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Plant communities of silver fir (*Abies alba*) forests in southeastern Bohemia

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Abstract

The vegetation of silver fir forests in southeastern Bohemia (Czech Republic) was studied using the Braun-Blanquet approach. On the basis of 57 phytosociological relevés, three associations were subjectively distinguished: (1) oligotrophic *Vaccinio vitis-idaeae-Abietetum*, (2) oligo-mesotrophic *Luzulo luzuloidis-Abietetum*, and (3) mesotrophic *Galio rotundifolii-Abietetum* (all of them with drier and wetter subtypes). Each association is characterised by species composition, basic soil properties (soil type, humus form), and distribution in the study area. Ellenberg indicator values and detrended correspondence analysis were used to visualize the similarity of vegetation types and detect the main ecological factors determining the proposed classification. The syntaxonomy of fir-dominated forests is discussed.

Keywords: *Abies alba*, coniferous forest, Czech Republic, phytosociology, site ecology.

Zusammenfassung

Die Pflanzengesellschaften der Tannenwälder in Südst-Böhmen

Die Vegetation der Tannenwälder wurde in Südst-Böhmen (Tschechien) mit Hilfe des Braun-Blanquet-Ansatzes untersucht. Drei Assoziationen von Tannenwäldern wurden subjektiv unterschieden, basierend auf 57 Vegetationsaufnahmen: (1) das *Vaccinio vitis-idaeae-Abietetum* auf oligotrophen Standorten, (2) das *Luzulo luzuloidis-Abietetum* auf oligo-mesotrophen Standorten und (3) das *Galio rotundifolii-Abietetum* auf mesotrophen Standorten (alle mit bodentrockeneren und -feuchteren Untereinheiten). Jede Assoziation wird mit Artenkombination, Bodeneigenschaften und Verbreitung im Untersuchungsgebiet beschrieben. Ellenberg-Zeigerwerte und Ordinationsmethoden werden verwendet, um die Ähnlichkeit der Vegetationstypen und die für die Vegetation wichtigen Umweltfaktoren darzustellen. Die Syntaxonomie der Tannenwälder wird diskutiert.

1. Introduction

Silver fir (*Abies alba*) is one of the most threatened tree species in the forests of Central Europe (MÍCHAL et al. 1992). Its strong decline began to be registered in the Czech Republic already in the 1970s. Today, it constitutes only about 1% of Czech forests, but its natural representation in a climax landscape is estimated to be 16–20% (MÁLEK 1983, ŠINDELÁŘ 1995). Although some improvement of the condition of fir health has been observed in the last decades (MÍCHAL & PETŘÍČEK 1999), silver fir forests are still considered as rare and threatened vegetation types in the Czech Republic (MORAVEC et al. 1995).

In the Czech Republic, where fir forests occur within the altitudinal range of beech forests, the dominance of fir on Cambisols and Podzols is considered to be a result of human impact (e.g. forest grazing, litter gathering, preference of fir in forest management, MÁLEK 1971, 1983, MÍCHAL & PETŘÍČEK 1999). Beech has been observed as the regenerating tree in some fir forests in these habitats (GRULICH 2006). Nevertheless, some authors map non-waterlogged fir forests as potential natural vegetation (NEUHÄUSLOVÁ et al. 1997, 1998). Fir is generally assumed to dominate only on soils periodically influenced by ground water (Planosols) (WALENTOWSKI 1998, BUČEK & LACINA 2000, WALENTOWSKI et al. 2005), but even in these habitats the expected proportion of naturally growing beech might be underestimated.

In the Czech Republic, fir-dominated forests occur mainly in the supracolline and submontane (ca 350–800 m a.s.l.) vegetation belts. More extensive stands are located in southern, western and central Bohemia, in southwestern Moravia, and in the Moravian Carpathians (BOUBLÍK 2005). In some historical documents from the 16th century, we can find refer-

ences to silver fir forests also in southeastern Bohemia (AMBROŽ 1948). The currently existing fir forests probably represent only small remnants of formerly more extensive stands (RYBNÍČEK & RYBNÍČKOVÁ 1978, MÁLEK 1983).

In the current vegetation of the Czech Republic, four associations of *Abies alba* forests have traditionally been distinguished within the *Luzulo-Fagion* and *Fagion* alliances (e. g. HUSOVÁ 1968, 1983, 1998, MORAVEC et al. 2000): the acidophilous communities *Deschampsio flexuosaef-Abietetum* (occurring on Cambisols) and *Luzulo pilosae-Abietetum* (on Planosols), the mesotrophic association *Saniculo europaeaef-Abietetum* (typical for Stagnic Cambisols), and the hygrophilous *Carici remotae-Abietetum* (occurring in contact with springs on Planosols or Gleysols). Scree forests dominated by fir are assigned to the alliance *Tilio-Acerion* (e. g. *Aceri-Carpinetum abietetosum*, *Lunario-Aceretum lunarietosum*, and *Arundo-Aceretum abietetosum*, MORAVEC et al. 2000). Up to now, fir forests in southeastern Bohemia have been mentioned only in a local study by BOUBLÍK (2002). The aim of this study is to describe all of the distinguished fir forest vegetation types in the study area, including ecology and distribution. Special attention was paid to the soil and humus properties. A new concept of classification of fir forests in this area is proposed and discussed.

2. Study area

The study area is located in the southeastern part of Bohemia. It is delimited by the towns of Nové Hrady in the south, Třeboň, Kardašova Řečice, Kamenice nad Lipou in the northwest and Strmilov, Kunžak and Staré Město pod Landštejnem in the east. The southern boundary of the area is the border between the Czech Republic and Austria (Fig. 1). The study area is situated in the supracolline and submontane vegetation belts (SKALICKÝ 1988), with the range of altitudes between 430 and 738 m.

The Třeboň basin (the western part) is filled by Mesozoic, Tertiary and Quaternary sediments (e. g. sandstones, conglomerates, claystones, clays, [gravel] sands, peats). The central and eastern hilly part of the study area (the southwestern part of the Českomoravská vrchovina hills – the Novobystřická and Křemešnická vrchovina hills) is formed mostly by Proterozoic gneisses together with migmatites and Palaeozoic granites and granodiorites (CHÁBERA et al. 1985).

Moderately warm climate predominates in this area, except for the highest altitudes above ca 650 m. These localities, situated in the east, belong to the cold climatic region (QUITT 1971). The mean annual temperature varies between 5.5 and 7.8 °C and the mean annual precipitation reaches ca 620–750 mm (SYROVÝ 1958; data for the period 1901–1950).

Cambisols and Podzols are the most widespread soil types. Planosols, Gleysols and Histosols are confined to the terrain depressions (mainly in the Třeboň basin). Leptosols occur rarely: we can find them on the summits and in the brook valleys in the central and the eastern hilly part of the study area. Arenosols are typical for sandy sediments in the Třeboň basin.

3. Material and methods

In this study, fir forests are defined as predominantly coniferous stands older than 60 years with at least 30% representation of fir. Beech is either absent or its proportion is less than 25%. The phytosociological data were collected subjectively using the Braun-Blanquet method. For the estimation of species cover and abundances, a modified 9-point Braun-Blanquet scale was mostly used (WESTHOFF & VAN DER MAAREL 1973). Plots were selected in order to represent all of the main fir forest vegetation types in the study area. In total, 57 relevés were collected by K.B. in 2000–2004. All of them are stored in the Czech National Phytosociological Database (CHYTRÝ & RAFAJOVÁ 2003) and 14 of them were published in BOUBLÍK (2002). The basic soil properties (soil type, subtype, variety, and humus form) were recorded in the centre of each phytosociological relevé. The degree of soil hydromorphism was determined on the basis of evaluation of the soil type, subtype, and variety according to the Czech soil classification system (NĚMEČEK et al. 2001). For our analyses, the degree of soil hydromorphism and the humus forms are expressed on ordinal scales. Concerning the humus forms, ordinal values from 1 to 7

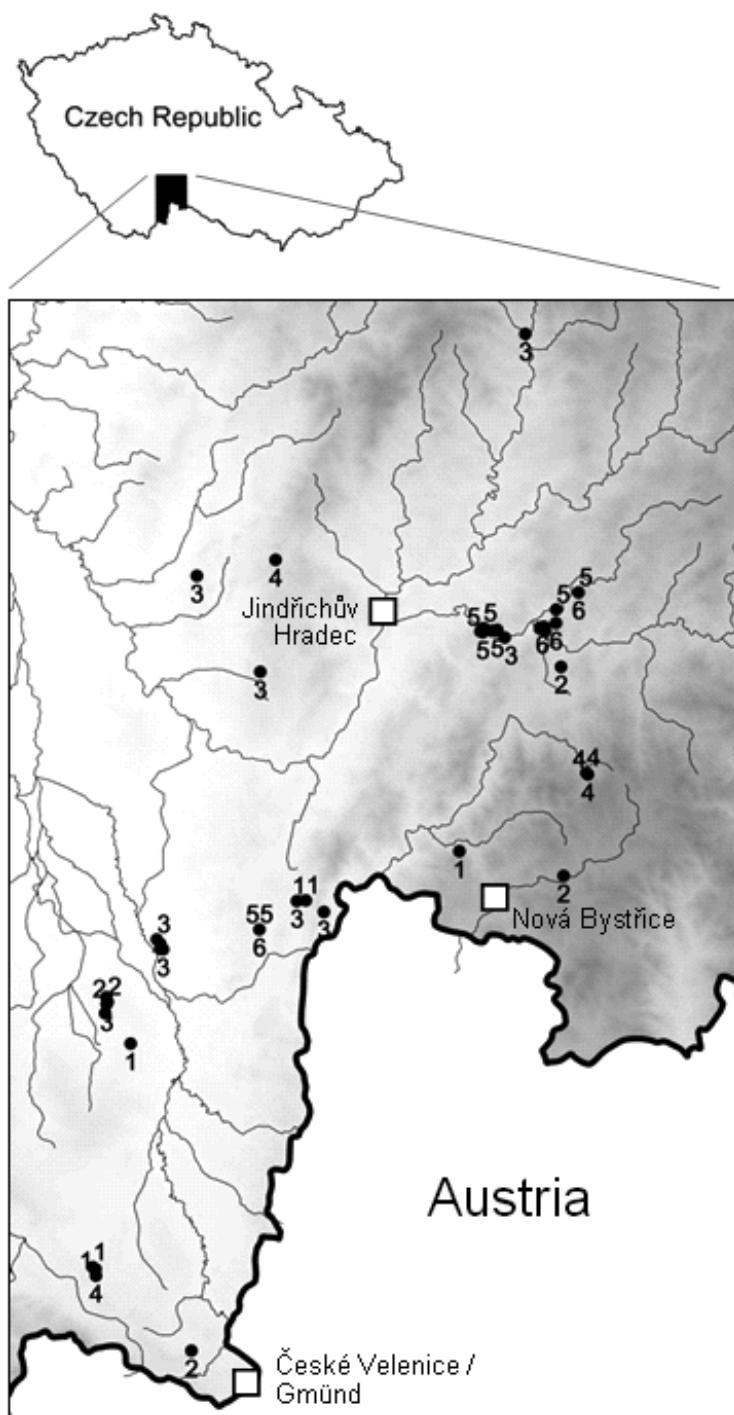
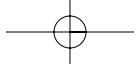


Fig. 1: Location of the study area within the Czech Republic and distribution of distinguished vegetation units in the study area (numbers of vegetation units correspond to Tab. 1).

Abb. 1: Lage des Untersuchungsgebiets in Tschechien und Vorkommen der einzelnen Vegetationsarten (die Nummern der Typen korrespondieren mit Tab. 1).



are ordered in accordance with the increasing humus quality (see Table 3); as for hydromorphism, ordinal values from 1 to 7 are ordered from the soils with no hydromorphic features to Gleysols (see Table 4).

Relevés were entered and stored using the programme TURBOVEG 2.0 (HENNEKENS & SCHAMINÉE 2001), transforming the species cover values from the ordinal Braun-Blanquet scale into a percentage scale. The classification of relevés was carried out subjectively based on species composition following the Braun-Blanquet approach (WESTHOFF & VAN DER MAAREL 1973). The value of species frequency was used for the preparation of a synoptic table in the programme JUICE 6.3 (TICHÝ 2002). The table of phytosociological relevés (Table 2) contains only the unpublished relevés.

To reveal major gradients in species composition and similarity between the distinguished vegetation types, detrended correspondence analysis (DCA) was performed using the package CANOCO 4.5 (TER BRAAK & ŠMILAUER 2002). The square root transformation of percentage cover species data and detrending by segments were used. For the interpretation of the first two ordination axes, the Ellenberg indicator values (EIV) for soil nutrients, light, continentality, soil reaction (pH), temperature, and soil moisture (ELLENBERG et al. 1992), together with the recorded humus form and the degree of soil hydromorphism, were projected *post hoc* in the resulting ordination diagram. The Ellenberg values for each relevé were calculated in the programme JUICE 6.3 (TICHÝ 2002) as the non-weighted average of values for vascular plants from merged vegetation layers. The EIVs were also used for the ecological calibration of the distinguished vegetation types. Box-and-whisker plots for particular EIVs were prepared using the package STATISTICA 7.0 (www.statsoft.com).

The species nomenclature follows KUBÁT et al. (2002) for vascular plant taxa and KUČERA & VÁŇA (2003) for bryophytes. The nomenclature of syntaxa is according to WALENTOWSKI (1998). The nomenclature of soil groups and subunits follows ISSS-ISRIC-FAO (1998). The concept of humus forms is according to NĚMEČEK et al. (2001).

4. Results

4.1. Vegetation types

Six relevé groups were subjectively distinguished in the fir forest vegetation of southeastern Bohemia (Table 1). The groups belong to three associations; within each association, two different subtypes correlated with soil moisture can be distinguished. The following description of species composition is valid only for the southeastern Bohemian stands. For the distribution of vegetation types see Fig. 1.

4.1.1. *Vaccinio vitis-idaeae-Abietetum* Oberdorfer 1957

(Table 1, cols 1–2, Table 2, rels 1–20)

The dominance of *Vaccinium myrtillus* or *Avenella flexuosa* and the absence of mesotrophic species in the herb layer are the typical features of the oligotrophic spruce-pine-fir forests, characterised by the lowest nutrient status in comparison with the other units (Fig. 2). Strongly acidic mor is the most frequent humus form (Table 3). The stands of this association occur in the whole area on granite colluvia (the Novobystřická vrchovina hills), fluvial gravel sands, and Mesozoic sediments (the Třeboň basin).

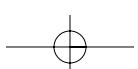
Two ecologically differentiated subtypes can be distinguished within this unit. The drier subtype occurs on soils with small or no influence of groundwater (Cambisols and Podzols). The wet subtype occurring on Planosols (Table 4) is differentiated e.g. by *Sphagnum girgensohnii* and *Molinia caerulea* agg.

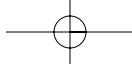
4.1.2. *Luzulo luzuloidis-Abietetum* Oberdorfer 1957

(Table 1, cols 3–4, Table 2, rels 21–38)

Oligo-mesotrophic spruce-fir woodlands are scattered in the whole study area. Except for the acidophilous species (*Vaccinium myrtillus*, *Avenella flexuosa*), the presence of oligo-mesotrophic plant taxa is important for its distinction from the previous association (e.g. *Mycelis muralis*, *Calamagrostis arundinacea*, *Rubus idaeus*, *Luzula pilosa*, and *Rubus* ser. *Glandulosi*). Mesotrophic species are usually absent.

Based on the differences in species composition reflecting the soil water regime, two ecological subtypes within the *Luzulo luzuloidis-Abietetum* can be distinguished. The subtype





of the drier habitats (on Cambisols – see Table 4) without differential species is situated in fluvial gravel sands, Mesozoic sediments (the Třeboň basin), granites, migmatites and paragneisses (the Českomoravská vrchovina hills). Various subtypes of moder are the most frequent humus forms (Table 3).

The wet subtype (similar to *Luzulo luzuloidis-Abietetum deschampsietosum cespitosae* sensu WALENTOWSKI 1998) occurs on waterlogged soils (Gleysols and Planosols) in the terrain depressions. Hygrophilous species, such as *Equisetum sylvaticum*, *Polytrichum commune*, *Sphagnum palustre*, *Lysimachia nemorum*, and *Deschampsia cespitosa* are the diagnostic species. Humus forms are mostly represented by hydromor and typical mor (Table 3).

4.1.3. *Galio rotundifolii-Abietetum Wraber (1955) 1959* (Table 1, cols 5–6, Table 2, rels 39–43)

Galio-Abietetum is a mesotrophic herb-rich spruce-fir forest. The association is differentiated by various *Fagetalia* species (e.g. *Senecio nemorensis* agg., *Impatiens noli-tangere*, *Carex digitata*, *Fragaria vesca*). The stands of the association are confined to the brook valleys east of the town of Jindřichův Hradec and the vicinity of the village of Staňkov.

Similarly to the two previous associations, two ecologically different subtypes can be distinguished. The subtype of the drier habitats occurs on Cambisols (Table 4), which is developed from paragneiss and granite rock debris. Moder is the most frequent humus form. This vegetation type represents the most warmth-demanding community in the study area (Fig. 2).

The habitat subtype of waterlogged soils (Planosols and Gleysols, which are developed on granite bedrock) is the rarest fir forest community of the study area. Moder is the typical humus form (Table 3). The surroundings of spring areas are the typical habitat of this vegetation subtype. Accordingly, species of forest springs from the alliance *Caricion remotae* form the differential species group (e.g., *Ajuga reptans*, *Plagiomnium undulatum*, *Valeriana dioica*, *Ranunculus repens*, *Carex remota*, *Equisetum sylvaticum*). Some of these species are also common in the wet type of *Luzulo luzuloidis-Abietetum* (see Table 1). This vegetation type is assigned to *Galio rotundifolii-Abietetum equisetetosum sylvatici* (MÜLLER in OBERDORFER 1992, WALENTOWSKI 1998).

4.2. Gradient analysis

The ordination diagram in Fig. 3 shows the distribution of the distinguished vegetation types along the first two ordination axes, together explaining 16.1% of the total species variability. The main division into associations distinguished by trophic level and soil reaction (from the oligotrophic and acidophilous *Vaccinio vitis-idaeae-Abietetum* to the mesotrophic *Galio rotundifolii-Abietetum*) follows the first ordination axis, which is correlated with EIV for nutrients and soil reaction and increasing quality of humus. The division into drier and wetter habitat subtypes corresponds with the second ordination axis, correlated mostly with EIV for moisture and degree of soil hydromorphism.

5. Discussion

In Germany, Austria, and Slovakia, the acidophilous communities of spruce-fir forests are assigned to the class *Vaccinio-Piceetea* (FAJMONOVÁ 1976, ŠOMŠÁK 1982, MUCINA & MAGLOCKÝ 1985, SEIBERT in OBERDORFER 1992, POTT 1992, WALLNÖFER 1993, WALENTOWSKI 1998). However, the occurrence of some stands in the middle altitudes in the habitats of climax mixed forests with a high proportion of *Fagus sylvatica* (WALENTOWSKI 1998, BOUBLÍK 2005) justifies the possible inclusion of these communities also into the class *Querco-Fagetea*. This concept was used in the syntaxonomy of the Czech fir forests (HUSOVÁ 1968, 1983, MORAVEC et al. 2000). Tables 1 and 2 show that the species of *Vaccinio-Piceetea* are frequent in the *Vaccinio vitis-idaeae-Abietetum* and, simultaneously, that the species of *Querco-Fagetea* are absent. Thus, we suggest that this unit be classified in the class *Vaccinio-*

Tab 1: Constancy table of fir forests in southeastern Bohemia.

The percentage constancies of species are shown. Diagnostic species for particular vegetation types are printed in bold. In total, 36 species occurring in only one column with percentage constancy < 15% were omitted. Layers: 3 – tree layer, 2 – shrub layer, 1 – herb layer, 0 – moss layer.

Tab. 1: Stetigkeitstabelle (in %) der Tannenwälder in Südst.-Böhmen.

Die diagnostischen Arten für die einzelnen Vegetationstypen sind fett gedruckt. 36 Arten mit Stetigkeiten < 15 % wurden ausgeschlossen. Schichten: 3 – Baum-, 2 – Strauch-, 1 – Kraut-, 0 – Moosschicht. VA – *Vaccinio vitis-idaeae-Abietetum*, VAw – *Vaccinio vitis-idaeae-Abietetum*, wet subtype/feuchter Subtyp, LA – *Luzulo luzuloidis-Abietetum*, LAW – *Luzulo luzuloidis-Abietetum*, wet subtype/feuchter Subtyp, GA – *Galio rotundifolii-Abietetum*, GAw – *Galio rotundifolii-Abietetum*, wet subtype/feuchter Subtyp.

Group number	Layer	1 VA 12	2 VAw 8	3 LA 18	4 LAW 5	5 GA 10	6 GAW 4
Tree species							
<i>Picea abies</i>							
<i>Picea abies</i>	3	92	100	78	100	70	100
<i>Picea abies</i>	2	100	88	61	100	20	25
<i>Picea abies</i>	1	100	100	89	100	100	100
<i>Abies alba</i>	3	100	100	100	100	100	100
<i>Abies alba</i>	2	58	25	33	20	30	.
<i>Abies alba</i>	1	100	100	100	100	100	100
<i>Pinus sylvestris</i>	3	58	.	22	40	30	.
<i>Pinus sylvestris</i>	1	17	12	6	40	.	25
<i>Sorbus aucuparia</i>	3	.	25	.	.	.	25
<i>Sorbus aucuparia</i>	2	17	.	39	40	60	75
<i>Sorbus aucuparia</i>	1	58	100	94	100	90	100
<i>Fagus sylvatica</i>	3	.	.	6	.	.	.
<i>Fagus sylvatica</i>	2	.	.	17	.	.	.
<i>Fagus sylvatica</i>	1	8	12	56	40	40	75
<i>Quercus robur</i>	3	.	50	33	.	10	25
<i>Quercus robur</i>	1	58	50	67	60	90	75
<i>Quercus petraea</i> agg.	3	8	25	11	.	.	.
<i>Quercus petraea</i> agg.	1	25	12	6	.	.	.
<i>Betula pendula</i>	3	.	.	6	.	10	.
<i>Betula pendula</i>	2	.	.	12	.	20	.
<i>Betula pendula</i>	1	42	25	6	20	20	50
<i>Populus tremula</i>	3	25
<i>Populus tremula</i>	2	50
<i>Populus tremula</i>	1	8	.	6	.	10	50
<i>Acer pseudoplatanus</i>	3	10	.
<i>Acer pseudoplatanus</i>	2	.	.	17	.	20	25
<i>Acer pseudoplatanus</i>	1	.	.	39	20	60	50
<i>Alnus glutinosa</i>	3	.	.	.	20	.	.
<i>Alnus glutinosa</i>	2	.	.	.	40	.	25
<i>Alnus glutinosa</i>	1	.	.	.	20	.	.
<i>Quercus rubra</i>	1	8	12	6	.	.	25
<i>Betula pubescens</i>	3	.	12
<i>Betula pubescens</i>	1	.	12
<i>Fraxinus excelsior</i>	2	10	.
<i>Fraxinus excelsior</i>	1	.	.	6	.	10	.
<i>Prunus avium</i>	1	10	25
<i>Larix decidua</i>	1	8
<i>Pinus strobus</i>	1	8
<i>Quercus</i> sp.	1	.	.	11	.	.	.
<i>Tilia</i> sp.	1	.	.	6	.	.	.
<i>Betula</i> sp.	1	.	.	6	.	.	.
<i>Tilia cordata</i>	1	10	.

Vaccinio-Abietetum - drier habitat subtype						
<i>Sphagnum capillifolium</i>	0	33
Vaccinio-Abietetum - wet habitat subtype						
<i>Molinia caerulea</i> agg.	1	.	38	.	.	.
<i>Herzogiella seligeri</i>	0	.	25	6	.	.
<i>Chiloscyphus profundus</i>	0	.	25	.	.	.
Luzulo-Abietetum - wet habitat subtype						
<i>Polytrichum commune</i>	0	.	.	.	80	.
<i>Sphagnum palustre</i>	0	.	.	.	60	.
<i>Calamagrostis epigejos</i>	1	.	.	22	60	10
<i>Lysimachia nemorum</i>	1	.	.	.	40	.
<i>Plagiochila asplenoides</i>	0	.	12	.	40	10
<i>Brachythecium oedipodium</i>	0	17	.	.	20	.
<i>Crepis paludosa</i>	1	.	.	.	20	.
<i>Sphagnum fallax</i>	0	.	.	.	20	.
<i>Circaea alpina</i>	1	.	.	.	20	.
<i>Carex echinata</i>	1	.	12	.	20	.
<i>Plagiothecium undulatum</i>	0	8	12	.	20	.
<i>Melampyrum pratense</i>	1	.	.	.	20	.
<i>Stellaria alsine</i>	1	.	.	.	20	.
<i>Calypogeia integrifistipula</i>	0	.	.	.	20	.
<i>Calypogeia muelleriana</i>	0	.	.	.	20	.
<i>Phegopteris connectilis</i>	1	.	.	.	20	10
<i>Impatiens parviflora</i>	1	.	.	11	20	10
<i>Lycopodium annotinum</i>	1	.	.	.	20	10
<i>Lepidozia reptans</i>	0	.	.	6	20	.
<i>Stellaria nemorum</i>	1	.	.	6	20	.
<i>Agrostis canina</i>	1	.	.	.	20	.
<i>Caltha palustris</i>	1	.	.	.	20	.
Vaccinio-Abietetum + Luzulo-Abietetum - wet habitat subtypes						
<i>Sphagnum girgensohnii</i>	0	8	100	.	60	.
Vaccinio-Abietetum + Luzulo-Abietetum						
<i>Leucobryum glaucum</i>	0	92	62	39	20	.
<i>Viscum album</i> ssp. <i>abietis</i>	3	33	12	11	20	.
<i>Bazzania trilobata</i>	0	75	75	11	40	10
<i>Dicranum polysetum</i>	0	33	50	11	40	10
Galio-Abietetum - drier habitat subtype						
<i>Melica nutans</i>	1	.	.	11	.	60
<i>Lonicera nigra</i>	2	.	.	17	.	50
<i>Lonicera nigra</i>	1	.	.	11	.	50
<i>Galeobdolon montanum</i>	1	50
<i>Galium sylvaticum</i>	1	50
<i>Galeopsis speciosa</i>	1	40
<i>Mercurialis perennis</i>	1	30
<i>Poa nemoralis</i>	1	.	.	6	.	30
<i>Lonicera xylosteum</i>	2	30
<i>Geranium robertianum</i>	1	30
<i>Pulmonaria obscura</i>	1	30
<i>Mnium spinulosum</i>	0	8	.	.	.	20
<i>Galeopsis bifida</i>	1	.	.	6	.	20
<i>Mnium spinosum</i>	0	.	.	6	.	20
<i>Chelidonium majus</i>	1	20
<i>Galeopsis pubescens</i>	1	20
<i>Campanula trachelium</i>	1	20
<i>Galium rotundifolium</i>	1	20
<i>Sambucus racemosa</i>	1	20
<i>Asarum europaeum</i>	1	20
<i>Lathyrus vernus</i>	1	20
Galio-Abietetum - wet habitat subtype						
<i>Ajuga reptans</i>	1	75
<i>Plagiomnium undulatum</i>	0	50
<i>Urtica dioica</i>	1	.	.	.	10	50

<i>Ranunculus repens</i>	1	50
<i>Anemone nemorosa</i>	1	50
<i>Valeriana dioica</i>	1	50
<i>Juncus effusus</i>	1	25
<i>Cirsium oleraceum</i>	1	25
<i>Eurhynchium praelongum</i>	0	25
<i>Viola riviniana</i>	1	25
<i>Epilobium sp.</i>	1	25
<i>Stachys sylvatica</i>	1	25
<i>Paraleucobryum longifolium</i>	0	25
<i>Epilobium montanum</i>	1	10	25
<i>Hieracium lachenalii</i>	1	.	.	11	.	10	25
<i>Rubus fruticosus agg.</i>	1	.	.	6	.	10	25
<i>Pteridium aquilinum</i>	1	.	.	6	.	.	25
<i>Dactylis sp.</i>	1	25
<i>Stellaria graminea</i>	1	10	25
<i>Chrysosplenium alternifolium</i>	1	25
<i>Brachythecium sp.</i>	0	25
<i>Cirsium palustre</i>	1	25
<i>Angelica sylvestris</i>	1	25
<i>Epilobium angustifolium</i>	1	25
<i>Chaerophyllum hirsutum</i>	1	25
<i>Cynodontium sp.</i>	0	.	.	6	.	.	25
<i>Brachythecium rutabulum</i>	0	.	12	6	.	.	25
<i>Rubus clusii</i>	1	25
<i>Festuca gigantea</i>	1	25
<i>Calamagrostis canescens</i>	1	25
<i>Myosotis nemorosa</i>	1	25
<i>Senecio germanicus</i>	1	.	.	11	.	10	25
<i>Sambucus nigra</i>	2	10	25
<i>Plagiochila porellaoides</i>	0	.	.	11	.	10	25
<i>Galio-Abietetum</i>							
<i>Senecio nemorensis agg.</i>	1	.	.	11	.	70	50
<i>Moehringia trinervia</i>	1	.	.	11	.	60	50
<i>Eurhynchium angustirete</i>	0	17	.	22	20	60	50
<i>Corylus avellana</i>	2	.	.	22	.	50	50
<i>Impatiens noli-tangere</i>	1	40	50
<i>Veronica officinalis</i>	1	.	.	6	.	40	25
<i>Hieracium murorum</i>	1	.	.	22	.	40	25
<i>Scrophularia nodosa</i>	1	.	.	6	.	40	50
<i>Solidago virgaurea</i>	1	.	.	6	.	40	25
<i>Carex digitata</i>	1	.	.	11	.	40	25
<i>Fragaria vesca</i>	1	.	.	6	.	30	50
<i>Senecio fuchsii</i>	1	.	.	6	20	30	50
<i>Agrostis capillaris</i>	1	.	.	6	.	30	50
<i>Atrichum undulatum</i>	0	.	.	6	.	20	50
<i>Brachythecium velutinum</i>	0	20	25
<i>Rubus sp.</i>	1	.	.	17	.	20	25
<i>Gymnocarpium dryopteris</i>	1	.	.	6	.	20	25
<i>Viola sp.</i>	1	20	25
<i>Rhizomnium punctatum</i>	0	20	25
<i>Luzulo-Abietetum + Galio-Abietetum - wet habitat subtypes</i>							
<i>Equisetum sylvaticum</i>	1	.	.	.	80	.	50
<i>Lysimachia vulgaris</i>	1	.	.	.	40	.	50
<i>Dicranodontium denudatum</i>	0	.	.	11	40	.	25
<i>Digitalis purpurea</i>	1	.	.	.	40	.	25
<i>Carex remota</i>	1	.	.	.	20	.	50
<i>Galium palustre</i>	1	.	.	.	20	.	25
<i>Rubus nessensis</i>	1	.	.	17	20	.	25

**Vaccinio-Abietetum + Luzulo-Abietetum + Galio-Abietetum - wet habitat
subtypes**

<i>Tetraphis pellucida</i>	0	.	38	.	20	.	25
<i>Deschampsia cespitosa</i>	1	.	12	.	80	10	75
<i>Soldanella montana</i>	1	.	12	6	40	10	25

Luzulo-Abietetum - drier habitat subtype + Galio-Abietetum

<i>Corylus avellana</i>	1	.	.	39	.	40	50
<i>Sambucus racemosa</i>	2	.	.	39	.	30	50
<i>Mycelis muralis</i>	1	.	.	33	.	90	50
<i>Prenanthes purpurea</i>	1	8	.	28	.	30	25
<i>Dryopteris filix-mas</i>	1	.	.	28	.	90	25

Luzulo-Abietetum + Galio-Abietetum

<i>Rubus idaeus</i>	1	.	.	50	80	90	100
<i>Luzula pilosa</i>	1	.	.	50	40	60	100
<i>Rubus ser. Glandulosi</i>	1	.	.	33	40	40	75
<i>Mnium hornum</i>	0	.	.	17	80	10	25

Others

<i>Avenella flexuosa</i>	1	100	100	72	100	80	50
<i>Vaccinium myrtillus</i>	1	100	100	89	100	80	100
<i>Polystrichastrum formosum</i>	0	100	88	94	80	100	100
<i>Dryopteris carthusiana</i>	1	75	88	83	80	70	75
<i>Thuidium tamariscinum</i>	0	67	50	61	60	50	100
<i>Dryopteris dilatata</i>	1	58	38	67	80	60	100
<i>Calamagrostis villosa</i>	1	50	100	22	80	10	50
<i>Maianthemum bifolium</i>	1	42	100	67	100	60	75
<i>Oxalis acetosella</i>	1	42	75	94	100	100	75
<i>Plagiothecium laetum</i>	0	33	50	56	40	40	25
<i>Carex brizoides</i>	1	25	50	39	40	20	75
<i>Plagiommium affine</i>	0	25	25	44	80	40	75
<i>Frangula alnus</i>	2	25	75	50	100	50	75
<i>Frangula alnus</i>	1	25	88	39	80	30	75
<i>Plagiothecium sp.</i>	0	17	38	6	60	10	25
<i>Carex pilulifera</i>	1	8	12	61	40	40	75
<i>Athyrium filix-femina</i>	1	8	12	50	80	70	100
<i>Calamagrostis arundinacea</i>	1	.	12	50	20	40	25
<i>Dicranum scoparium</i>	0	67	62	44	.	60	25
<i>Hypnum cupressiforme</i> agg.	0	42	38	67	.	70	25
<i>Pohlia nutans</i>	0	33	62	17	40	40	.
<i>Pleurozium schreberi</i>	0	92	100	78	40	60	.
<i>Dicranella heteromalla</i>	0	.	25	17	.	20	25
<i>Convallaria majalis</i>	1	.	.	6	20	20	.
<i>Hylocomium splendens</i>	0	.	12	6	.	10	.
<i>Cladonia sp.</i>	0	.	12	6	.	.	.
<i>Polypodium vulgare</i>	1	.	.	6	.	10	.
<i>Polygonatum multiflorum</i>	1	.	.	6	.	10	.
<i>Plagiothecium denticulatum</i>	0	.	.	6	.	10	.

Sources of relevés:

Group 1: Tab. 2, rels 1–12

Group 2: Tab. 2, rels 13–20

Group 3: Tab. 2, rels 21–33; Boublík (2002), Tab. 1, rels 27, 29–31, 36

Group 4: Tab. 2, rels 34–38

Group 5: Tab. 2, rels 39–41; Boublík (2002), Tab. 1, rels 14, 28, 32–35, 37

Group 6: Tab. 2, rels 42–43; Boublík (2002), Tab. 1, rels 22, 26

Tab. 2: Phytosociological relevés of fir forests from southeastern Bohemia

Tab. 2: Pflanzensoziologische Aufnahmen der Tannenwälder in Südost-Böhmen

Rels/Aufn. 1–12 *Vaccinio vitis-idaeae-Abietetum*, 13–20 *Vaccinio vitis-idaeae-Abietetum*, wetter subtyp/feuchter Subtyp, 21–33 *Luzulo luzuloidis-Abietetum*, 34–38 *Luzulo luzuloidis-Abietetum*, wetter subtype/feuchter Subtyp, 39–41 *Galio rotundifolii-Abietetum*, 42–43 *Galio rotundifolii-Abietetum*, wetter subtype/feuchter Subtyp. (m = 2m [5%], a = 2a [6–12.5%], b = 2b [12.5–25%])

Other species:

E - *Viscum album* subsp. *laxum* 10: +, *Betula pubescens* 20: m, *Fagus sylvatica* 29: b, *Alnus glutinosa* 37: m

E₂ – *Lonicera nigra* 25: +, *Populus tremula* 43: r, *Sambucus nigra* 43: r.

juveniles: *Pinus strobus* 6-7; *Larix decidua* 9; *Abies alba* 43; *A. concolor* 15; *A. pseudoplatanus* 45; *A. spicata* 45; *Tilia* 15.

Piceetea. The assignment of the Czech stands of *Luzulo luzuloidis-Abietetum* to higher syntaxa is more complicated because of the common occurrence of *Vaccinio-Piceetae* and *Quercoco-Fagetea* species.

The concept used for the classification of *Abies alba* forests in this paper reflects the differences in nutrient supply, soil reaction, and soil water regime (WALENTOWSKI 1998, WALENTOWSKI et al. 2005). HUSOVÁ (1968, 1983) classified acidophilous fir forests in the supracolline and submontane areas of the Czech Republic in the association *Deschampsio flexuosae-Abietetum* Husová 1968. In Germany, however, fir forests of this trophic level are assigned to the *Luzulo luzuloidis-Abietetum* (SEIBERT in OBERDORFER 1992, POTT 1992, WALENTOWSKI 1998). This association is also reported from Slovakia (MUCINA & MAGLOCKÝ 1985, DRAŽIL in STANOVÁ & VALACHOVIC 2002). The comparison of the relevés of acidophilous stands classified in the *Deschampsio-Abietetum* by HUSOVÁ (1968, 1983) with the original description of the association *Luzulo luzuloidis-Abietetum* (OBERDORFER 1957) indicates two differences: 1) presence of montane or oceanic species in the *Luzulo luzuloidis-Abietetum* (e.g., *Blechnum spicant*, *Luzula sylvatica*, *Rhytidiodelphus loreus*) and 2) presence of species of lower altitudes such as *Campanula persicifolia* and *Quercus robur* in *Deschampsio-Abietetum* (Boublík ined.). We do not consider these differences as a sufficient reason for distinguishing a separate association for the fir forests in lower altitudes. We propose therefore the classification of oligo-mesotrophic fir-dominated forests into the association *Luzulo luzuloidis-Abietetum*, regardless of the presence of the montane/oceanic species or the species of lower altitudes.

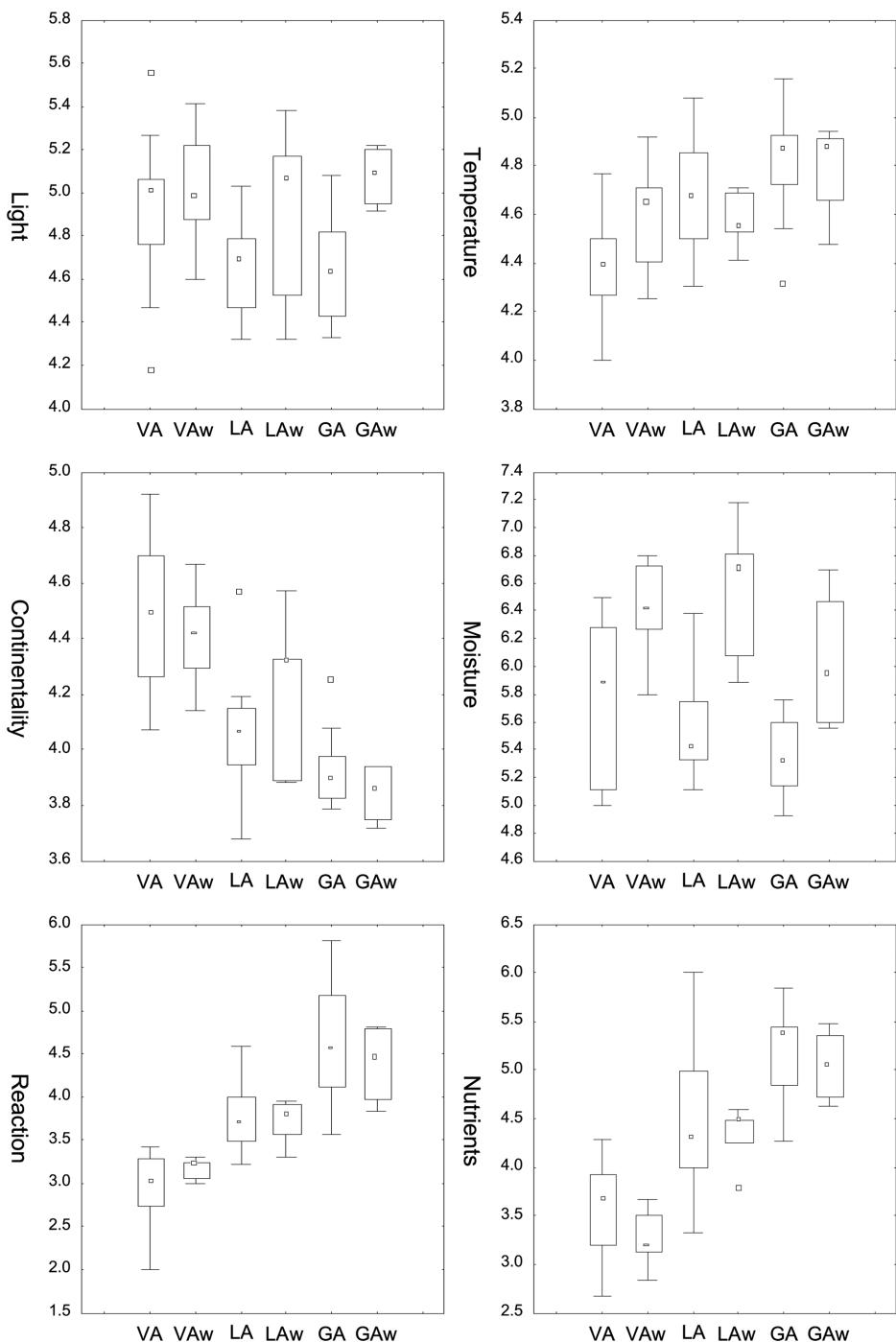


Fig. 2: Box-and-whisker plots of the Ellenberg indicator values (ELLENBERG et al. 1992) for the fir communities. For the explanation of the abbreviations of vegetation units see Tab. 1.

Abb. 2: Box-and-Whisker Diagramme der Zeigerwerte nach ELLENBERG et al. (1992) für die Gesellschaften der Tannenwälder. Erklärung der Abkürzungen der Vegetationstypen s. Tab. 1.

Tab. 3: Frequency of humus forms in particular vegetation units. Transitional humus subforms between 3–5 and 5–7 were not recorded. For the explanation of the abbreviations of vegetation units, see Tab. 1.

Tab. 3: Häufigkeit der Humusformen in den einzelnen Vegetationstypen. Die Übergänge zwischen 3–5 und 5–7 wurden nicht aufgenommen. Erklärung der Abkürzungen der Vegetationstypen s. Tab. 1.

Humus form	Community					
	VA	V Aw	LA	L Aw	GA	G Aw
1 - typical mor and hydromor	9	8	5	4		
2 - transition between 1 and 3				1		
3 - mor-like moder	2		8		6	1
5 - typical moder	1		5		4	1
7 - mull-like moder						2

Tab. 4: Frequency of the degrees of soil hydromorphism and soil types in particular vegetation units. For the explanation of the abbreviations of vegetation units see Tab. 1.

Tab. 4: Häufigkeit der Stufen des Bodenwasser-Einflusses und der Bodentypen. Erklärung der Abkürzungen der Vegetationstypen s. Täb. 1.

Degree of soil hydromorphism + soil type	Community					
	VA	V Aw	LA	L Aw	GA	G Aw
1 - without hydromorphic features (Cambisols, Podzols, Leptosols)	5		14		7	
2 - stagnic variety of Cambisols			2		2	1
3 - stagnic subtype of Cambisols	3		1		1	
4 - transition between Cambisols and Planosols	1		1			
5 - Planosols	3	7	1	1		1
6 - transition between Planosols and Gleysols		1				2
7 - Gleysols					4	

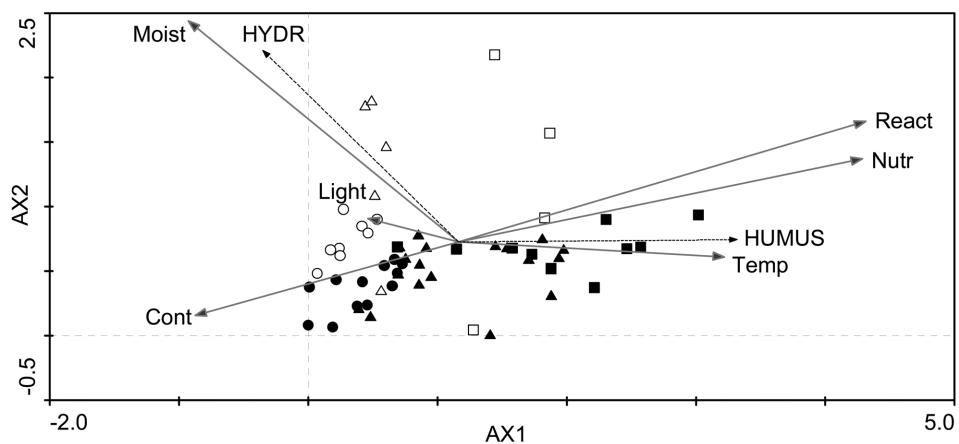
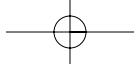


Fig. 3: Ordination diagram (biplot) of vegetation relevés based on DCA with passive projection of environmental variables: Ellenberg indicator values (ELLENBERG et al. 1992) for moisture (Moist), light (Light), continentality (Cont), nutrients (Nutr), soil reaction (React) and temperature (Temp); HUMUS = humus quality, HYDR = degree of soil hydromorphism.

Abb. 3: Ordinationsdiagramm der Vegetationsaufnahmen auf Grundlage der DCA-Analyse mit den passiven Variablen: Zeigerwerte (ELLENBERG et al. 1992) für Feuchtigkeit (Moist), Licht (Light), Kontinentalität (Cont), Nährstoff- oder Stickstoffversorgung (Nutr), Bodenreaktion (React) und Wärme (Temp); HUMUS = Humusqualität des Oberbodens, HYDR = Einfluss des Bodenwassers.

● = *Vaccinio vitis idaeae-Abietetum*, ○ = *Vaccinio vitis idaeae-Abietetum*, wet subtype/feuchter Subtyp, ▲ = *Luzulo luzuloidis-Abietetum*, △ = *Luzulo luzuloidis-Abietetum*, wet subtype/feuchter Subtyp, ■ = *Galio rotundifolii-Abietetum*, □ = GAw – *Galio rotundifolii-Abietetum*, wet subtype/feuchter Subtyp.



According to the Czech vegetation survey (MORAVEC et al. 2000), some of the relevés presented in this study within the *Galio rotundifolii-Abietetum* were previously classified into a more nutrient-demanding subassociation of the *Deschampsio flexuosa-Abietetum* (i.e., *Deschampsio-Abietetum calamagrostietosum arundinaceae* Husová 1983) (BOUBLÍK 2002). However, the frequent presence of mesotrophic species in these relevés suggests their classification into the mesotrophic association *Galio rotundifolii-Abietetum* would be more appropriate.

The wet fir forests have so far been presented in the Czech literature as acidophilous *Luzulo pilosae-Abietetum* Mráz 1957 and mesotrophic *Carici remotae-Abietetum* Husová 1998 (HUSOVÁ 1998, HUSOVÁ in MORAVEC et al. 2000). Because of the low number of the differential species of *Luzulo pilosae-Abietetum* in comparison with *Luzulo luzuloidis-Abietetum* (BOUBLÍK 2005) and many common species in the stands of *Galio rotundifolii-Abietetum* and *Carici remotae-Abietetum* (see Table 1), we consider these vegetation types to be only subunits within the *Luzulo luzuloidis-Abietetum* and *Galio rotundifolii-Abietetum*, respectively (in agreement with OBEDORFER 1992 and WALENTOWSKI 1998).

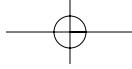
The mesotrophic fir forests were previously classified into the association *Saniculo europeae-Abietetum* Husová (1968) 1998 (HUSOVÁ 1998, HUSOVÁ in MORAVEC et al. 2000). If we take into account its species composition and ecology, this association is closely related to the *Galio rotundifolii-Abietetum*. We do not consider the differences in species composition, caused mostly by the geographical distribution of some species (WRABER 1959), to be a sufficient reason for distinguishing the Czech mesotrophic fir forests on the association level. We propose to classify them as *Galio rotundifolii-Abietetum*.

Acknowledgments

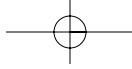
Our thanks are due to Milan Chytrý, Jiří Kolbek, and Petr Petřík for valuable comments on the previous version of the manuscript, to Radim Hédl, Klement Rejšek, and Milan Žárník for their help with soil classification, to Jiří Košnar for the determination of bryophytes, and to Ching Feng Li for preparation of the map of the study area. Ondřej Matějka and Toby Spribille kindly improved our English. We thank Petr Petřík for the translation of the text into German and Hartmut Dierschke for editing the final version. The study was supported by grant no. 206/05/0020 from the Grant Agency of the Czech Republic, by the institutional long-term research plans AV0Z60050516 of the Academy of Sciences of the Czech Republic (K.B.) and MSM 0021622416 (D.Z.).

Localities, sampling dates and relevé numbers in Czech National Phytosociological Database (CHYTRÝ & RAFAJOVÁ 2003) for relevés in Table 2:

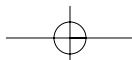
- 1 – Majdalena village, between the Nový Hospodář pond and the U Tikalských settlement, 4.5.2001, 347071
- 2 – Kaproun village, in the valley ca 0.6 km WNW of the railway stop, 7.7.2002, 347391
- 3 – Hradiště village (near Nová Bystrice), ca 0.5 km NW of the village, 6.10.2002, 347434
- 4–6 – Mirochov village, 2 km ESE of the village, 26.8.2003, 347622, 347624, 347626
- 7 – Staňkov village, the Maluškov forest ca 1.5 km NW of the village, 29.8.2003, 347629
- 8 – Hranice u Nových Hradů village, ca 0.5 km SE of the Hořejší Chalupy settlement, 1.9.2003, 347636
- 9 – Hranice u Nových Hradů village, ca 0.25 km SE of the Hořejší Chalupy settlement, 1.9.2003, 347637
- 10 – Hranice u Nových Hradů village, ca 0.3 km S of the Hořejší Chalupy settlement, 1.9.2003, 347638
- 11 – Suchdol nad Lužnicí town, 3 km NW of the railway station, 6.9.2003, 347643
- 12 – Majdalena village, between the Nový Hospodář pond and the U Tikalských settlement, 14.9.2003, 347648
- 13–14 – Stržovice village, ca 0.4 km S of the railway station, 9.6.2002, 347049, 347050
- 15 – Stržovice village, ca 0.5 km SSW of the railway station, 9.6.2002, 347051
- 16 – Majdalena village, the Sv. Barbora forest district, 2.5 km WSW of the Majdalena (Chlum u Třeboně) railway station, 11.8.2003, 347621

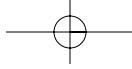


- 17 - České Velenice town, the Obecní les forest ca 2.6 km NW of the railway station, 1.9.2003, 347634
- 18 - Majdalena village, the Ráj forest 0.9 km W of the Stará Paseka hill (469 m) 3 km SW of the village, 6.9.2003, 347640
- 19 - Majdalena village, the Ráj forest 1.1 km WSW of the Stará Paseka hill (469 m) 3 km SW of the village, 6.9.2003, 347642
- 20 - Blato village, close to the northern bank of the Osika pond ca 1.5 km SW of the church in the village, 5.9.2004, 347879
- 21 - Majdalena village, between the Nový Hospodář pond and the U Tikalských settlement, 4.5.2001, 347072
- 22 - Majdalena village, ca 0.5 km N of the U Janů settlement, ca 2.2 km N of the village, 4.5.2001, 347073
- 23 - Kamenice nad Lipou town, the Bradlo hill 1 km S of the town centre, above the left bank of the Včelníčka brook, 7.9.2002, 347402
- 24 - Mirochov village, ca 3.3 km ESE of the village, 14.6.2003, 347518
- 25 - Malý Ratmírov village, ca 0.9 km NW of the village, ca 0.5 km W of the Ratmírovský vrch hill (582 m), 15.6.2003, 347521
- 26 - Mirochov village, 2 km ESE of the village, 26.8.2003, 347625
- 27-28 - Staňkov village, the Maluškov forest ca 1.5 km NW of the village, 29.8.2003, 347630, 347631
- 29 - Mnich village (near Kardašova Řečice), ca 1.8 km SW of the village, 31.8.2003, 347633
- 30 - Hatín village, forest close to the NE margin of the village, 5.9.2003, 347639
- 31 - Majdalena village, the Ráj forest 1.1 km W of the Stará Paseka hill (469 m) 3 km SW of the village, 6.9.2003, 347641
- 32 - Kaproun village, in the valley ca 0.6 km W of the railway stop, 12.9.2003, 347645
- 33 - Majdalena village, under the Nový Hospodář pond, 14.9.2003, 347647
- 34-35 - Kaproun village, in the valley ca 0.6 km W of the railway stop, 7.7.2002, 347393, 347394
- 36 - Obora settlement (near Byňov village), 1 km NNW of the settlement, 1.9.2003, 347635
- 37 - Mnich village (near Kardašova Řečice), the Sv. Barbora forest district, near the railway 2.3 km E of the village, 7.9.2003, 347644
- 38 - Kaproun village, in the valley ca 0.6 km W of the railway stop, 12.9.2003, 347646
- 39 - Mutyněves village, 1 km ENE of the village, 14.6.2002, 347376
- 40-41 - Staňkov village, the Maluškov forest ca 1.5 km NW of the village, 29.8.2003, 347627, 347628
- 42 - Mutyněves village, 1 km ENE of the village, 14.6.2002, 347377
- 43 - Staňkov village, the Maluškov forest ca 1.5 km NW of the village, 29.8.2003, 347632


Header data for relevés in Table 2:

Relevé	Area (m ²)	Altitude (m)	Aspect	Slope (°)	Cover (%)			
					E ₃	E ₂	E ₁	E ₀
1	300	438	-	0	85	1	25	20
2	300	610	W	2	70	10	60	65
3	150	570	W	4	65	40	35	80
4	375	500	W	2	60	45	15	25
5	200	495	WNW	3	65	20	20	65
6	400	495	-	0	70	10	25	80
7	300	470	ENE	2	70	40	50	40
8	150	495	NW	3	70	10	10	40
9	225	490	W	2	65	15	35	45
10	300	490	N	10	75	5	15	80
11	150	463	-	0	70	20	35	55
12	400	438	-	0	80	2	15	60
13	400	540	-	0	70	2	30	70
14	400	540	-	0	65	25	20	70
15	300	540	-	0	65	3	60	60
16	400	460	-	0	65	25	20	40
17	150	480	N	2	70	25	50	85
18	300	460	-	0	75	20	15	65
19	300	457	-	0	75	5	20	85
20	150	635	-	0	70	25	40	40
21	400	438	-	0	75	15	20	40
22	500	437	-	0	80	30	65	75
23	400	540	SW	15	70	2	35	5
24	200	505	SSW	10	60	30	25	70
25	300	550	W	5	65	5	35	5
26	225	490	NNE	3	65	45	10	45
27	375	480	-	0	70	2	25	90
28	225	475	N	3	70	10	20	70
29	400	475	NNE	3	80	2	10	55
30	225	485	W	2	80	20	30	5
31	150	460	-	0	75	0	5	70
32	225	610	W	3	70	5	50	55
33	300	437	-	0	75	1	35	3
34	375	605	WSW	3	70	10	45	90
35	150	605	-	0	60	50	25	50
36	150	485	-	0	60	45	30	60
37	100	505	-	0	60	10	60	65
38	300	603	-	0	65	10	20	80
39	400	550	W	5	70	1	55	70
40	400	480	E	5	80	3	35	70
41	300	475	E	3	65	5	50	60
42	150	540	W	3	75	5	30	80
43	400	475	-	0	70	2	50	60





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