der Gefässpflanzen Mitteleuropas. 2. erweiterte Aufl.* Gustav Fischer Verlag, Stuttgart. 318 pp.

Frahm J.-P. & Frey W., 1992: *Moosflora.* Ed. 3. E. Ulmer, Stuttgart. 522 pp.

Hadač E., Jeník V. & Březina P., 1969: Rostlinná společenstva Trojrohého plesa ve Vysokých Tatrách [Die Pflanzengesellschaften des Bergsees Trojrohé pleso in der Hohen Tatra]. *Zbornik Prác o Tatranskom Národnom Parku,* 11: 481–494 (in Czech, English Summary).

Hartmann F.K., 1953: Waldgesellschaften der deutschen Mittelgebirge und des Hügellandes. *Umschaudienst. Akademie d. Landesplanung, Landschaftsgestaltung,* Hannover, 4–6: 147–182.

Hartmann F.K. & Jahn G., 1967: *Waldgesellschaften des mitteleuropäischen Gebirgsraumes nördlich der Alpen.* Gustav Fischer Verlag, Stuttgart, 636 pp.

Hennekens S.M., 1996: *TURBOVEG. Software package for input, processing and presentation of phytosociological data.* Wageningen, Lancaster.

Hennekens S.M. & Schaminee J.H.J., 2001: TURBOVEG, a comprehensive data base management system for vegetation data. *J. Veget. Sci.*, Uppsala, 12/4: 589–591.

Hill M.O., 1979: *TWINSPAN. A Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes.* Cornell University, Ithaca.

Hilitzer A., 1929: Geobotanický rozbor vegetace Jezerní stěny na Šumavě [Geobotanical analysis of the vegetation of the Jezerní Stěna Mt. in the Bohemian Forest]. *Věstník 6. Sjezdu Čs. přírodozpytců, lékařů a inženýrů,* sect. natur., Praha 1928/3: 100–102 (in Czech).

Husová M., Jirásek J. & Moravec J., 2002: *Jehličnaté lesy* [*Coniferous forests*]. In: Přehled vegetace České republiky [Vegetation Survey of the Czech Republic]. Moravec J. (ed.), vol. 3: 1–128. vydavatelství Praha (in Czech, English Summary).

Jirásek J., 1996: Společenstva přirozených smrčin České republiky [Gesellschaften natürlicher Fichtenwälder in der Tschechischen Republik]. *Preslia,* 67: 225–259 (in Czech, German Summary).

Krahulec F., 1979: *Smrčiny kulminační části Králického Sněžníku* [*Spruce forests of the culmination part of the Králický Sněžník Mts.*] *1–2.* Dissertation, Charles University, Prague, 72 pp. (Library of Department of Botany, Faculty of Nature Sciences, Charles University, Prague) (in Czech).

Kučera S., 1978–1990: Materiály z Modravských slatí [Materials from the Modravské Slatě bogs]. In: *Šumavské studie.* Pecharová E. & Rada P. (eds), pp. 65–111, ed. Institute of Botany of AS CR, Třeboň (in Czech).

Kučera S., 1991: Geobotanické posouzení centrální části Národního parku Šumava pro účely zonace a managementu. Materiály z Modravských slatí [Geobotanische Beurteilung des Zentralteiles des NP Šumava. Materiale aus den Filzen von Modrava]. In: *Šumavské studie,* Pecharová E. & Rada P. (eds), pp. 7–11. ed. Institute of Botany of AS CR, Třeboň (in Czech).

Mikyška R., 1972: Die Wälder der böhmischen mittleren Sudeten und ihrer Vorberge. *Rozpravy Československé Akademie Věd,* 82/3: 1–162.

Moravec J. (ed.), 1994: *Fytocenologie (Nauka o vegetaci)* [*Phytocenology*]. Academia, Praha. 404 pp. (in Czech).

Moravec J. (ed.), 1995: Rostlinná společenstva České republiky a jejich ohrožení [Red list of plant communities of the Czech Republic and their endangerment]. Ed. 2. *Severočeskou Přírodou,* Suppl. 1995: 1–206 (in Czech, English Summary).

Moravec J., Husová M., Neuhäusl R. & Neuhäuslová Z., 1982: Die Assoziationen mesophiler und hygrophiler Laubwälder in der Tschechischen Sozialistischen Republik. In: *Vegetace ČSSR,* ser. A, 12: 1–292 (in German, Czech Summary).

Nesvadbová J. (ed.), 1994: Rašeliniště a podmáčené smrčiny u Nové Hůrky (Šumavské pláně) [Moore und vernäßte Fichtenwälder bei der Gemeinde Nová Hůrka (Neuhürken, Böhmerwalder Hochebenen)]. *Erica,* 3: 39–51 (in Czech).

Neuhäuslová Z. (ed.), 1998, 2001: *Mapa potenciální přirozené vegetace České republiky. Textová část* [*Map of potential natural vegetation of the Czech Republic. Explanatory Text*]. Academia, Praha, 342 pp. Reprint 2001 (in Czech, English Summary).

Neuhäuslová Z. (ed.), 2001: The Map of potential natural vegetation of the Šumava National Park. *Silva Gabreta,* Suppl. 1: 1–189 (in Czech, English and German).

Neuhäuslová Z. & Eltsova V., 2001: Das *Sphagno-Piceetum* im Nationalpark Šumava (Böhmerwald). *Silva Gabreta,* 6: 111–124.

Neuhäuslová Z. & Eltsova V., 2002a: The *Bazzanio-Piceetum* in the Bohemian Forest (Šumava Mts.). Czech Republic. *Feddes Repert.,* 113/5–6: 367–379.

Neuhäuslová Z. & Eltsová V., 2002b: Das *Soldanello-Piceetum* in Südböhmen. *Verhandlungen der Zoologisch-Botanischen Gesellschaft Österreich*, 139: 123–133.

Neuhäuslová Z. & Wild J., 2000: Dynamics of spruce forests in the Šumava National Park, Czech Republic. In: *Biodiversity and dynamics of ecosystems in North Eurasia*, vol. 4, pars 1, p. 78–79. Novosibirsk.

Oberdorfer E., 1957: Süddeutsche Pflanzengesellschaften. *Pflanzensoziologie*, 10: 1–564.

Pettermann R. & Seibert P., 1979: Die Pflanzengesellschaften des Nationalparks Bayerischer Wald mit einer farbigen Vegetationskarte. In: *Nationalpark Bayerischer Wald*. Bayer. Staatsminist. Ernährung, Landwirtschaft und Forsten, Grafenau, 4: 1–142.

Pišta F., 1975: Smrčiny ve východní části kvildských plání [Spruce forest in the eastern part of the Plateaus of the Bohemian Forest/Šumava]. *Lesnictví*, 21 (48): 527–552 (in Czech).

Poelt J., 1969: *Bestimmungsschlüssel Europäischer Flechten*. Cramer, Lehre.

Quitt E., 1971: Klimatické oblasti Československa [Climatic regions of Czechoslovakia]. *Studia Geographica*, Brno, 16: 1–64 (in Czech, German and English Summary).

Soukup J., 1981: Přirozené smrčiny západních a jihozápadních Čech [Die natürlichen Fichtenwälder in West- und Südwestböhmen]. *Studie ČSAV*, 7/1981: 1–127 (in Czech, German Summary).

Soukup J., 1985: Vrcholový fenomen hory Můstek na Šumavě [Das Gipfelphänomen des Berges Můstek (Brückel) im Šumava-Gebirge (Böhmerwald)]. *Zpravodaj muzejí západočeského kraje, Příroda*, 30–31: 19–31 (in Czech).

Soukup J., 1993: Poznámky k charakteristice vegetace lesu, rašelinišť, pramenišť a některých antropogenních bezlesí Brd [Comments to the characteristics of forest, peatbogs, spring areas and some cleared areas vegetation in the Brdy Mts.]. In: *Příroda Brd a perspektivy její ochrany*. Referát OÚ Příbram, p. 39–44.

Soukup J. & Šandová M., 1972: Pflanzengesellschaften des Hochmoores Rokytská slať (Weißfäller Filz) im Šumava Gebirge. *Folia Musei Rerum Naturalium Bohemiae Occidentalis, Botanica*, 1: 1–27.

Soukup J. & Štěpán J., 1971: Vegetace šumavských karů [Vegetation der Böhmerwalder Kare]. *Rozpravy Československé akademie věd*, ser. math.-natur., 81/1: 1–57 (in Czech, German Summary).

Stöcker G., 1967: Der Karpatenbirken-Fichtenwald des Hochharzes. *Pflanzensoziologie*, 15: 1–123.

Stöcker G., 1968: Das *Anastrepto-Piceetum* im Harz und Riesengebirge (Krkonoše). *Opera Corvontica*, 5: 135–155.

Sýkora T. & Hadač E., 1984: Příspěvek k fytogeografii Adršpašsko-Teplických skal [Contribution to the phytogeography of the Adršpach-Teplice rock complex]. *Preslia*, 56: 359–376 (in Czech, English Summary).

Šoltés R., 1976: Phytozönotische Analyse des Verbandes *Vaccinio-Piceion* Br.-Bl. 1938 in den Westkarpaten. *Acta Facultatis Rerum Naturalium Universitatis Comenianae*, Botanica, 24: 139–167.

ter Braak C.J.F. & Šmilauer P., 1998: *CANOCO references manual and user's guide to CANOCO for Windows: Software for Canonical Community Ordination (version 4)*. CPRO-DLO, Wageningen.

Trautmann W., 1952: Pflanzensoziologische Untersuchungen der Fichtenwälder des Bayerischen Waldes. *Forstwissenschaftliches Centralblatt*, 71: 289–313.

Tüxen R., 1937: Die Pflanzengesellschaften NW–Deutschlands. *Mitteilungen der Floristisch-Soziologischen Arbeitsgemeinschaft Niedersachsen*, Hannover, 3: 1–170.

Vorel J., 1968: *Stupňovitost lesních biogeocenóz pohraniční horské části Šumavy [Vegetation belts of biogeocoenoses in the mountain border part of the Šumava Mts.]*. Disertation, ÚHÚVLS, Velká Bystřice, 320 pp. (ÚHÚVLS, Velká Bystřice) (in Czech).

Westhoff V. & van der Maarel E., 1973: The Braun-Blanquet approach. In: *Ordination and classification of communities*, Whittaker R.H., Handbook Vegetation Science, 5: 617–726.

Wild J., Neuhäuslová Z., & Soukup J., 2003: Changes of the Šumava spruce forests since the 1970ies. *Forest Ecology and Management* (in press).