Calcicolous beech forests and related vegetation in the Czech Republic: a comparison of formalized classifications

Vápnomilné bučiny České republiky a příbuzná vegetace – srovnání formalizovaných klasifikací

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A syntaxonomical synthesis of calcicolous forests dominated by *Fagus sylvatica* (*Cephalanthero-Fagenion* suballiance) in the Czech Republic was carried out using the Braun-Blanquet approach. Relevés included in the analyses were selected following formalized approach by using an expert-delimited group of 38 calcicolous and/or xerothermophilous species. Only one association *Cephalanthero-Fagetum* was distinguished, which usually occurs on limestone, calcareous sandstone and calcareous sandy marlite; however, can be found also on base-rich siliceous bedrock (e.g. basalt, phonolite). Based on TWINSPAN analysis, three subassociations were recognized within the *Cephalanthero-Fagetum*: (i) *Cephalanthero-Fagetum seslerietosum caeruleae* on shallow rocky soils with frequent dominance of *Sesleria caerulea* and presence of petrophytes, (ii) *Cephalanthero-Fagetum typicum* on dry, shallow soils with a significant presence of light-demanding, thermophilous, and calcicolous species, and (iii) *Cephalanthero-Fagetum actaeetosum spicatae* on deeper, sufficiently moist soils with an abundance of mesophilous, nitrophilous and acidophilous species. The name *Cephalanthero-Fagetum actaeetosum spicatae* is a new nomenclatural combination. The relationships between *Cephalanthero-Fagetum* and similar forest vegetation types containing xerothermophilous and/or calcicolous species in the Czech Republic are discussed. The main gradients in species composition of *Cephalanthero-Fagetum* subassociations were revealed by gradient analysis. The Ellenberg indicator values, altitude, slope, and 'southness' were used to interpret these gradients. Using unconstrained ordination analysis (DCA) the syntaxonomical interpretation indicated three relatively distinct groups. Moreover, further DCA analysis revealed the well-defined position of *Cephalanthero-Fagetum* within Czech beech forests. The results of the above delimitation of *Cephalanthero-Fagetum* were compared with the results based on Cocktail-defined species groups improved by similarity-based assignment of relevés (using frequency-positive fidelity index). When the Cocktail-based formulas for beech forests were applied to the relevés selected by our 38-species diagnostic group, the correspondence between these two approaches was only 36%. However, at the lower subassociation level, the highest correspondence occurred for *Cephalanthero-Fagetum seslerietosum* (84%). The reason for this high correspondence is that the species composition includes many specialists (i.e. good diagnostic species) and it occurs at the end of an ecological gradient. To sum up, it is possible to define vegetation units accurately using strict formulas, as opposed to the less rigorous 'soft' traditional approach. However, both approaches fail when defining central units.

K e y w o r d s : *Cephalanthero-Fagenion*, Cocktail, deciduous forests, *Fagus sylvatica*, fidelity, frequency-positive fidelity index, ordination, species group approach, syntaxonomy, TWINSPAN

Introduction

The *Cephalanthero-Fagenion* Tüxen et Oberdorfer 1958 suballiance comprises Central European calcicolous herb-rich beech forests occurring on base-rich substrates, mainly on calcareous bedrock (Ellenberg 1988, Oberdorfer 1992, Moravec et al. 2000, Willner 2002). This vegetation differs from other beech forest communities in including many species groups containing calcicolous or xerothermophilous species (e.g. *Arabis hirsuta*, *Cephalanthera rubra*, *Carex alba*, *Galium glaucum*, *Sesleria caerulea* and *Viola hirta*). Most of these species have a sub-Mediterranean distribution range and often occur also in thermophilous oak forests (*Quercetalia pubescenti-petraeae*) and dry grasslands on base-rich substrates (e.g. *Bromion*, *Seslerio-Festucion pallentis*, *Geranion sanguinei*, *Calamagrostion variae*). Stands of *Cephalanthero-Fagenion* occur in France, the Alps (Germany, Austria, Switzerland), the Carpathians (Slovakia, Poland) and the Hercynian area (Germany, Czech Republic, Poland) (e.g. Oberdorfer 1957, 1992, Mucina & Maglocký 1985, Pott 1992, Mucina et al. 1993, Keller et al. 1998, Moravec et al. 2000, Matuszkiewicz 2001, Willner 2002, Bardat et al. 2004). The centre of the variability of this suballiance is in the Alps and the Carpathians. In SE Europe, the suballiance is replaced by the floristically and ecologically similar suballiance *Ostryo-Fagenion* (Willner 2002, compare also with Tzonev et al. 2006).

In the Czech Republic, stands of *Cephalanthero-Fagenion* forests are rare. The classification of Czech calcicolous beech forests needs to be re-evaluated for the following reasons. In the past three decades, a rather simple classification of this suballiance has been proposed, distinguishing one association (*Cephalanthero-Fagetum*) with no internal variability (Moravec et al. 1982, 2000). This association was characterized in the following way: (i) mesic environmental conditions, (ii) calcareous bedrock (limestone, calcareous sandstone, calcareous marlite), (iii) soil type rendzic leptosol and its transitions to cambisols, and terra fusca, (iv) frequent occurrence of calcicolous orchids, and (v) species composition typical of forests of lower altitudes. The thermophilous part of the calcicolous beech forests has been neglected in this delimitation, which does not reflect the natural variability of this forest type in the Czech Republic. Further, communities floristically similar to *Cephalanthero-Fagetum* occurring on base-rich substrates without or with small amounts of calcium carbonate (e.g. basalt, diabase, phonolite) were classified as a part of herb-rich mesophilous beech forests of the *Eu-Fagenion* suballiance.

Currently, the differences in traditional (non-formalized) and formalized vegetation classifications are frequently discussed, both theoretically and practically by using large data sets. The traditional approach, previously widely used in the Czech Republic, is based on expert knowledge of natural species co-occurrence (Moravec et al. 1995). The formalized classification can either be unsupervised or supervised by the researcher (compare Bruelheide & Chytrý 2000, Chytrý 2000, Kočí et al. 2003). The recently introduced supervised Cocktail method (Bruelheide 1995, 2000, Kočí et al. 2003; see also Havlová 2006) imitates traditional subjective classification but is formalized and repeatable. Innovatively, artificial neural networks resulting from the learning process of a computer program are used as a surrogate phytosociologist to classify vegetation (Černá & Chytrý 2005).

In the present paper the calcicolous beech forest is formally defined by compiling a formula composed of one relatively large diagnostic species group. Such definition is compared with the formalized classification of the same vegetation type by the Cocktail method using similarity-based assignment of relevés.

The aims of this paper are (i) to define the calcicolous beech forests in the Czech Republic using a supervised formalized definition, (ii) to analyse their internal variability, (iii) to analyse and discuss the relationships to other beech forests, (iv) to find the major gradients responsible for the variation in species composition of *Cephalanthero-Fagenion* communities, and (v) to compare the results of two formalized definitions of the same vegetation unit.

Materials and methods

Data set selection: formalized definition of calcicolous beech forests

Phytosociological relevés sampled according to the Braun-Blanquet approach (Westhoff & van der Maarel 1973) were selected as follows:

First, from the Czech National Phytosociological Database (Chytrý & Rafajová 2003), 2217 relevés dominated by *Fagus sylvatica* (at least 25% cover in tree layer), including our relevés, were accepted regardless of the original assignment to vegetation units by the authors of these relevés (stored in the header data field 'Syntaxon code' in the database).

Second, a diagnostic species group was formed of calcicolous and/or xerothermophilous species, which have high values according to Ellenberg et al. (2001) for soil reaction (most of them with values higher than 7), light, or temperature. This species group was based both on our field experience and comparison with diagnostic species of corresponding vegetation types in other countries (Oberdorfer 1992, Mucina et al. 1993, Willner 2002). However, it was not realistic to include all eligible species, so the following were excluded: (i) species of deeper, loamy soils in flat terrain (e.g. *Festuca heterophylla*, *Serratula tinctoria*), (ii) species associated with human-induced habitats or which occur on siliceous bedrocks (e.g. *Digitalis grandiflora*, *Euphorbia cyparissias*, *Melica transsilvanica*), and (iii) species which also often occur in mesic habitats (e.g. *Corallorhiza trifida*, *Epipactis helleborine* agg., *Lathyrus niger*, *Neottia nidus-avis*, *Sorbus torminalis*). Finally, the diagnostic species group consisted of 38 species (listed in Appendix 1). At least two of the 38-species diagnostic group had to be present in a relevé in order for it to be selected as calcicolous beech forest.

Third, this species group was used for the formalized selection of relevés used in subsequent analyses (internal variability, comparison with Cocktail-based classification).

In total 128 relevés were selected. We excluded eight of these 128 relevés as we considered them to be different units (see Discussion).

Internal variability of calcicolous forests

A divisive classification of 120 relevés assigned to calcicolous beech forests was carried out. All records of bryophytes and lichens were omitted in order to standardize the different sampling effort. Relevés were classified using the TWINSPAN method (Hill 1979; see e.g. Roleček 2005) embedded within the JUICE program (Tichý 2002). Pseudospecies cut levels were set to 3 and values of cut levels to 0%, 5% and 25%. Five relevés were selected as a minimum group size for division. Diagnostic species for particular vegetation units were determined using the phi coefficient as a measure of fidelity (Chytrý et al. 2002) in a synoptic table. The phi coefficient was used for clusters of equalized size (Tichý & Chytrý 2006). Only species with both a significant concentration in particular vegetation units (using Fisher's exact test and significance level $P < 0.01$) and phi coefficient ≥ 0.30 were considered to be diagnostic species. Fisher's test excluded some scarce species that could become diagnostic by chance.

Gradient analysis of material from calcicolous forests

To reveal the main gradients in *Cephalanthero-Fagenion* vegetation in the data set of 120 relevés, unimodal-based ordinations using Canoco for Windows 4.5 (ter Braak & Šmilauer 2002) software were performed. For the gradient analysis, the semi-quantitative species covers were square-root transformed and the default options according to Lepš & Šmilauer (2003) were followed in the Canoco program. Supplementary variables were derived from species data in relevés and used in constrained ordinations: Ellenberg indicator values (Ellenberg et al. 2001) for light, soil moisture, temperature, soil nutrients, soil reaction and continentality. In the data sets analysed vegetation layers were not merged or deleted.

For the unconstrained ordination, Detrended Correspondence Analysis (DCA) with geographical position index as a covariate (to filter out spatial dependency of closest relevés) was calculated in the JUICE program (Tichý & Holt 2006). This index is based on assignment of the same number to relevés in the same grid-cell (here with the size of 0.75' N × 1.25' E, i.e. 2.1 km^2) within a virtual grid. The TWINSPAN group membership was projected to DCA scatter-plot.

For the assessment of the species composition–environment relationship, Canonical Correspondence Analysis (CCA) with geographical coordinates as covariates was performed (ordination diagram not shown). From the head of each relevé, the altitudes, slopes and folded aspects were used as environmental variables in the CCA. The aspect had to be rescaled ('folded') about the north-south line from 0–360° to 0–180°. In this sense, the folded aspect expresses 'southness' of a site. Nine relevés were excluded, as they contained no header data. In the CCA, inter-species distances and other steps identical to those in the DCA were followed. Additionally, a manual forward selection of the three factors used was launched with 999 Monte Carlo permutation tests testing the significance of canonical axes at significance level $P < 0.001$.

In order to show relations of calcicolous beech forests to the rest of beech-dominated vegetation in the Czech Republic, a second DCA analysis was performed using another data set with 2217 relevés (see Data set selection). All these relevés were analyzed using both original authors' indication of vegetation alliances and that of the 120 relevés selected by 38-species diagnostic group.

Cocktail method combined with fidelity index

First, we took a set of definitions[1] of beechwood associations prepared with the help of the Cocktail method by K. B. and R. H. for the project Vegetation of the Czech Republic (Chytrý 2007) and applied it to the group of 120 relevés. The Cocktail-definitions are formed both by species groups and the dominance of species joined by logical operators such as AND, OR, and AND NOT. The species groups are based on statistical tendency (measured by phi coefficient) of joint occurrence of species, which are more frequent than would be expected by chance (Bruelheide 2000, Kočí et al. 2003). It should be noted that

[1] In these definitions we used 25% thresholds of *Fagus sylvatica* dominance rather than the 50% threshold employed in beech forests definitions in the new vegetation survey of the Czech Republic.

the data set used for the formation of Cocktail groups is geographically stratified, which increases its representativeness (Knollová et al. 2005).

Second, for the relevés matching two or more vegetation units (i.e. the transitional ones) when selected by the Cocktail-definitions, a frequency-positive fidelity index (FPFI) was calculated (Tichý 2005). The FPFI compares the similarity of the species composition of a selected relevé and a group of relevés, upweighting the diagnostic species of the relevé group with respect to quantitative proportions among species (Tichý 2005).

We do not want to discuss other methodological aspects (the standardization of material and methods etc.) used in the new Czech vegetation survey because they are thoroughly discussed elsewhere (Chytrý 2007, Roleček 2007).

Finally, the results obtained by two formalized definitions, i.e. (i) the selection using the 38-species diagnostic group and (ii) the classification using the Cocktail method with FPFI, were compared.

Nomenclature

The nomenclature follows mostly Kubát et al. (2002) for plant species names and Moravec et al. (1995) and Willner (2002) for syntaxa. If not, the authors' names are given. The nomenclature of soil units (with the exception of terra fusca) follows World reference base for soil resources (ISSS-ISRIC-FAO 1998). The concept of altitudinal vegetation belts is that of Skalický (1988).

Results

Classification of calcicolous beech forests in the Czech Republic

The formalized selection using the diagnostic species group of 38 calcicolous and/or xerothermophilous species assigned 120 relevés to calcicolous beech forest of the *Cephalanthero-Fagenion* suballiance. Because of local geographical origin of one of four TWINSPAN clusters, we joined it to the next closest cluster in the subsequent TWINSPAN analysis of this data set. According to the similar fundamental floristic composition of all the three groups, we classify them within one association (*Cephalanthero-Fagetum* Oberdorfer 1957). *Cephalanthero-Fagetum* is a calcicolous beech forest occurring in colline and supracolline vegetation belts in the Czech Republic. Three types recognized by TWINSPAN represent the subassociations whose frequencies in the field are well reflected by the number of relevés analysed (Table 1, columns 1–3):

1. Dry calcicolous beech forest on rocky outcrops
Cephalanthero-Fagetum seslerietosum caeruleae Oberdorfer 1957 (Table 1, column 1)

The stands of this subassociation represent dwarf, often former coppiced beech forests on rendzic leptosols, which develop on rocky outcrops of limestone, calcareous sandstone and calcareous sandy marlite. *Sesleria caerulea* usually predominates in the herb layer and the presence of petrophytes (*Asplenium ruta-muraria*, *A. trichomanes*) and species of the *Diantho lumnitzeri-Seslerion* (Soó 1971) Chytrý et Mucina in Mucina et al. 1993 alliance are characteristic features. The stands contain a high proportion of juvenile trees and shrubs. It occurs at 270–590 m a.s.l. especially in the Moravian and Bohemian Karst, the Jizera river valley, the Džbán hills and the foothills of the Bohemian Forest (Fig. 1).

Table 1. – Combined frequency table of *Cephalanthero-Fagetum* and related communities in the Czech Republic. The percentage constancies (in the *Cephalanthero-Fagetum* subassociations) and categorical constancies (in other communities) of species are shown. The upper indices are phi coefficients (× 100). The values of diagnostic species for particular vegetation types and differential species of the *Cephalanthero-Fagenion* suballiance used for data set selection (see Appendix 1) are in bold. Species that occurred in less than three columns and had no differential value (226 species) were omitted from the table. Layers: 3 – tree layer, 2 – shrub layer, 1 – herb layer, j – juvenile. Vegetation types: CFs – *Cephalanthero-Fagetum seslerietosum*, CFt – *Cephalanthero-Fagetum typicum*, CFa – *Cephalanthero-Fagetum actaeetosum*, Car – transition vegetation type between *Cephalanthero-Fagetum* and Carpathian thermophilous beech forests, CaF – *Calamagrostio arundinaceae-Fagetum* (Hartmann et Jahn 1967) Sýkora 1972, mbSB – montane calcicolous spruce-beech forest. *Galium pusillum* agg. includes *Galium pumilum* and probably also *G. valdepilosum.*

Group no. Vegetation type No. of relevés	Layer	1 CFs 37	2 CFt 74	3 CFa 9	4 Car 3	5 CaF 5	6 mbSB 2
Sesleria caerulea	1	**92**$^{87.8}$	8	.	.	.	.
Viola collina	1	**70**$^{71.1}$	8	.	.	.	.
Anthericum ramosum	1	**51**$^{55.9}$	8	.	.	I	.
Rosa canina agg.	j	**59**$^{55.7}$	16	.	II	.	.
Cardaminopsis arenosa	1	**46**$^{54.1}$	5	.	.	I	.
Vincetoxicum hirundinaria	1	**62**$^{52.8}$	12	11	II	IV	.
Campanula rotundifolia agg.	1	**35**$^{48.0}$	3	.	.	II	.
Campanula rapunculoides	1	**81**$^{46.4}$	53	11	II	.	.
Picea abies	2	**30**$^{43.1}$	3	.	.	.	.
Asplenium ruta-muraria	1	**24**$^{42.0}$	.	.	II	.	.
Berberis vulgaris	j	**35**$^{41.7}$	8	.	.	.	.
Teucrium chamaedrys	1	**24**$^{39.8}$	1	.	.	.	.
Asplenium trichomanes	1	**30**$^{39.6}$	5	.	II	.	.
***Sorbus aria* agg.**	2	**30**$^{39.6}$	5	.	.	IV	.
Asperula tinctoria	1	**22**$^{39.4}$	.	.	.	.	.
Pinus sylvestris	3	**32**$^{39.1}$	8	.	.	II	.
Campanula persicifolia	1	**51**$^{38.7}$	30	.	II	.	.
Bupleurum falcatum	1	**24**$^{37.8}$	3	.	II	.	.
Carex humilis	1	**22**$^{37.1}$	1	.	.	.	.
Rhamnus cathartica	j	**27**$^{36.9}$	5	.	II	.	.
Digitalis grandiflora	1	**27**$^{36.9}$	5	.	II	II	V
Polygala chamaebuxus	1	**19**$^{34.3}$	1	.	.	.	.
Silene nutans	1	**24**$^{34.1}$	5	.	.	I	.
Cotoneaster integerrimus	j	**27**$^{33.7}$	8	.	.	.	.
Sorbus aucuparia	j	**62**$^{32.6}$	12	44	.	I	V
Tilia sp.	j	**19**$^{32.0}$	3	.	.	.	.
***Sorbus aria* agg.**	j	**19**$^{32.0}$	3	.	.	I	.
Euonymus verrucosa	j	**16**$^{31.2}$	1	.	II	.	.
Fagus sylvatica	j	**92**$^{31.1}$	58	67	V	I	.
Taxus baccata	j	**14**$^{30.7}$	.	.	.	.	.
Pulmonaria officinalis s. lat.	1	.	**58**$^{69.3}$	.	II	.	V
Stellaria holostea	1	3	**42**$^{53.7}$	.	.	.	.
Asarum europaeum	1	3	**39**$^{51.5}$	.	IV	.	.
Carpinus betulus	3	22	**54**$^{46.9}$	.	II	.	.
Melittis melissophyllum	1	3	**34**$^{46.8}$	.	IV	.	.
Campanula trachelium	1	14	**45**$^{45.1}$	.	IV	.	.
Galium sylvaticum agg.	1	41	**69**$^{41.4}$	11	II	I	.
Lathyrus niger	1	3	**27**$^{40.5}$	.	II	.	.
Viola mirabilis	1	.	**22**$^{39.4}$	.	.	.	.
Vicia sepium	1	.	**22**$^{39.4}$	.	.	.	.
Carex montana	1	3	**26**$^{39.2}$	.	.	.	.

Lilium martagon	1	14	**47**$^{38.6}$	11	II	.	V
Crataegus sp.	j	22	**43**$^{37.1}$	.	IV	.	.
Aegopodium podagraria	1	.	**19**$^{36.7}$	.	.	.	.
Lathyrus vernus	1	43	**86**$^{36.0}$	47	IV	.	.
Quercus petraea agg.	3	19	**39**$^{35.5}$	.	IV	III	.
Melica nutans	1	38	**73**$^{35.3}$	33	IV	II	.
Tilia cordata	3	5	**24**$^{34.1}$	.	.	.	.
Carex muricata agg.	1	3	**20**$^{33.5}$	.	.	.	.
Pyrethrum corymbosum	1	38	**58**$^{33.1}$	11	II	II	.
Veronica chamaedrys agg.	1	8	**35**$^{31.2}$	11	.	.	.
Galium odoratum	1	11	**77**$^{31.0}$	78	V	.	III
Heracleum sphondylium	1	.	**14**$^{30.7}$	.	.	.	.
Acer campestre	2	3	**18**$^{30.5}$	.	II	.	.
Avenella flexuosa	1	11	5	**67**$^{61.7}$	.	IV	V
Daphne mezereum	2	3	14	**67**$^{61.7}$	IV	.	V
Cephalanthera damasonium	1	22	50	**100**$^{61.2}$	II	.	.
Orthilia secunda	1	5	3	**56**$^{59.4}$	II	.	III
Epipactis helleborine agg.	1	24	30	**89**$^{58.4}$	.	.	III
Dentaria enneaphyllos	1	.	3	**44**$^{55.8}$	.	.	.
Cephalanthera rubra	1	5	22	**67**$^{54.1}$	II	.	.
Actaea spicata	1	3	42$^{1.6}$	**78**$^{53.2}$	II	.	V
Mycelis muralis	1	19	50	**89**$^{51.4}$	V	I	V
Solidago virgaurea	1	14	4	**56**$^{51.4}$	II	I	V
Neottia nidus-avis	1	5	27	**67**$^{50.6}$	.	.	.
Epilobium montanum	1	5	14	**56**$^{50.3}$	.	.	V
Epipactis microphylla	1	.	.	**33**$^{50.0}$	.	.	.
Petasites albus	1	.	.	**33**$^{50.0}$	.	.	.
Corallorhiza trifida	1	.	3	**33**$^{46.4}$	.	.	.
Euphorbia amygdaloides	1	.	3	11	**V**	.	.
Carex pilosa	1	.	3	.	**V**	.	.
Cephalanthera longifolia	1	.	5	.	**IV**	.	.
Carex sylvatica	1	.	8	.	**IV**	.	.
Viburnum opulus	j	.	5	.	**IV**	.	.
Pimpinella major	1	3	5	.	.	.	**V**
Asplenium viride	1	5	.	.	.	.	**V**
Polygonatum verticillatum	1	.	1	.	.	.	**V**
Aconitum variegatum	1	.	.	.	.	.	**V**
*Bupleurum *vapincense*	1	.	.	.	.	.	**V**
Gentiana asclepiadea	1	.	.	.	.	.	**V**
Geranium sylvaticum	1	.	.	.	.	.	**V**
Pleurospermum austriacum	1	.	.	.	.	.	**V**
Polystichum lonchitis	1	.	.	.	.	.	**V**
Ranunculus nemorosus	1	.	.	.	.	.	**V**
Arabis sudetica	1	.	.	.	.	.	**III**
Campanula bohemica	1	.	.	.	.	.	**III**
Galium sudeticum	1	.	.	.	.	.	**III**
Homogyne alpina	1	.	.	.	.	.	**III**
Listera ovata	1	.	.	.	.	.	**III**
Melampyrum sylvaticum	1	.	.	.	.	.	**III**
Fagus sylvatica	3	100	100	100	V	V	V
Fagus sylvatica	2	54	49	33	V	II	V
Hieracium murorum	1	92	73	67	IV	III	V
Luzula luzuloides	1	8	26	11	II	IV	III
Senecio nemorensis agg.	1	8	24	56	II	I	V
Mercurialis perennis	1	68	86	67	II	II	.
Convallaria majalis	1	41	43	22	II	III	.
Poa nemoralis	1	19	68$^{23.4}$	67	IV	I	.

Carex digitata	1	76	55	44	V	.	III
Fragaria vesca	1	30	26	56	II	.	III
Oxalis acetosella	1	3	12	22	II	.	III
Vaccinium myrtillus	1	14	1	22	.	II	III
Rubus idaeus	1	5	7	22	.	I	III
Maianthemum bifolium	1	.	20	44	II	I	III
Hepatica nobilis	1	65	$84^{28.7}$	44	II	.	.
Fraxinus excelsior	j	59	45	56	IV	.	.
Acer pseudoplatanus	j	59	43	33	IV	.	.
Quercus petraea agg.	j	38	43	11	IV	.	.
Picea abies	j	$22^{11.9}$	3	22	II	.	.
Tilia platyphyllos	j	19	7	11	II	.	.
Berberis vulgaris	2	16	3	11	II	.	.
Crataegus sp.	2	8	15	22	II	.	.
Bromus ramosus agg.	1	5	$48^{22.9}$	44	II	.	.
Viola reichenbachiana	1	5	$45^{20.0}$	44	IV	.	.
Anemone nemorosa	1	8	$41^{28.2}$	22	II	.	.
Sanicula europaea	1	8	32	56	II	.	.
Dactylis glomerata agg.	1	5	$27^{25.1}$	11	IV	.	.
Veronica officinalis	1	5	11	22	IV	.	.
Brachypodium sylvaticum	1	3	22	33	IV	.	.
Tilia cordata	j	3	16	11	II	.	.
Polypodium vulgare	1	8	3	11	II	.	.
Galium pusillum agg.	1	19	5	22	.	I	.
Lonicera xylosteum	2	11	24	.	II	II	.
Picea abies	3	19	15	.	.	I	V
Calamagrostis arundinacea	1	11	11	.	.	V	V
Acer pseudoplatanus	2	8	9	.	.	I	III
Ajuga reptans	1	.	$20^{22.7}$	11	IV	.	V
Scrophularia nodosa	1	.	11	22	II	.	III
Acer platanoides	j	51	38	78	.	.	.
Cornus sanguinea	j	41	28	11	.	.	.
Acer campestre	j	35	45	11	.	.	.
Lonicera xylosteum	j	30	31	11	.	.	.
Galium mollugo agg.	1	$27^{27.7}$	3	11	.	.	.
Pimpinella saxifraga	1	$22^{22.9}$	1	11	.	.	.
Hedera helix	1	19	34	11	.	.	.
Fraxinus excelsior	3	19	11	11	.	.	.
Acer platanoides	3	16	30	44	.	.	
Sorbus torminalis	3	16	12	11	.	.	.
Arabis hirsuta agg.	1	16	7	33	.	.	.
Hieracium lachenalii	1	14	7	22	.	.	.
Inula conyzae	1	14	4	22	.	.	.
Daphne mezereum	j	5	$36^{26.1}$	22	.	.	.
Geranium robertianum	1	5	20	22	.	.	.
Urtica dioica	1	5	5	11	.	.	.
Rosa sp.	j	3	19	11	.	.	.
Alliaria petiolata	1	3	11	11	.	.	.
Cardamine impatiens	1	3	9	33	.	.	.
Aquilegia vulgaris	1	3	9	22	.	.	.
Galeobdolon montanum	1	3	8	22	.	.	.
Myosotis sylvatica	1	3	7	11	.	.	.
Galium rotundifolium	1	3	4	11	.	.	.
Juglans regia	j	3	4	11	.	.	.
Hypericum perforatum	1	3	3	22	.	.	.
Carpinus betulus	j	51	41	.	IV	.	.
Polygonatum odoratum	1	35	18	.	II	.	.

Corylus avellana	j	27	12	.	IV	.	.
Sorbus torminalis	j	24	23	.	II	.	.
Fragaria moschata	1	22	28	.	II	.	.
Carpinus betulus	2	22	19	.	II	.	.
Primula veris	1	16	32	.	IV	.	.
Prunus avium	j	16	16	.	II	.	.
Cornus mas	2	11	8	.	II	.	.
Arabis pauciflora	1	11	4	.	II	.	.
Hieracium sabaudum	1	8	12	.	II	.	.
Cornus mas	j	8	11	.	II	.	.
Acer platanoides	2	8	5	.	II	.	.
Euonymus verrucosa	2	8	1	.	II	.	.
Melampyrum pratense	1	5	16	.	II	.	.
Rosa canina agg.	2	5	3	.	II	.	.
Hylotelephium maximum	1	5	1	.	II	.	.
Corylus avellana	2	38	23	.	.	II	.
Festuca ovina	1	14	5	.	.	II	.
Cotoneaster integerrimus	2	11	1	.	.	II	.
Ribes alpinum	2	3	4	.	.	II	.
Ribes uva-crispa	2	3	3	.	.	I	.
Taraxacum sect. *Ruderalia*	1	24	16	.	.	.	III
Sorbus aucuparia	2	16	4	.	.	.	V
Dentaria bulbifera	1	3	15	.	II	.	.
Viola riviniana	1	5	15	.	II	.	.
Vaccinium vitis-idaea	1	5	.	.	.	I	III
Melica uniflora	1	.	11	22	II	.	.
Acer pseudoplatanus	3	.	22 [24.3]	11	.	I	.
Prenanthes purpurea	1	.	16	22	.	.	III
Dryopteris filix-mas	1	.	7	11	.	.	III
Phyteuma spicatum	1	.	12	.	II	.	V

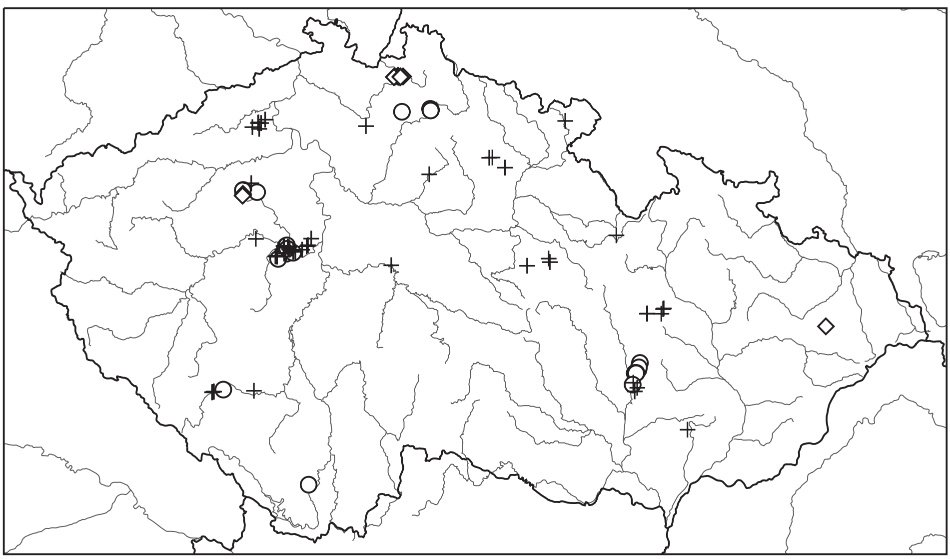

Fig. 1. – Distribution of the *Cephalanthero-Fagetum* subassociations in the Czech Republic based on the relevés analysed: ○ *Cephalanthero-Fagetum seslerietosum*, + *Cephalanthero-Fagetum typicum*, ◇ *Cephalanthero-Fagetum actaeetosum*.

This vegetation type was not recognized in previous vegetation surveys of the Czech Republic (Moravec et al. 1982, 2000), although beech stands with *Sesleria caerulea* were reported by Sýkora (1969) from N Bohemia and by Horák (1979) from the region of Moravian Karst.

The habitats of *C.-F. seslerietosum* are similar to those of *Seslerio albicantis-Tilietum cordatae* Chytrý et Sádlo 1997 (Chytrý & Sádlo 1997), with which *C.-F. seslerietosum* can create mosaics (e.g. in the Moravian Karst).

2. Dry-mesic calcicolous beech forest
Cephalanthero-Fagetum typicum Oberdorfer 1957 (Table 1, column 2)

The characteristic feature of this subassociation is a high frequency of light-demanding or thermophilous calcicolous species (species of *Carpinion*, *Quercetalia pubescenti-petraeae*, and *Festuco-Brometea*). The stands are taller than those of the previous subassociation. It occurs at altitudes of 280–625 m on drier, shallow soils (rendzic leptosols or cambisols). The stands of this subassociation are relatively frequent in Bohemia, especially in the Bohemian Karst and the České středohoří Mts. In Moravia, it is recorded only in the Moravian Karst, the Javoříčko Karst and the Ždánický les forest (Fig. 1).

The subassociation *primuletosum veris*, which was described by Winterhoff (1963) (sub *Carici-Fagetum primuletosum veris*), partly corresponds to subassociation *Cephalanthero-Fagetum typicum* and partly to *Cephalanthero-Fagetum seslerietosum* (see also Dierschke 1989). Winterhoff distinguished four subassociations: *primuletosum veris*, *typicum*, *actaeetosum* and *luzuletosum*. In his concept, the subassociation *primuletosum veris* represents the most xeric subtype of this association but the border between this unit and the typical subassociation was drawn in a different way. Since Winterhoff (1963) published only synthetic tables, unfortunately no type relevé can be chosen from his material.

3. Mesic calcicolous beech forest
Cephalanthero-Fagetum actaeetosum spicatae (Winterhoff 1963) Boublík, Petřík, Sádlo, Hédl, Willner, Černý et Kolbek **comb. nov. hoc loco** (Table 1, column 3)

[Basionym: *Carici-Fagetum actaeetosum spicati* Winterhoff 1963: 32]

This subassociation is, besides the presence of calcicolous herbs, characterized by the dominance of mesophilous or nitrophilous species of the *Fagetalia* order and, in some cases, by the presence of acidophilous species. The stands have the character of high-grown forest and occur at 375–505 m a.s.l. in rather moist or shady habitats with deep soils (usually transition between rendzic leptosols and cambisols). It is recorded in the northern and central part of the Czech Republic (the Ještědský hřbet range, the Džbán hills, and N Moravia; Fig. 1).

Stands with acidophilous species similar to some Czech relevés are described as *Carici-Fagetum luzuletosum* by German authors (Lohmeyer 1955, Winterhoff 1963, Dierschke 1989). No such discrete subassociation was revealed in our data set.

Gradient analysis of environmental factors

Using mostly indirect measurement of environmental correlates, three significant environmental factors explain 6.9% of the variation in species data (of this 45% by slope, 30% by

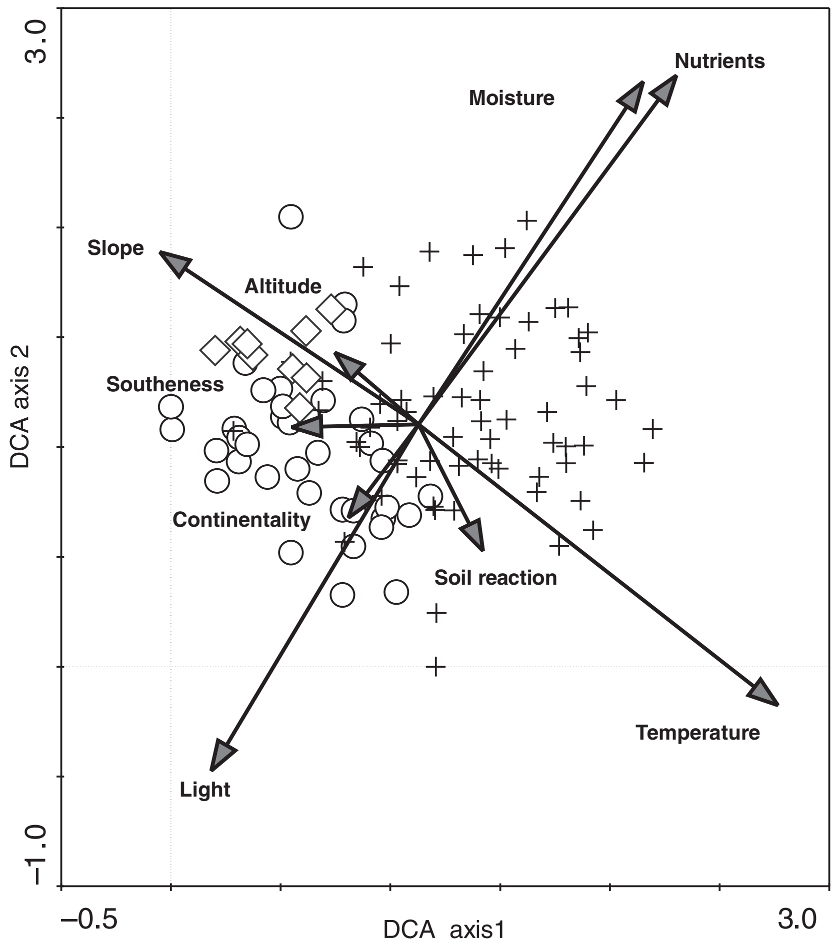

Fig. 2. – Detrended correspondence analysis (DCA) ordination diagram of *Cephalanthero-Fagetum* relevés (n = 111) with supplementary environmental data. The first two ordination axes explain 12.1% of variation in species composition. 'Southness' expresses the exposition of a site to the south. ○ *Cephalanthero-Fagetum seslerietosum*, + *Cephalanthero-Fagetum typicum*, ◇ *Cephalanthero-Fagetum actaeetosum*.

altitude and 25% by folded aspect; expressed as conditional effects of variables) in the constrained ordination. (As the resulting pattern was similar, the CCA ordination graph was replaced by a DCA graph with passive projection of environmental factors; Fig. 2.) The first axis is positively correlated with nutrients and slope, and negatively with temperature. The second axis represents gradient in folded aspect ('southness') and altitude on one hand and moisture, soil reaction and nutrient supply on the other. Moisture and nutrient values are intercorrelated contrary to the negative relationship between Ellenberg's values for moisture and light. About 4.3% of the data variation is distorted by spatial dependency calculated using geographical position index.

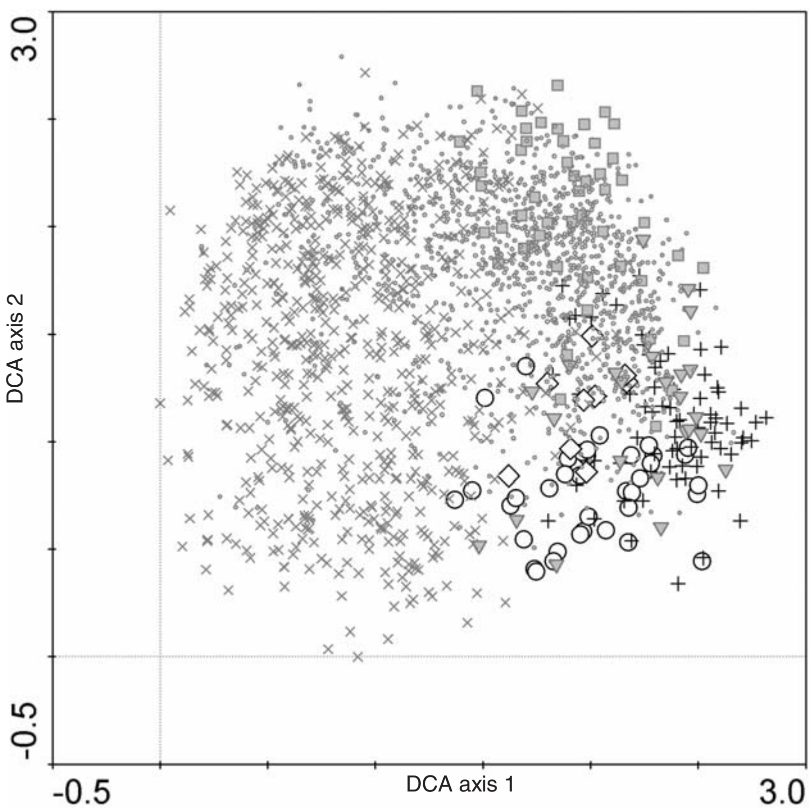

Fig. 3. – Detrended correspondence analysis (DCA) ordination diagram based on 2217 relevés with > 25% coverage of *Fagus sylvatica* in the tree layer. The symbols in black: ○ *Cephalanthero-Fagetum seslerietosum*, + *Cephalanthero-Fagetum typicum*, ◇ *Cephalanthero-Fagetum actaeetosum*; the symbols in grey: ▼ *Carpinion*, ■ *Tilio-Acerion*, ○ *Fagion*, ✕ *Luzulo-Fagion* and *Genisto germanicae-Quercion* (assignment of relevés to vegetation alliances was based on the original indication stored in the header data of relevés in the Czech National Phytosociological Database). In total, 130 unclassified relevés (lacking this indication) are not shown.

Unconstrained gradient analysis with supplementary data gave three groups in ordination space, which were interpreted as subassociations (Fig. 2). The relevés within the *Cephalanthero-Fagetum typicum* are related to warm sites and contain many indicator species with high demands of temperature and good nutrient supply. The relevés of the *C.-F. seslerietosum* subassociation occur typically at the most open and continental habitats on steep slopes. The *C.-F. actaeetosum* subassociation is distributed at higher altitudes on steep slopes and wetter, relatively shaded habitats with high soil nutrient content. Although most stands of this unit are exposed on the southern parts of slopes, the thermophytes are rare due to higher altitude (see arrow of temperature indicator values).

A well-delimited position based on floristic composition of calcicolous beech forests as a whole (not so for their subunits) is shown in Fig. 3. There are significant relationships to *Carpinion* and other *Fagion* communities according to how they were classified by the original authors in the Czech National Phytosociological Database. The overlap is mostly due to *Cephalanthero-Fagetum typicum*.

The comparison of two formalized approaches

When the Cocktail-based formulas for beech forests are applied to the relevés selected by our 38-species diagnostic group (i.e. 100%), the correspondence between these two approaches is not very high – only 36% (Table 2). At the lower classification level, the highest correspondence is in subassociation *C.-F. seslerietosum* (84%), as opposed to *C.-F. actaeetosum* with 89% of transitional relevés among any beech association. The Cocktail definitions assign some relevés to other beech forest communities of *Eu-Fagenion*. Further, 29% of the relevés assigned to transitional vegetation types were classified using the FPFI. The majority of these relevés were assigned to *Galio odorati-Fagetum* and *Cephalanthero-Fagetum* according to the FPFI value (Table 2). Only two relevés were further assigned to the *Cephalanthero-Fagetum* within all the beech forest relevés of the Czech Republic, i.e. in relevés not included in the set selected by the 38-species diagnostic group (see Appendix 2 for composition of species groups and Appendix 3 for *Cephalanthero-Fagetum* and beech forests Cocktail definitions).

Table 2. – (A) The number of relevés selected by the 38-species diagnostic group definition of *Cephalanthero-Fagetum* (n = 120) assigned to Cocktail-based definitions of beech forests recognized in the Czech Republic (see Appendix 2 for the composition of the Cocktail species groups). (B) The number of remaining relevés (n = 35) transitional to other communities further classified using the frequency-positive fidelity index (FPFI). (C) Final comparison of these two formalized definitions supported by FPFI.

Assignment	A	B	C
Cephalanthero-Fagetum	43	9	52 (43.3%)
Galio odorati-Fagetum	4	20	24 (20.0%)
Mercuriali-Fagetum	27	1	28 (23.3%)
Luzulo-Fagetum	–	2	2 (1.7%)
Carpathian thermophilous beech forests	–	3	3 (2.5%)
Unclassified relevés	11		11 (9.2%)

Discussion

Relationship of Cephalanthero-Fagetum to similar communities in the European context

Because of the similar floristic composition of the three units recognized in the material, and because of the fuzziness of their delimitation at the supraregional level, they were classified within a single association with three subassociations. This approach corresponds with the concept used for classification of calcicolous *Fagus*-forests in Germany (Dierschke 1989, Oberdorfer 1992). Most German authors use the name *Carici-Fagetum* Moor 1952 for such stands. However, we consider the *Carici-Fagetum* as a community of the SW part of Central Europe, characterized by the presence of W European species such as *Acer opalus* Miller, *Ilex aquifolium*, *Helleborus foetidus*, and *Teucrium scorodonia* (Willner 2002). Thus, the name *Cephalanthero-Fagetum* Oberdorfer 1957 is used, in accordance with most Czech authors (Moravec et al. 2000).

According to Willner (2002), the other associations of the suballiance *Cephalanthero-Fagenion* in Central Europe are: *Carici-Fagetum* s. str. (for description see above), *Cyclamini-Fagetum*, *Taxo-Fagetum*, *Helleboro nigri-Fagetum* and *Poo stiriacae-Fagetum*.

Cyclamini-Fagetum is a south-eastern community, mainly distributed in E Austria. It differs from *Cephalanthero-Fagetum* by species with a southern distribution such as *Carex alba*, *Daphne laureola* L. and *Salvia glutinosa* (these species are also present in *Carici-Fagetum* s.str.), as well as by species with a south-eastern distribution such as *Cyclamen purpurascens* and *Veratrum nigrum*. *Taxo-Fagetum*, *Helleboro nigri-Fagetum* and *Poo stiriacae-Fagetum* are xerothermophilous beech forests occurring in the lower montane belt of the Alps and Jura mountains, with a high proportion of Alpine-dinaric calcicolous species such as *Lonicera alpigena* L., *Adenostyles glabra* DC., *Veronica urticifolia* Jacq., *Helleborus niger*, *Poa stiriaca* Fritsch et Hayek and others. Within all of these regional associations, subunits with *Sesleria caerulea* can be distinguished, occurring on rocky slopes. To unite these subunits to a wide *Seslerio-Fagetum* (e.g. Mucina et al. 1993), however, does not accord with the predominant geographical gradient in the floristic pattern of calcicolous beech forests (Willner 2002).

Relationship of Cephalanthero-Fagetum to similar communities within the Czech Republic

Within the Czech Republic, we focus now on the classification of colline and supracolline beech forests on base-rich substrates (basalt, phonolite, spilite, diabase) containing calcicolous and/or xerothermophilous species (e.g. *Bupleurum longifolium* subsp. *longifolium*, *Melittis melissophyllum*, *Trifolium alpestre*). These communities are usually assigned to the regional Central Bohemian association (*Tilio cordatae-Fagetum*) or local association of the N Bohemian volcanic hills (*Tilio platyphylli-Fagetum*) (Moravec et al. 1982, 2000). In these cases, the continuum between *Cephalanthero-Fagenion* and *Eu-Fagenion* communities is apparent. However, we suggest classifying the stands with calcicolous or xerothermophilous species as *Cephalanthero-Fagetum*. The Bohemian supracolline beech forests without such species should be ranked either as *Galio odorati-Fagetum* Sougnez et Thill 1959 nom. cons. et mut. propos. or *Mercuriali perennis-Fagetum sylvaticae* Scamoni 1935 nom. invers. propos. (compare with Dierschke 1989, Oberdorfer 1992, Willner 2002, Dengler et al. 2004).

For the selection of relevés of calcicolous beech forest, at least two species from the 38-species diagnostic group had to be present. However, the final data set contained some relevés, which were regarded as either belonging to another vegetation unit (based on our expert opinion) or whose syntaxonomical evaluation was questionable. These are (i) Moravian beech forests with species of the Carpathian floristic element, (ii) supracolline beech forests dominated by *Calamagrostis arundinacea* occurring on volcanic hills in N Bohemia, and (iii) montane spruce-beech forest occurring on calcium carbonate bedrock in the Krkonoše Mts.

(i) The presence of calcicolous and xerothermophilous species is a significant feature of colline Carpathian beech forests similar to *Cephalanthero-Fagetum* (Moravec et al. 1982, 2000, Chytrý et al. 2001) and these species are not only limited to the more extreme habitats. As a criterion for assigning this transition community to Carpathian thermophilous beech forest, at least two species occurring within the Czech Republic especially in the Carpathians (Carex pilosa group: *Carex pilosa*, *Euphorbia amygdaloides*, *Galium schultesii*, *Hacquetia epipactis*; Appendix 2), had to be present in a relevé. There are three such relevés in the data set (Table 1, column 4). Species typical of Central Carpathian beech forests – *Cirsium erisithales*, *Clematis alpina* L. (Mill.), *Valeriana* *tripteris*, *Hesperis nivea* Baumg., *Cortusa mathiolii* – do not occur in Czech stands, which complicates the evaluation of Czech communities. The syntaxonomical evaluation of such communities will depend on the concept used to classify beech forest in the W Carpathians and goes outside the scope of this paper.

(ii) We place the supracolline beech forests of dry, slightly base-rich, siliceous bedrock of volcanic hills in N Bohemia dominated by *Calamagrostis arundinacea* (Table 1, column 5) in the *Luzulo-Fagion* alliance because of their acidophilous character and the low number of calcicolous and xerothermophilous species. For Bohemia, the stands are mentioned by Sýkora (1972) as *Calamagrostio arundinaceae-Fagetum* (Hartmann et Jahn 1967) Sýkora 1972 but they also have close floristic affinities to the association *Melampyro-Fagetum* Oberdorfer 1957 known also from the Czech Republic (Willner 2002).

(iii) Due to their occurrence on bedrock rich in calcium carbonate (similar to *Cephalanthero-Fagenion*), relevés of montane spruce-beech forest were included in the synoptic table despite the absence of species from the diagnostic species group (Table 1, column 6). This community can be found as a single stand in the vicinity of the Obří důl glacial cirque in the Krkonoše Mts. It is characterized by the occurrence of calcicolous petrophytes (e.g. *Asplenium viride*, *Polystichum lonchitis*) and heliophilous species (e.g. *Digitalis grandiflora*) as well as montane species such as *Gentiana asclepiadea* or *Homogyne alpina*. Its floristic composition is related to the Alpine associations *Asplenio-Piceetum* (Oberdorfer 1992, Mucina et al. 1993) and *Saxifrago rotundifoliae-Fagetum* (Willner 2002), however, its syntaxonomical position is unclear.

Is the epithet 'calcicolous' adequate for Cephalanthero-Fagenion communities?

The term 'calcicolous/calciphilous' is commonly used as an epithet for *Cephalanthero-Fagenion* communities (see national overviews listed in Introduction). As we show, *Cephalanthero-Fagenion* communities can also occur on soils where calcium carbonate is not significantly represented but still contributes to the cation exchange capacity. In such cases, the calcium content corresponds well to pH (soil reaction) and so justifies the use of surrogate measures in ecological research, such as indicator values (e.g. Ellenberg 1988, Ellenberg et al. 2001). Often, the basicity determined by Ellenberg indicator values is related to higher temperature and lower moisture values (e.g. Ewald 2003). Often, the term 'calcicolous' is inconsistently used and the relationship of many species to calcium carbonate should be tested in the laboratory. Hence, we use the term 'calcicolous' to avoid possible misinterpretation and another complicated description.

Relevé and species group selection

In general, the output of a relevé selection from any data set depends basically on three conditions: (i) the size and representativeness (composition) of the data set used, (ii) the composition and size of the species group used and (iii) the threshold fidelity values used. In addition, the structure of the data set and the species group composition depend on the vegetation types included, i.e. on the character of the region surveyed and at what scale (Kuželová & Chytrý 2004, Knollová et al. 2005, Petřík & Bruelheide 2006).

In principle, the more species the diagnostic species group contains, the fuzzier the delimitation of vegetation types. The more restricted the threshold values, the fewer relevés that fall into the selected types. We attempted to make our selection criteria more restrictive, selecting only relevés that had at least three species from the 38-species diagnostic group. This pilot procedure resulted in a similar selection of relevés except for the acidophilous and species-poor beech forest community *Calamagrostio arundinaceae-Fagetum* (Hartmann et Jahn 1967) Sýkora 1972 (because only *Rubus saxatilis*, *Sorbus aria* agg. and *Vincetoxicum hirundinaria* from the diagnostic species group were present) and, partially, some mesophilous types of *Cephalanthero-Fagetum actaeetosum*, which were not selected.

Chytrý & Tichý (2003) considered that the sharpness of the delimitation of *Cephalanthero-Fagenion* was low (the sharpness corresponded to the number or quality of diagnostic species in a vegetation unit, relative to the average species richness of its stands) in the statistical revision of the diagnostic species of vegetation units traditionally used in the Czech Republic. As for uniqueness (i.e. whether there are other similar vegetation units in a classification system), the calcicolous beech forests were similar to oak-hornbeam forests of the *Carpinion* alliance. As these authors discussed, these results could be related to either fragmentary occurrence or erroneous delimitation of *Cephalanthero-Fagenion* in the Czech Republic. In addition, the number of relevés used for that analysis was rather low, n = 42, compared to our 120 relevés. The floristic affinities between *Cephalanthero-Fagenion* and *Carpinion* have also been discussed in the German literature (e.g. Oberdorfer 1992). However, most authors agree that *Cephalanthero-Fagenion* should be included into *Fagion*, and not *Carpinion*, because of the dominance of *Fagus sylvatica.*

Correspondence between two formalized approaches

The correspondence between the two formalized approaches was generally low except for the subgroup *Cephalanthero-Fagetum seslerietosum*, which consists of many specialists (i.e. good diagnostic species). In other words, it is easier to define a unique calcareous forest (dry subassociation on rocky outcrops) than a related community (central mesic subassociation *C.-F. typicum*) that occurs in the centre of a hypothetical ecological gradient. Similarly, the poorly delimited subassociation *C.-F. actaeetosum* overlaps another suballiance *Eu-Fagenion* (additionally classified as meso-eutrophic *Mercuriali perennis-Fagetum*). Logically, we can ask if it is possible to define any beech community using a large set of species groups. We suppose this approach fails in the case of central associations lacking good diagnostic species (Willner 2006) such as *Galio odorati-Fagetum* (*Eu-Fagenion*) and *Luzulo-Fagetum* (*Luzulo-Fagion*). Nevertheless, it is useful for defining communities situated at the ends of ecological gradients with a unique species composition including many specialists.

When comparing two formalized definitions (i.e. selection by 38-species diagnostic group and Cocktail-definitions) in this paper, a relatively large number of relevés was classified either as a transitional type of beech forest associations or remained unclassified (38%).

Using formalized approaches, we can define vegetation units consistently if strict formulas are used, which is in contrary to the less rigorous 'soft' traditional approach (e.g. Chytrý 2000). We used the formal definition of diagnostic species group intentionally in order to unify selection criteria for relevés independently of the authors' original assignment to vegetation units. Selection employing the original authors' assignment probably influenced the results obtained by Knollová & Chytrý (2004) or Roleček (2007).

Our two formalized definitions resulted in different outcomes. First, the 38-species diagnostic group definition (coined in this paper) encompasses a widely varied group of calcicolous beech forests. The newly proposed definition attempted to include the whole of the variability of the Czech calcicolous beech forests. Therefore, our definition of diagnostic species group contains many species chosen independently of any statistical analysis. Second, the Cocktail-based formula is narrower, with fewer species used in the definition. So, overlaps between definitions tend to be larger when using broad definitions. However, both approaches fail when defining central units.

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Souhrn

Přinášíme výsledky syntaxonomické revize společenstev vápnomilných bučin podsvazu *Cephalanthero-Fagenion* v České republice. Snímky vápnomilných bučin musely obsahovat alespoň 25 % buku ve stromovém patře, muselo se jednat o květnaté porosty a podle našich kritérií musely obsahovat alespoň dva druhy z námi sestavené skupiny 38 vápnomilných a/nebo xerotermofilních taxonů (Appendix 1). Uvedené definici odpovídá 120 fytocenologických snímků řazených námi podle základního společného druhového složení k asociaci *Cephalanthero-Fagetum*. Tyto snímky byly dále metodou divizivní klasifikace (TWINSPAN) rozděleny na čtyři skupiny, jež jsme dále po sloučení dvou skupin interpretovali jako tři subasociace.

Cephalanthero-Fagetum seslerietosum caeruleae je zakrslá bučina skalních výchozů vápenců, opuk či vápnitých pískovců s půdami typu rendzina či pararendzina. V porostech obvykle dominuje *Sesleria caerulea*, hojné jsou petrofyty a druhy pěchavových trávníků. Subasociace osidluje podobné biotopy jako asociace suťových lesů *Seslerio albicantis-Tilietum cordatae*, se kterou místy tvoří mozaiky. *Cephalanthero-Fagetum typicum* se vyznačuje vysokou účastí druhů světlomilných a je vázána na mělčí půdy typu kambických rendzin či rendzin, případně kambizemí. *Cephalanthero-Fagetum actaeetosum spicatae* představuje vysokokmenný les hlubších půd, ve kterém jsou hojné nebo dominují mezotrofní nebo nitrofilní druhy nebo jsou časté druhy acidofilní. Jméno subasociace *Cephalanthero-Fagetum actaeetosum spicatae* představuje novou nomenklatorickou kombinaci.

Náplň asociace *Cephalanthero-Fagetum* v České republice tvoří vápnomilné bučiny kolinního a suprakolinního vegetačního stupně s účastí druhů, které se v ČR chovají jako vápnomilné, suchomilné či teplomilné. Proto se podle tohoto kritéria společenstva vápnomilných bučin nemusejí vyskytovat jen na vápnitých substrátech (vápencích, opukách, vápnitých pískovcích), ale najdeme je také na bazických silikátových horninách (např. čedič, znělec, diabas) v Českém středohoří či na Křivoklátsku, kde se překrývají s dosud rozlišovanými regionálními asociacemi *Tilio cordatae-Fagetum* a *Tilio platyphylli-Fagetum* řazenými tradičně do podsvazu *Eu-Fagenion* (Moravec et al. 2000). Porosty bez účasti těchto bazifytů dosud řazené do výše zmíněných regionálních jednotek považujeme za společenstva asociací *Galio odorati-Fagetum* nebo *Mercuriali perennis-Fagetum sylvaticae*.

Jsou diskutovány rovněž příbuzné vegetační typy obsahující vápnomilné a/nebo xerotermofilní druhy. Karpatské kolinní bučiny vyskytující se ve východní části ČR vykazují přechodné typy k asociaci *Cephalanthero-Fagetum* a jejich hodnocení necháváme otevřené, protože záleží na pojetí použité pro podobné porosty v Západních Karpatech. Porosty *Calamagrostio arundinaceae-Fagetum* (Hartmann et Jahn 1967) Sýkora 1972 (Sýkora 1972) vyskytující se na vulkanických kopcích v severních Čechách obsahují sice některé druhy z naší diagnostické skupiny, ale základní druhová skladba ukazuje na příslušnost ke svazu *Luzulo-Fagion*. Smrkové bučiny bazických podkladů z montánních poloh Obřího dolu v Krkonoších představují z hlediska ČR atypické

porosty, které obsahují reliktní či horské taxony (*Bupleurum longifolium* subsp. *vapincense*, *Campanula bohemica*, *Homogyne alpina*, *Pleurospermum austriacum*). Syntaxonomická příslušnost těchto porostů není jasná.

Výsledky nepřímé ordinace (DCA) částečně ukázaly floristickou diferenciaci v našem materiálu, stejně jako ojedinělé postavení vápnomilných bučin v rámci bukových lesů ČR. Pro odhalení příčin variability ve floristickém složení byly použity Ellenbergovy indikační hodnoty, nadmořská výška, sklon, orientace ke světovým stranám a poloha snímku na gradientu sever–jih. Vzhledem k tomu, že se jedná často o maloplošné a lokální porosty, byly geografické pozice snímků vzaty při analýzách jako kovariáty k odstranění prostorové závislosti. Složení uvedených subasociací je nejvíce určeno sklonitostí, nadmořskou výškou a expozicí (resp. polohou více na jih).

Výsledky klasifikace podle námi navržené skupiny 38 druhů jsme porovnali s výsledky získanými jiným formalizovaným přístupem, založeným na vytváření skupin diagnostických druhů metodou Cocktail (použita při přípravě nového přehledu vegetace České republiky, cf. Chytrý 2007). Použili jsme definice všech asociací bučin ČR (srov. Appendix 2 a 3) k tomu, abychom ukázali, nakolik jsou obě definice vápnomilných bučin srovnatelné. Shoda mezi snímky vybranými na základě naší diagnostické skupiny a těmi, které byly vybrány pomocí Cocktailových definic, byla poměrně malá (36 %). Navíc až 38 % snímků nebylo možno zařadit pomocí Cocktailu jednoznačně do žádné z definic bučin v ČR. Pokud se ale podíváme na nižší úroveň subasociace, zjistíme 84% shodu mezi oběma přístupy u dobře definované subasociace *C.-F. seslerietosum* narozdíl od nevyhraněné centrální subasociace *C.-F. typicum*, postrádající dobré diagnostické druhy. Důvodem zjištěné vysoké shody je floristická skladba subasociace *C.-F. seslerietosum* sestávající převážně z druhů–specialistů a také její ojedinělé postavení na pomyslných křídlech ekologického gradientu. Ukázalo se, že metoda Cocktail s následným přiřazováním snímků pomocí indexu podobnosti FPFI zachycuje užší jádra vegetačních jednotek, zatímco definice pomocí široké druhové skupiny se vztahuje na širší variabilitu vápnomilných bučin.

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Appendix 1. – Diagnostic species group of calcicolous and/or xerothermophilous species used for selection of calcicolous beech forests.

Anthericum liliago, *A. ramosum*, *Aquilegia vulgaris*, *Arabis pauciflora*, *Berberis vulgaris* (shrub layer), *Brachypodium pinnatum*, *Bupleurum falcatum*, *B. longifolium* subsp. *longifolium*, *Calamagrostis varia*, *Carex flacca*, *C. humilis*, *C. montana*, *Cephalanthera damasonium*, *C. rubra*, *Cornus mas* (shrub layer), *Cypripedium calceolus*, *Epipactis atrorubens*, *E. microphylla*, *Galium glaucum*, *Hypericum montanum*, *Laserpitium latifolium*, *Melica picta*, *Melittis melissophyllum*, *Peucedanum cervaria*, *Primula veris*, *Rubus saxatilis*, *Sesleria caerulea*, *Sorbus aria* agg. (shrub layer), *Teucrium chamaedrys*, *Trifolium alpestre*, *Veratrum nigrum*, *Viburnum lantana* (shrub layer), *Vicia dumetorum*, *V. pisiformis*, *Vincetoxicum hirundinaria*, *Viola collina*, *V. hirta*, *V. mirabilis*.

Appendix 2. – Composition of species groups used in the Cocktail definitions of beech forests.

Asarum europaeum group: *Asarum europaeum*, *Campanula trachelium*, *Polygonatum multiflorum*, *Pulmonaria officinalis* s. lat.
Carex digitata group: *Campanula persicifolia*, *Carex digitata*, *Clinopodium vulgare*, *Pyrethrum corymbosum*
Carex pilosa group: *Carex pilosa*, *Euphorbia amygdaloides*, *Galium schultesii*, *Hacquetia epipactis*
Cephalanthera damasonium group: *Cephalanthera damasonium*, *C. rubra*, *Corallorhiza trifida*, *Epipactis helleborine* agg.
Galium odoratum group: *Dentaria bulbifera*, *Galium odoratum*, *Mycelis muralis*, *Viola reichenbachiana*
Geranium sanguineum group: *Anthericum ramosum*, *Geranium sanguineum*, *Polygonatum odoratum*, *Vincetoxicum hirundinaria*
Hieracium sabaudum group: *Hieracium sabaudum*, *Hieracium murorum*, *Hieracium lachenalii*, *Luzula luzuloides*, *Melampyrum pratense*
Lathyrus niger group: *Carex montana*, *Festuca heterophylla*, *Lathyrus niger*, *Melittis melissophyllum*
Lathyrus vernus group: *Galium sylvaticum*, *Hepatica nobilis*, *Lathyrus vernus*, *Melica nutans*

Mercurialis perennis group: *Actaea spicata*, *Galeobdolon luteum* agg., *Geranium robertianum*, *Mercurialis perennis*
Trientalis europaea group: *Calamagrostis villosa*, *Homogyne alpina*, *Trientalis europaea*
Vaccinium myrtillus group: *Avenella flexuosa*, *Dicranum scoparium*, *Polytrichum formosum*, *Vaccinium myrtillus*

Appendix 3. – Cocktail definitions of beech forests overlapping relevés selected by 38-species diagnostic group.

Cephalanthero-Fagetum: *Fagus sylvatica* cover > 25% AND (*Geranium sanguineum* group OR *Lathyrus niger* group OR *Cephalanthera damasonium* group OR *Sesleria caerulea* cover > 5%) AND NOT *Carex pilosa* group
Galio odorati-Fagetum: *Fagus sylvatica* cover > 25% AND *Galium odoratum* group AND NOT *Mercurialis perennis* group
Mercuriali perennis-Fagetum sylvaticae: *Fagus sylvatica* cover > 25% AND *Mercurialis perennis* group
Carpathian thermophilous beech forests: *Fagus sylvatica* cover > 25% AND *Carex pilosa* cover > 5% AND *Carex pilosa* group
Luzulo-Fagetum: *Fagus sylvatica* cover > 25% AND (*Vaccinium myrtillus* group OR *Hieracium sabaudum* group) AND NOT (*Trientalis europaea* group OR *Lathyrus vernus* group OR *Asarum europaeum* group OR *Carex digitata* group OR *Galium odoratum* group OR *Mercurialis perennis* group OR *Calamagrostis villosa* cover > 5%)