

# Plant community variability within potential natural vegetation units: a case study from the Bohemian Karst

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**ABSTRACT:** Based on a map of potential natural vegetation (PNV), actual vegetation was studied in the Mramor locality (106.4 ha). A total of 188 relevés were examined using stratified random sampling. A comparison was made between trends in vegetation variability throughout the entire locality and variability within the defined PNV units. The stratification of the locality according to PNV units was only partly representative of the main trends in vegetation variability, especially at ecologically distinctive sites. On the other hand, in areas with a relatively limited ecological gradient, the sites were “oversampled”. The variability of plant communities within PNV units was high. The results of this case study suggest that the need for delineation of PNV units which are homogeneous in terms of production, site and phytocoenosis is overestimated. This delineation neither corresponds to the characteristics of actual ecosystems nor is necessary for the application of a PNV system. A more suitable unit for the development of such a system would be, for example, forest type series.

**Keywords:** vegetation classification; vegetation variability; potential natural vegetation; oak forest; Bohemian Karst

## Formalized sampling approaches

The subjective selection of phytocoenological plots, which were traditionally used for many decades, is being replaced by a formalized selection process. The main reasons for this change were the requirement of a representative set of samples from surveyed territories and the desire to eliminate tautological statements of evidence (e.g. CHYTRÝ 2000). One of the methods widely used in this formalized approach to data collection is stratified random sampling (e.g. HIRZEL, GUIBAN 2002). Unlike entirely random sampling, stratified random sampling enables the more effective placement of plots along important gradients of variability and in general provides more information about vegetation rarity and diversity (HESSBURG et al. 2000). However, this type of selection requires more detailed data on

the studied territory. In studies of phytocoenosis, stratified random sampling is applied primarily on the coarse landscape level (e.g. COOPER, LOFTUS 1998; CAWSEY et al. 2002; HURST, ALLEN 2007). In such cases, the landscape is stratified in advance, e.g. according to climatic characteristics, geological bedrock, altitude, or the classification of aerial photographs. Random sampling is subsequently applied in territorial segments within a specific category. The choice of underlayers for stratification at fine spatial levels (tens to hundreds of hectares) is problematic, as commonly used underlayers are too coarse (e.g. geological maps at a scale of 1:25,000–1:50,000) and better data sources are not generally available. There arises a question whether the forest map of potential natural vegetation (PNV) would be applicable for this purpose. In the Czech Republic, such a map is available at a scale of 1:10,000 (and even 1:5,000 in

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national nature reserves) for all forest stands in the country (ANONYMOUS 1971/1976). Other countries could make use of similarly constructed systems for the purposes of stratification (e.g. POJAR et al. 1987; PYATT et al. 2001; SCHWARZ 2005).

### The potential natural vegetation map

Research into PNV is currently paid considerable attention (e.g. CHYTRÝ 1998; NEUHÄUSLOVÁ et al. 1998; ZERBE 1998; BUČEK, LACINA 2002; RICOTTA et al. 2002; BOHN et al. 2003). PNV maps are a part of the groundwork for future landscape use planning (e.g. ZELENKOVÁ 2000) as well as for assessments of the stability and naturalness of contemporary ecosystems (PETŘÍČEK, MÍCHAL 1999). PNV maps exist for all forest stands in the Czech Republic, and were constructed using a Typological System developed by the Forest Management Institute (TSFMI) (ANONYMOUS 1971/1976 – further extended by PLÍVA (1991), MIKESKA and KUSBACH (1999), PRŮŠA (2001), VIEWEGH et al. (2003)). This TSFMI was primarily created for the applied function of landscape classification to be used in future resource planning. While other systems of PNV classification exist (e.g. NEUHÄUSLOVÁ et al. 1998), this study uses the concept of “forest type” (FT) (e.g. ZLATNÍK 1956; VIEWEGH 1997). The concept behind this classification was defined for the “Central European space”, and it assumes that we can distinguish between types of potential natural vegetation – in this case forest types (FT) – based on the differentiation of “permanent” ecological site conditions. This idea is similar to the theory of PNV by TÜXEN (1956) (see KOWARIK 1987; ZERBE 1998; CHYTRÝ 1998), according to which such vegetation that would be the most competitive for given site conditions is “interpreted” into the landscape. The factors of time and succession are eliminated (cf. STUMPEL, KALKHOVEN 1978). In the TSFMI classification, FT is a mapping unit of PNV. Unlike other systems that map potential natural vegetation, this system requires uniformity of soil, production and phytocoenosis within a mapping unit. Therefore, a difference in soils, production or phytocoenosis at a specific landscape segment calls for new FT. Subsequently, FTs are aggregated into superstructural units according to their ecological affinity. During this stage, the search for ecological factors which lead to differences in the vegetation composition is of key importance for general modelling of the structure and development of plant communities (e.g. AUSTIN 2002; RICOTTA et al. 2002).

As the future development of the structure of plant communities is not known, units of the PNV

represent selected units of existing vegetation (usually, the vegetation least affected by humans and most stable in time). There are only a few possible methods to verify the correctness of the PNV concept (ZERBE 1998), but the theoretical assumption of the homogeneity of forest types can be verified by analyzing the variability of actual (namely near-natural) vegetation.

Our objectives in this study are:

- To assess whether the Czech PNV map is useful as groundwork for the stratification of the territory in studying actual vegetation.
- To test whether the variability of actual vegetation contradicts the concept of PNV according to the TSFMI.
- To check whether the FTs delineated in the PNV map are homogeneous in terms of phytocoenosis.

## MATERIALS AND METHODS

### Area descriptions

The Bohemian Karst is a geomorphic part of the Brdy Region (DEMEK et al. 2006). Mean annual total precipitation is about 500 mm; mean annual temperature is 8–9°C (TOLASZ et al. 2007; www.chmu.cz/). There are significant differences between day and night temperatures during the growing season, with maximums of 40°C at a ground level on southern slopes.

The studied area (Mramor) covers 106.4 ha and is situated in the southern part of the Bohemian Karst (Fig. 1). The highest elevations in the territory are the summits of Mramor (472 m a.s.l.) and Šamor (481 m a.s.l.), while the lowest elevations are at an altitude of about 350 m a.s.l. The territory is geologically homogeneous, with bedrock built of Devonian limestones. Ecological conditions vary considerably



Fig. 1. Study area: The Bohemian Karst Protected Landscape Area (in grey) with the studied Mramor locality

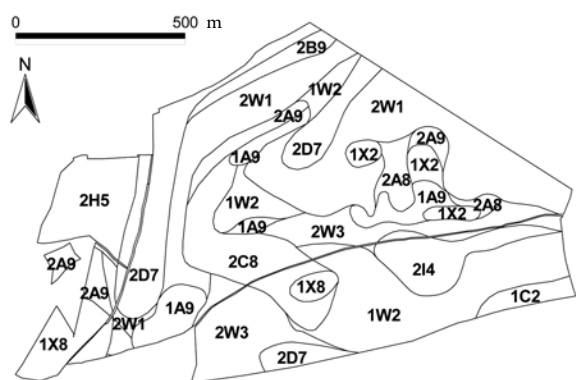


Fig. 2. The map of potential natural vegetation in the Mramor locality (ZELENKOVÁ 2000). Forest types (in alphabetic order): 1A9 – *Aceri-Carpineto-Quercetum lapidosum* on limestones, 1C2 – *Carpineto-Quercetum subxerothermicum* with *Poa nemoralis*, 1W2 – (*Fagi-*) *Carpineto-Quercetum calcarium*, 1X2 – *Corneto-Quercetum (xerothermicum)* on Rendzic Leptosols, 1X8 – *Corneto-Quercetum (xerothermicum)* on Lithic Leptosols (Rendzic), 2A8 – *Aceri-Fageto-Quercetum lapidosum* on warm slopes, 2A9 – *Aceri-Fageto-Quercetum lapidosum* on shady slopes, 2B9 – *Fageto-Quercetum mesotrophicum* with *Alliaria petiolata*, 2C8 – *Fageto-Quercetum subxerothermicum* on limestones with *Brychypodium pinnatum*, 2D7 – *Fageto-Quercetum acerosum deluvium* on limestones, 2H5 – *Fageto-Quercetum illimerosum mesotrophicum* with *Luzula luzuloides* and *Carex montana*, 2I4 – *Fageto-Quercetum illimerosum acidophilum* with *Melampyrum pratense*, 2W1 – *Fageto-Quercetum calcarium* with *Mercurialis perennis*, 2W3 – *Fageto-Quercetum calcarium* with *Galium odoratum*. The territory is crossed by three roadways

throughout the study area, resulting in a wide range of habitats, from diluvial sites on northern slopes to exposed southern slopes with shallow soils. Soils can be classified as Lithic Leptosols (Rendzic), Rendzic Leptosols (Humic and Eutric), Chromic Cambisols and Chromic Luvisols (ISSS-ISRIC-FAO 1998; DRIESSEN et al. 2001; MICHÉLI et al. 2006). The study area is within Conservation Zone 1 of the Bohemian Karst Protected Landscape Area, and the dominant plant communities are subjected to limited human impact. The map of PNV for the area is shown in Fig. 2 (ZELENKOVÁ 2000). We assume that the quality of PNV mapping achieved in the model territory is at a similar level as in the remaining area of the Czech Republic.

There are historical records of the tree composition in the area. In 1645, forests surrounding the village of Liteň (1 km from the Mramor study site) were described as being composed predominantly of oak, and other historical sources also mention beech, hornbeam and pine (NOŽIČKA 1957; NOVÁK,

TLAPÁK 1974). A similar tree species composition was described in both 1711 and 1808; NOŽIČKA (1957) and NOVÁK and TLAPÁK (1974) reported a low proportion of aspen and fir in the following years. In spite of the fact that during the subsequent 150 years, deciduous lowland coppiced (low) forests throughout the Czech Republic were routinely changed to high forests with a large amount of spruce and Scotch pine, the Mramor site was still depicted as coppiced forest on stand maps from 1902. At present, the Mramor forests are dominated by *Quercus petraea* agg., *Tilia cordata*, *Fagus sylvatica* and *Carpinus betulus*, with mixed – sexual and/or asexual – origin. The occurrence of allochthonous tree species (*Robinia pseudacacia*, *Aesculus hippocastanum*, *Larix decidua*, *Picea abies*, *Quercus cerris*) is minimal.

### Field sampling

Plots for relevés were selected by formalized manner with the use of stratified random sampling (e.g. HIRZEL, GUIBAN 2002). In the first step, the Mramor territory was divided into seven site types (ST), which we obtained by merging the forest types (ZELENKOVÁ 2000) according to their ecological affinity. Site types were usually identical with individual edaphic categories of the PNV system, but we made exceptions in well-founded cases (e.g. it is difficult to separate FTs 2B9, 2W1, 2W3 in karst regions – ŠAMONIL 2005, 2007a,b; ŠAMONIL, VIEWEGH 2005). These ST types were established specifically for this study and are not a part of the PNV system. Some specific forest types (1X2, 1X8, and 2I4; see Fig. 2) were not merged due to their exceptional character. Thus, the site type in these cases was identical to that defined by forest type. Defined forest types were then subjected to random sampling. The entire Mramor territory was covered by a graticule with  $25 \times 25 \text{ m}^2$ , which were then selected at random to determine relevés. The affiliation of the square centre was decisive in determining the square allocation to a specific ST. If the selected square was in an environment that was significantly anthropogenically modified (e.g. roadside landing, old road), it was replaced by the next chosen square. In site types that were larger than 5% of the total territory area, a total of 32 squares were selected; for other site types 20 squares were selected (Fig. 3).

Phytocoenological plots of  $20 \times 20 \text{ m}$  were delineated in the field, using navigation by a Garmin GPS with an approximate positioning error of 5 m. Vegetation was recorded according to the 11-member classification of abundance and dominance by

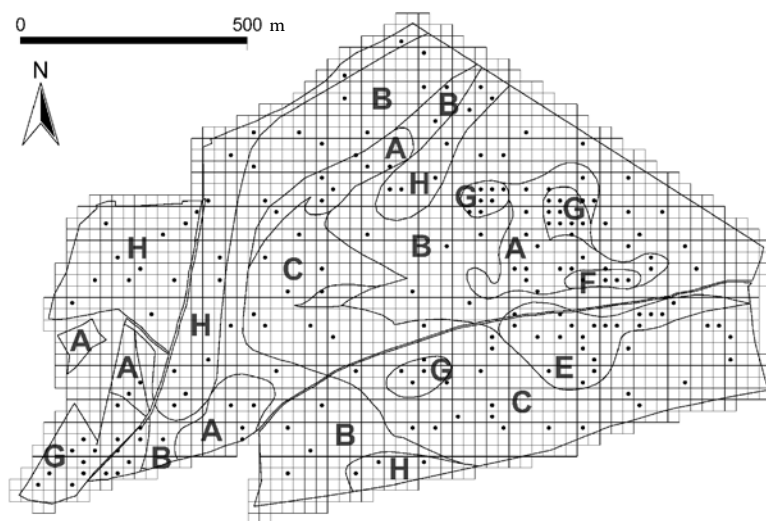


Fig. 3. Site types created through the merging of forest types according to their ecological affinity: A (Forest Types 1A9, 2A8, 2A9), B (2B9, 2W1, 2W3), C (1W2, 1C2, 2C8), D (2D7, 2H5), E (2I4), F (1X2), G (1X8). The territory was covered by a grid at a grain of 25 × 25 m. According to site types, squares were generated by random selection for the creation of relevés (marked with a dot). The territory is divided by three roadways

ZLATNÍK (1953) – a modified Braun-Blanquet classification. Vertical stratification according to ZLATNÍK (1975) was used. A total number of 188 relevés were created in June and July, 2005 and 2006. Only vascular plant taxa were recorded; mosses and lichens were not assessed. The nomenclature followed KUBÁT et al. (2002).

### Data analysis

Relevés were recorded in the Turboveg for Windows 2.07 a database programme (HENNEKENS, SCHAMINÉE 2001). For subsequent analyses, the tree species layers were merged based on their random overlapping; e.g. the sum of two layers was calculated as  $c_s = c_x + (100 - c_x) \times c_y$ , where  $c_s$  is the resulting overall cover, and  $c_x$  and  $c_y$  are taxon covers in layers  $x$  and  $y$  expressed in percent (TICHÝ, JASON 2006).

In order to study vegetation variability, the entire set of 188 relevés was classified by means of the hierarchic divisive classification TWINSpan (HILL 1979) (Table 1). Analysis was performed with four levels of the set division. Quantitative characteristics of the occurrence of plant taxa were taken into consideration by adjusting 3 pseudospecies with the limiting values of cover at 0, 5 and 25%. This resulted in the division of the set of relevés into 12 groups, for which fidelity and constancy of plant taxa were calculated. Taxon fidelity, i.e. the concentration of species occurrence in vegetation units, was measured using the phi coefficient (SOKAL, ROHLF 1995; CHYTRÝ et al. 2002). The phi coefficient ( $\Phi$ ) of association between species and units is a statistical measure of the association between two categories. This phi coefficient was calculated according to the formula

$$\Phi = (N \times np - n \times Np) / \sqrt{\{n \times Np \times (N - n) \times (N - Np)\}}$$

where:

$N$  – number of relevés in the data set,

$Np$  – number of relevés in the target unit (in this case the TWINSpan category),

$n$  – number of occurrences of the species in the data set,

$np$  – number of occurrences of the species in the target unit.

Calculated phi coefficient values range from –1 to 1, but are then multiplied by 100. The highest phi value of 1 (recalculated to 100) is achieved if the species occurs in all relevés of the unit and is absent elsewhere. Calculations were performed and the resulting tables produced in Juice 6.4.55 software (TICHÝ 2002).

Next, vegetation variability was studied within the defined site types and in the PNV units. The constancy and fidelity of plant taxa were calculated according to the site types (Table 2), identically to the calculation of vegetation characteristics among TWINSpan categories. The classification of relevés according to the PNV system was then compared with categorization according to TWINSpan using a contingency table. At the same time, we evaluated how the species composition of individual relevés agrees with their classification according to the PNV system using the Frequency-Positive Fidelity Index (FPFI) (TICHÝ, JASON 2006). In some cases, the frequency and/or fidelity of plant species indicated a possible reclassification of the relevé to another PNV unit (forest type). We also calculated the successfulness of the PNV classification; user's accuracy and producer's accuracy (e.g. CONGALTON 1991; NILSSON 1998; see also ČERNÁ, CHYTRÝ 2005 – sensitivity and positive predictive power) were evaluated for individual forest types.

Detrended correspondence analysis (DCA) was used in order to compare vegetation variability within the entire study area with vegetation vari-



Table 1 to be continued

Number of TWINSPAN category	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Taxon/Number of relevés	3	4	2	1	3	23	20	36	80	11	3	2
<i>Primula veris</i>	.	50	.	.	67	74 <sup>38.3</sup>	10	47	11	.	.	.
<i>Carex muricata</i> agg.	.	.	.	.	.	30 <sup>36.8</sup>	5	19	1	.	.	.
<i>Viola mirabilis</i>	.	.	.	.	33	43 <sup>34.9</sup>	5	22	1	9	.	.
<i>Brachypodium pinnatum</i>	.	.	.	100	67	83 <sup>34.0</sup>	45	28	9	36	.	.
<i>Euphorbia cyparissias</i>	.	.	.	.	100	61 <sup>33.6</sup>	40	14	1	.	.	.
<i>Alliaria petiolata</i>	.	.	.	100	67	96 <sup>31.4</sup>	.	17	26	73	100	50
<i>Hylotelephium maximum</i>	.	.	.	.	33	22 <sup>22.0</sup>	.	.	.	9	.	.
<i>Anemone nemorosa</i>	.	.	.	.	.	.	70 <sup>61.6</sup>	6	31	9	.	.
<i>Trifolium alpestre</i>	.	.	.	.	.	13	35 <sup>47.7</sup>	.	.	.	.	.
<i>Veronica chamaedrys</i>	.	.	.	.	.	9	35 <sup>46.2</sup>	6	1	.	.	.
<i>Carex montana</i>	.	.	.	.	.	17	40 <sup>43.1</sup>	11	4	.	.	.
<i>Sorbus torminalis</i>	.	.	.	.	.	43	70 <sup>42.0</sup>	47	29	18	.	.
<i>Viola riviniana</i>	.	.	.	.	33	17	10	67 <sup>32.1</sup>	54	36	.	50
<i>Poa nemoralis</i>	.	25	.	100	67	83	70	92 <sup>26.0</sup>	69	45	33	.
<i>Astragalus glycyphyllos</i>	33	50	.	.	33	39	50	50 <sup>20.4</sup>	8	.	.	.
<i>Convallaria majalis</i>	.	.	.	.	.	.	.	3	19 <sup>38.5</sup>	.	.	.
<i>Galium sylvaticum</i>	.	.	.	.	.	17	5	17	45 <sup>35.1</sup>	36	.	.
<i>Tilia cordata</i>	.	25	.	.	.	52	.	36	75 <sup>34.5</sup>	82	33	.
<i>Luzula luzuloides</i>	.	.	.	.	.	.	15	31	35 <sup>34.1</sup>	.	.	.
<i>Melampyrum pratense</i>	.	.	.	.	.	9	.	28	31 <sup>33.5</sup>	.	.	.
<i>Pulmonaria obscura</i>	.	.	.	.	.	30	10	44	70 <sup>31.9</sup>	73	67	.
<i>Fagus sylvatica</i>	.	.	.	.	.	13	35	33	62 <sup>30.9</sup>	73	33	.
<i>Hepatica nobilis</i>	.	.	.	.	67	83	65	78	90 <sup>27.3</sup>	91	67	.
<i>Lilium martagon</i>	.	.	.	.	.	.	.	14	41 <sup>25.0</sup>	36	67	.
<i>Galium odoratum</i>	.	.	.	.	100	87	100	100	100 <sup>21.8</sup>	100	100	100
<i>Stellaria holostea</i>	.	.	.	.	33	43	5	19	50 <sup>20.6</sup>	27	33	50
<i>Corydalis cava</i>	.	.	.	.	.	4	.	.	5	36 <sup>51.3</sup>	.	.
<i>Dentaria enneaphyllos</i>	.	.	.	.	.	.	.	.	1	27 <sup>49.3</sup>	.	.
<i>Polygonatum multiflorum</i>	.	.	.	.	.	.	.	6	15	55 <sup>47.9</sup>	33	.
<i>Acer pseudoplatanus</i>	33	75	.	.	67	.	5	11	20	100 <sup>47.5</sup>	33	.
<i>Ulmus glabra</i>	.	.	.	.	33	4	.	.	2	36 <sup>37.0</sup>	.	.
<i>Actaea spicata</i>	.	.	.	.	.	9	.	3	12	55 <sup>33.6</sup>	100	.
<i>Sambucus nigra</i>	.	.	.	.	.	.	.	.	45	30.8	.	100
<i>Geranium robertianum</i>	.	.	.	100	100	26	.	3	5	73 <sup>21.5</sup>	100	50
<i>Picea abies</i>	.	.	.	.	.	.	.	6	1	.	100 <sup>66.1</sup>	100
<i>Urtica dioica</i>	.	.	.	.	.	4	.	.	4	36	100 <sup>59.6</sup>	100
<i>Convolvulus arvensis</i>	100 <sup>62.8</sup>	75 <sup>43.5</sup>	50	.	.	.	.	.	.	.	.	.

Table 1 to be continued

Number of TWINSPAN category	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Taxon/Number of relevés	3	4	2	1	3	23	20	36	80	11	3	2
<i>Eryngium campestre</i>	100 <sup>55.3</sup>	75 <sup>37.4</sup>	—	100	—	—	—	—	—	—	—	—
<i>Festuca rupicola</i>	100 <sup>42.4</sup>	100 <sup>42.4</sup>	100	—	100	—	—	3	—	—	—	—
<i>Arrhenatherum elatius</i>	100 <sup>42.4</sup>	100 <sup>42.4</sup>	100	—	100	—	—	3	—	—	—	—
<i>Achillea millefolium</i> agg.	100 <sup>39.5</sup>	100 <sup>39.5</sup>	100	—	100	—	4	35	—	3	—	—
<i>Fragaria viridis</i>	100 <sup>39.4</sup>	100 <sup>39.4</sup>	100	—	100	—	33	4	—	5	—	—
<i>Securigera varia</i>	100 <sup>38.9</sup>	100 <sup>38.9</sup>	100	—	100	—	33	17	—	—	—	—
<i>Sorbus aria</i>	—	—	—	—	100 <sup>82.2</sup>	35 <sup>21.4</sup>	5	—	2	—	—	—
<i>Pyrethrum corymbosum</i>	—	—	—	—	33	91 <sup>46.9</sup>	85 <sup>42.5</sup>	58	—	25	—	—
<i>Silene nutans</i>	—	—	—	—	—	39 <sup>33.8</sup>	40 <sup>34.7</sup>	11	—	9	—	—
<i>Clinopodium vulgare</i>	67	50	50	—	100	83 <sup>28.6</sup>	70 <sup>20.8</sup>	22	—	—	—	—
<i>Fragaria vesca</i>	—	—	—	100	67	91 <sup>27.7</sup>	65	89 <sup>26.2</sup>	41	27	67	—
<i>Asarum europaeum</i>	—	—	—	—	—	—	—	3	51 <sup>25.7</sup>	82 <sup>49.6</sup>	33	50
<i>Acer campestre</i>	67	100	50	100	100	96	75	97 <sup>19.3</sup>	59	64	—	—
<i>Rosa species</i>	100	100	100	100	33	74 <sup>16.3</sup>	10	39	8	—	—	—
<i>Crataegus species</i>	100	75	100	100	100	87 <sup>15.4</sup>	40	86 <sup>14.9</sup>	40	18	—	—
<i>Cornus sanguinea</i> ssp. <i>sanguinea</i>	67	75	100	100	100	87 <sup>18.9</sup>	20	83 <sup>16.7</sup>	11	27	—	—

ability according to site types (Fig. 4), using Canoco for Windows 4.5 (TER BRAAK, ŠMILAUER 2002; LEPSŠ, ŠMILAUER 2003). All 188 relevés were included in the analysis. The data were centred, standardized in the direction of relevés and species, and logarithmically transformed. The transformation was made according to the formula

$$y' = \log(y + 1)$$

where:

$y'$  – quantitative variable of taxon cover entered into the DCA analysis,

$y$  – percentage cover value.

This transformation suppressed the significance of dominant taxa in the analysis.

A map of actual vegetation at the Mramor site was plotted on the basis of the 188 relevés (Fig. 5), which were classified by the Zürich-Montpellier System of Vegetation Classification (BRAUN-BLANQUET 1921). The occurrence and hierarchical level of vegetation unit in individual PNV segments reflect the variability of plant communities within PNV units. The relevés were classified according to works published by CHYTRÝ (1997), MORAVEC et al. (2000), CHYTRÝ et al. (2001), CHYTRÝ and TICHÝ (2003), KNOLLOVÁ and CHYTRÝ (2004). We also used an expert system

for the classification of relevés at [www.sci.muni.cz/botany/vegsci/](http://www.sci.muni.cz/botany/vegsci/) (since the expert system has not been published yet, we gave a major emphasis on previously published sources).

## RESULTS

Plant communities situated in the most exposed parts of southern slopes were separated by the first TWINSPAN division (Table 1). The potential natural vegetation classification in these areas was *Corneto-Quercetum (xerothermicum)* on Lithic Leptosols (Rendzic) (Forest Type 1X8, Site Type G). The corresponding set of 20 relevés taken at 1X8 contained the appropriate plant taxa, with high fidelity values (Table 2). The floristic separation of these relevés was enhanced by the fact that Site Type G was at the border of the studied ecological gradient. At the same time, these relevés were internally very heterogeneous, entirely filling Classes I–IV and partly filling Classes VI, VIII and IX in the TWINSPAN classification (Table 1, 3). In the DCA analysis, this set of relevés represented a significant part of the most important vegetation variability gradient (the horizontal axis in Fig. 4). This natural variability was markedly reduced in only a single unit (G, Forest Type 1X8). Relevés studied at



Table 2. The synoptic table of 188 relevés from Mramor that were divided according to site types (Fig. 3) into 7 groups (capital letters). Data on individual taxa are presented in A<sup>B</sup> form, where A is to express the taxon constancy – frequency of occurrence (%), index <sup>B</sup> represents the taxon fidelity (see Materials and Methods). Taxa are arranged by fidelity, classes are arranged by floristic similarity. Values accentuated in the table are fidelity values over 20 (light grey) and higher than 40 (dark grey). Only those taxa whose fidelity to at least one of site types is ≥ 10 are shown

Site type	C		F		G		A		D		E		B	
Taxon/Number of relevés	32		20		20		32		32		20		32	
<i>Trifolium alpestre</i>	31	53.0	.	---	.	---	.	---	.	---	.	---	.	---
<i>Carex montana</i>	44	48.5	.	---	10	---	6	---	.	---	5	---	.	---
<i>Silene nutans</i>	44	40.7	25	---	.	---	3	---	.	---	10	---	.	---
<i>Pyrethrum corymbosum</i>	84	34.4	75	---	20	---	38	---	28	---	35	---	19	---
<i>Veronica chamaedrys</i>	25	33.1	.	---	10	---	6	---	.	---	.	---	.	---
<i>Viola hirta</i>	44	32.3	20	---	35	---	3	---	.	---	5	---	.	---
<i>Campanula persicifolia</i>	28	29.6	20	---	.	---	6	---	3	---	.	---	.	---
<i>Hierochloa australis</i>	25	28.3	25	---	.	---	.	---	.	---	.	---	.	---
<i>Hylotelephium maximum</i>	.	---	30	48.6	.	---	3	---	.	---	.	---	.	---
<i>Sorbus aria</i>	6	---	40	45.5	.	---	9	---	.	---	5	---	.	---
<i>Viola mirabilis</i>	9	---	50	42.8	10	---	12	---	.	---	15	---	.	---
<i>Sesleria caerulea</i>	.	---	20	42.0	.	---	.	---	.	---	.	---	.	---
<i>Vincetoxicum hirundinaria</i>	12	---	40	41.7	.	---	16	---	.	---	.	---	.	---
<i>Cardamine impatiens</i>	.	---	20	38.1	.	---	3	---	.	---	.	---	.	---
<i>Campanula rapunculoides</i>	69	---	85	34.8	20	---	59	---	28	---	10	---	28	---
<i>Anthericum ramosum</i>	22	---	45	34.7	15	---	19	---	.	---	.	---	3	---
<i>Primula veris</i>	31	---	60	29.1	45	---	34	---	6	---	10	---	9	---
<i>Fraxinus excelsior</i>	3	---	.	---	70	73.7	6	---	3	---	.	---	.	---
<i>Festuca rupicola</i>	.	---	.	---	55	71.5	.	---	.	---	.	---	.	---
<i>Arrhenatherum elatius</i>	.	---	.	---	55	71.5	.	---	.	---	.	---	.	---
<i>Fragaria viridis</i>	3	---	5	---	55	65.5	.	---	.	---	.	---	.	---
<i>Prunus spinosa</i>	6	---	15	---	65	63.9	3	---	.	---	.	---	.	---
<i>Eryngium campestre</i>	.	---	.	---	35	56.2	.	---	.	---	.	---	.	---
<i>Convolvulus arvensis</i>	.	---	.	---	35	56.2	.	---	.	---	.	---	.	---
<i>Achillea millefolium</i> agg.	25	---	.	---	55	55.9	.	---	.	---	.	---	.	---
<i>Galium glaucum</i>	12	---	15	---	60	54.3	.	---	.	---	10	---	.	---
<i>Securigera varia</i>	3	---	20	---	50	52.8	.	---	.	---	.	---	.	---
<i>Helianthemum grandiflorum</i> ssp. <i>obscurum</i>	.	---	.	---	30	51.8	.	---	.	---	.	---	.	---
<i>Agrimonia eupatoria</i>	.	---	.	---	30	51.8	.	---	.	---	.	---	.	---
<i>Knautia arvensis</i>	.	---	.	---	30	51.8	.	---	.	---	.	---	.	---
<i>Dianthus carthusianorum</i>	.	---	.	---	25	47.1	.	---	.	---	.	---	.	---
<i>Sanguis orbaminor</i>	6	---	.	---	30	45.7	.	---	.	---	.	---	.	---
<i>Hypericum perforatum</i>	12	---	25	---	65	45.4	6	---	.	---	30	---	3	---
<i>Dactylis glomerata</i>	.	---	.	---	20	42.0	.	---	.	---	.	---	.	---
<i>Scabiosa ochroleuca</i>	.	---	.	---	20	42.0	.	---	.	---	.	---	.	---



Table 2 to be continued

Site type	C		F		G		A		D		E		B	
Taxon/Number of relevés	32		20		20		32		32		20		32	
<i>Lotus corniculatus</i>	.	---	.	---	20	42.0	.	---	.	---	.	---	.	---
<i>Prunus avium</i>	16	---	10	---	50	37.3	12	---	12	---	10	---	3	---
<i>Cornussanguinea</i> ssp. <i>sanguinea</i>	47	---	65	---	85	32.3	34	---	19	---	60	---	9	---
<i>Rosa</i> sp.	28	---	40	---	65	31.4	16	---	12	---	35	---	12	---
<i>Corydalis cava</i>	.	---	5	---	.	---	25	41.8	.	---	.	---	.	---
<i>Dentaria enneaphyllos</i>	.	---	.	---	.	---	12	33.0	.	---	.	---	.	---
<i>Mercurialis perennis</i>	31	---	60	---	5	---	84	31.5	69	---	.	---	72	---
<i>Alliaria petiolata</i>	22	---	65	---	40	---	69	29.7	31	---	.	---	12	---
<i>Ulmus glabra</i>	.	---	5	---	5	---	22	29.6	.	---	.	---	6	---
<i>Viola reichenbachiana</i>	.	---	.	---	.	---	3	---	75	66.8	.	---	31	---
<i>Aegopodium podagraria</i>	.	---	.	---	.	---	3	---	25	43.6	.	---	.	---
<i>Sanicula europaea</i>	6	---	10	---	.	---	19	---	53	39.5	5	---	25	---
<i>Lapsana communis</i>	.	---	.	---	.	---	.	---	19	36.7	.	---	3	---
<i>Scrophularia nodosa</i>	.	---	.	---	.	---	.	---	12	33.0	.	---	.	---
<i>Rubus idaeus</i>	.	---	.	---	.	---	3	---	16	32.7	.	---	.	---
<i>Urtica dioica</i>	.	---	5	---	.	---	12	---	25	32.4	.	---	.	---
<i>Mycelis muralis</i>	6	---	10	---	.	---	28	---	38	30.7	.	---	6	---
<i>Picea abies</i>	.	---	.	---	.	---	.	---	19	30.1	10	---	.	---
<i>Avenella flexuosa</i>	6	---	.	---	.	---	3	---	12	---	45	47.6	3	---
<i>Melampyrum pratense</i>	6	---	20	---	.	---	9	---	28	---	65	44.0	19	---
<i>Pinus sylvestris</i>	.	---	.	---	5	---	.	---	.	---	20	36.1	.	---
<i>Luzula luzuloides</i>	16	---	20	---	5	---	16	---	38	---	60	35.4	9	---
<i>Lilium martagon</i>	9	---	10	---	.	---	38	---	25	---	.	---	59	39.9
<i>Polygonatum multiflorum</i>	3	---	.	---	.	---	12	---	19	---	.	---	31	30.6
<i>Poa angustifolia</i>	41	30.5	.	---	60	53.1	.	---	.	---	.	---	.	---
<i>Anemone nemorosa</i>	47	29.4	.	---	.	---	22	---	16	---	.	---	47	29.4
<i>Clinopodium vulgare</i>	59	27.8	60	28.4	45	---	12	---	3	---	20	---	.	---
<i>Brachypodium pinnatum</i>	59	26.3	70	35.7	35	---	25	---	.	---	20	---	.	---
<i>Sorbus torminalis</i>	66	24.8	20	---	35	---	31	---	9	---	75	32.7	19	---
<i>Bupleurum falcatum</i>	41	23.2	50	33.0	20	---	9	---	.	---	10	---	.	---
<i>Melica nutans</i>	38	---	65	29.7	5	---	59	24.8	9	---	30	---	12	---
<i>Crataegus</i> sp.	53	---	75	---	90	24.6	62	---	38	---	90	24.6	16	---
<i>Tilia cordata</i>	25	---	75	---	5	---	84	28.7	38	---	40	---	78	23.5
<i>Asarum europaeum</i>	3	---	10	---	5	---	34	---	56	30.2	.	---	62	36.1
<i>Pulmonaria obscura</i>	25	---	30	---	20	---	56	---	75	24.5	35	---	75	24.5

Site Type G were phytocoenologically classified into several alliances – *Berberidion*, *Quercion pubescenti-petraeae* and *Carpinion* (Table 4).

In other STs and FTs, the relevés were also classified into several vegetation units (Table 4). However, the individual site types as a whole usually contained

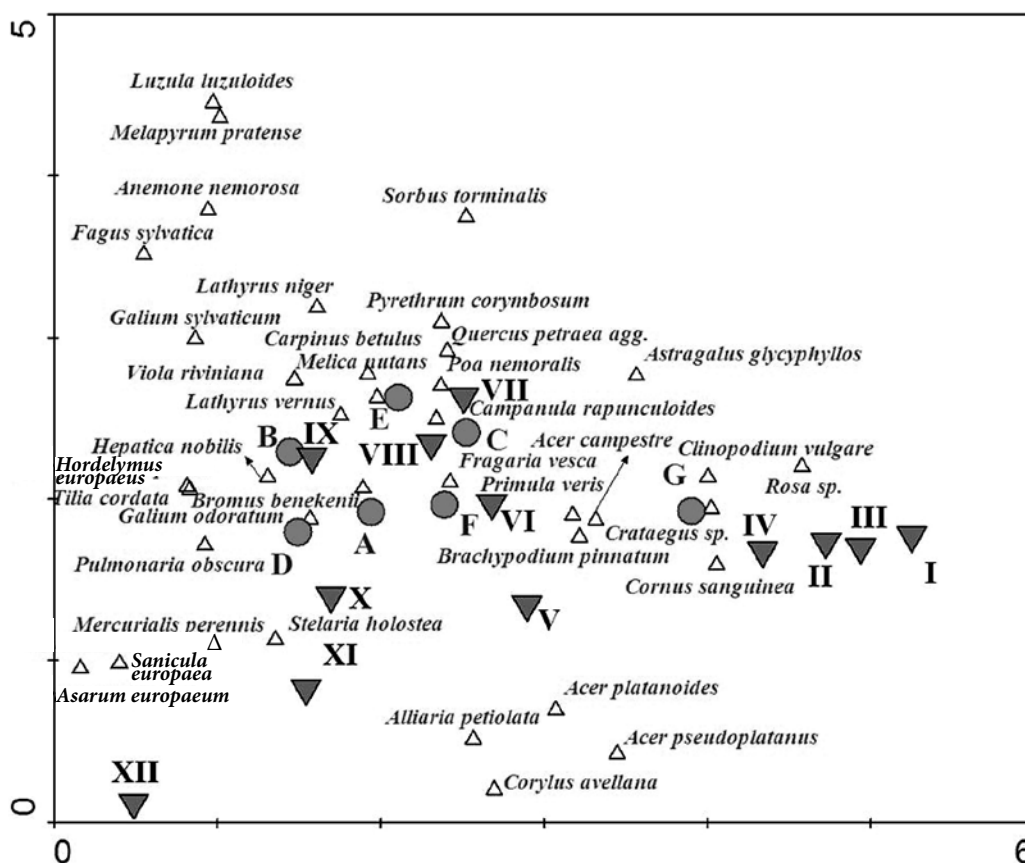


Fig. 4. Detrended correspondence analysis (DCA) of the set of 188 relevés from Mramor. Horizontal and vertical axes show the most significant directions of variability in the data set (non-canonical axes 1 and 2). The analysis results in passive projections (supplementary variable) of the centres of relevés classified by site types (letters A–G) and by TWINSpan classes (Roman numerals I–XII) (see Material and Methods). Taxa whose weight in the analysis was  $\geq 6\%$  are shown

taxa with high fidelity (Table 2). The floristically most poorly separated set was that belonging to Site Type B, with only a very few high-fidelity taxa. Neverthe-

less, the high internal variability was not a reason for the worse separation of this set; on the contrary, relevés in this unit were very similar. From the set of

Table 3. Contingency table between relevé classification according to the potential natural vegetation system (ZELENKOVÁ 2000) and relevé categorization within TWINSpan categories

	Unit of potential natural vegetation (forest type)														Total
	1A9	1C2	1W2	1X2	1X8	2A8	2A9	2B9	2C8	2D7	2H5	2I4	2W1	2W3	
I					3										3
II					4										4
III					2										2
IV					1										1
V				3											3
VI	3		1	10	3				6						23
VII		1	14						4			1			20
VIII	6		4	1	6						5	12		2	36
IX	7		2	6	1	7	1	2		18	3	7	20	6	80
X							8			1			2		11
XI										3					3
XII										2					2
Total	16	1	21	20	20	7	9	2	10	24	8	20	22	8	188

Table 4. The occurrence of plant communities (see Materials and Methods) according to site types and forest types in the Mramor locality (a total of 188 relevés)

Site type	Forest type	Unit of vegetation classification	No. of relevés
F	1X2	<i>Corno-quercetum</i>	11
		<i>Melampyro nemorosi-Carpinetum typicum</i>	7
		<i>Melampyro nemorosi-Carpinetum primuletosum veris</i>	2
G	1X8	<i>Berberidion</i>	10
		<i>Corno-Quercetum</i>	4
		<i>Melampyro nemorosi-Carpinetum primuletosum veris</i>	4
		<i>Melampyro nemorosi-Carpinetum typicum</i>	2
C	1C2	<i>Melampyro nemorosi-Carpinetum typicum</i>	1
	1W2	<i>Melampyro nemorosi-Carpinetum typicum</i>	20
		<i>Corno-Quercetum</i>	1
	2C8	<i>Melampyro nemorosi-Carpinetum typicum</i>	4
		<i>Corno-Quercetum</i>	6
B	2W1	<i>Melampyro nemorosi-Carpinetum typicum</i>	15
		<i>Cephalanthero-Fagetum</i>	7
	2W3	<i>Melampyro nemorosi-Carpinetum typicum</i>	8
	2B9	<i>Melampyro nemorosi-Carpinetum typicum</i>	2
H	2H5	<i>Melampyro nemorosi-Carpinetum typicum</i>	8
	2D7	<i>Melampyro nemorosi-Carpinetum typicum</i>	24
A	1A9	<i>Melampyro nemorosi-Carpinetum typicum</i>	9
		<i>Melampyro nemorosi-Carpinetum primuletosum veris</i>	6
		<i>Corno-Quercetum</i>	1
	2A8	<i>Melampyro nemorosi-Carpinetum typicum</i>	6
		<i>Aceri-Carpinetum</i>	1
	2A9	<i>Aceri-Carpinetum</i>	9
E	2I4	<i>Melampyro nemorosi-Carpinetum luzuletosum</i>	10
		<i>Melampyro nemorosi-Carpinetum typicum</i>	10

32 relevés belonging to Site Type B (LTs 2B9, 2W1, 2W3), 28 relevés were classified in Class IX according to the TWINSpan classification (Table 1). Rather, the similarity of the site-relevant relevés to relevés from other site types was responsible for the poor separation. According to the TWINSpan classification and DCA analysis, the most similar site type was D, followed by E and A. These site types are ecologically hardly distinctive, and the relevant forest types differed only little in floristic terms.

The relation between the species composition of relevés and their classification according to the PNV system is shown in Table 5. Based on FPF values, it was clear that some relevés could possibly be

reclassified. Some of the forest types were difficult to specify floristically, and total accuracy was only 46.3%. The lowest user's accuracy values were in FTs 1C2, 2B9 and 2W3, while the lowest producer's accuracy values were in FTs 2W1 and 2D7. This was primarily due to the considerable overlay of these latter FTs with FT 2B9. Pursuant to the FPF values it was not possible to mutually differentiate the FTs 1C2 and 1W2. On the other hand, FTs 2H5 and 2I4, with a higher presence of acidophilous taxa, were well differentiated.

The map of the actual Mramor vegetation is shown in Fig. 5. A large part of the territory is characterized by communities of the *Melampyro nemorosi-Carpi-*

Table 5. Contingency table between relevé classification according to the potential natural vegetation system (ZELENKOVÁ 2000) and their reclassification according to the Frequency-Positive Fidelity Index (FPFI)

	Classification of relevés to PNV units according to ZELEŇKOVÁ (2000)														User's accuracy (%)	
	1A9	1C2	1W2	1X2	1X8	2A8	2A9	2B9	2C8	2D7	2H5	2I4	2W1	2W3		TOTAL
Reclassification of relevés to PNV units according to FPFI	1A9	6		6	1				1						14	42.9
	1C2		1	4	1										6	16.7
	1W2			9					3						12	75.0
	1X2				6										6	100.0
	1X8					10									10	100.0
	2A8	3		1	4		5			1					14	35.7
	2A9							3							3	100.0
	2B9	6		1	3	1	2	2		11			14	1	47	4.3
	2C8			1		2			5						8	62.5
	2D7									6					6	100.0
	2H5									1	6				7	85.7
	2I4					1						16			17	94.1
	2W1												5		8	62.5
	2W3	1		5	1	4			1	2	2	4	3	7	30	23.3
TOTAL	16	1	21	20	20	7	9	2	10	24	8	20	22	8	188	
Producer's accuracy (%)	37.5	100.0	42.9	30.0	50.0	71.4	33.3	100.0	50.0	25.0	75.0	80.0	22.7	87.5		46.3

Reclassification of relevés to PNV units according to FPFI

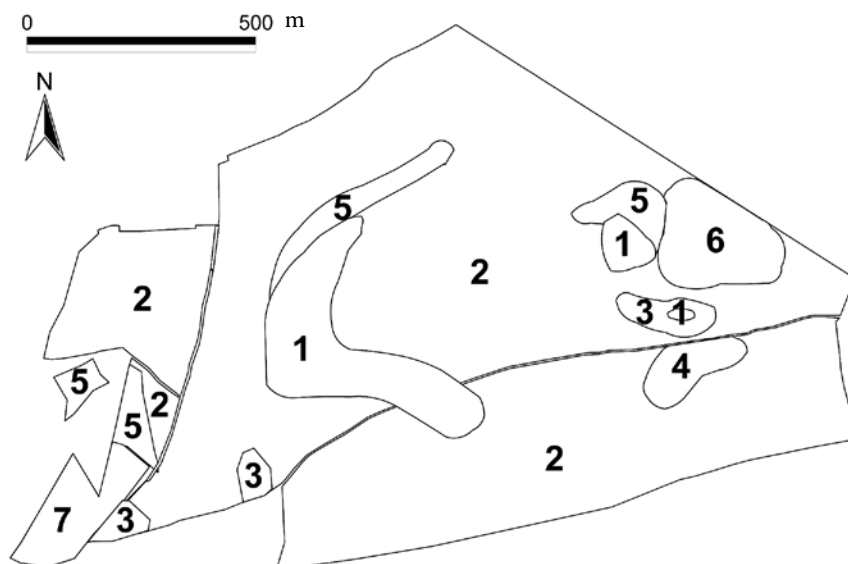


Fig. 5. The map of the actual Mramor vegetation made on the basis of phytocoenological classification of 188 relevés (see Material and Methods). 1 – *Corno-quercetum* (Máthé et Kovács 1962), 2 – *Melampyro nemorosi-Carpinetum typicum* (Passarge 1962), 3 – *Melampyro nemorosi-Carpinetum primuletosum veris* (Klika 1942, Neuhäusl in Moravec et al. 1982), 4 – *Melampyro nemorosi-Carpinetum luzuletosum* (Mikyška 1956, Neuhäusl in Moravec et al. 1982), 5 – *Aceri-Carpinetum* (Klika 1941), 6 – *Cephalanthero-Fagetum* (Oberdorfer 1957), 7 – mosaic of the communities of *Quercion pubescenti-petraeae* (Braun-Blanquet 1932 nom. mut. propos.) and *Berberidion* (Braun-Blanquet 1950) alliances. The territory is divided by three communications

*netum typicum* subassociation, which occurred in nearly all PNV units (Forest Types 1X2, 1X8, 1C2, 1W2, 2C8, 2W1, 2W3, 2B9, 2H5, 2D7, 1A9, 2A8, 2I4 – see Fig. 2, Table 4). Communities belonging to the *Corno-Quercetum* association showed a similarly broad distribution.

## DISCUSSION

### Actual vegetation based on the map of potential natural vegetation

The stratification of this locality according to units from the PNV map only partly represents the main trends in vegetation variability. In particular, at ecologically extreme sites where the PNV system of ANONYMOUS (1971/1976) distinguishes only one unit (e.g. Forest Type 1X8), there is insufficient coverage of the actual vegetation variability, which is highest precisely at these areas. In addition to the communities belonging to the alliances *Berberidion*, *Quercion pubescenti-petraeae* and *Carpinion*, there are, for example, communities of the *Festucion valesiace* alliance or communities of the *Trifolio-Geranietae sanguinei* class found in the Bohemian Karst at Site Type 1X8 (e.g. ŠAMONIL 2005). Thus, the question is whether these com-

munities were not recorded at the Mramor locality due to their absence or due to the insufficient site coverage by the relevés. In contrast, at areas where there is a relatively limited ecological gradient, the PNV classification distinguishes a number of units. Variables according to which the gradient is divided (e.g. the production of stands) do not reflect the vegetation species composition. These places were relatively “oversampled” with respect to the actual level of vegetation variability (altogether, 116 relevés corresponded to the community of *Melampyro nemorosi-Carpinetum typicum* subassociation). The stratification strategy used would have likely achieved better results in a territory with less variable ecological gradients or concentrating on sites at the edges of these gradients.

### Study of the potential natural vegetation

The significance of our results for the study of PNV is limited due to the fact that it only deals with the vegetation species composition, not taking into consideration other variables according to which the PNV is classified (production, soil conditions; ANONYMOUS 1971/1976). However, the vegetation variability clearly shows possible limitations of this system. The variability in actual “natural” vegetation changes unevenly across the PNV system. In

ecologically distinctive localities, e.g. rock steppes, the natural variability of plant communities is higher within the same forest type than it is at less distinctive sites even covering several edaphic categories and forest altitudinal vegetation zones. It can be expected that similarly heterogeneous development – but in an “ecologically” different direction – will also be exhibited by the development of soil conditions and production of phytocoenoses (see e.g. HOLUŠA et al. 2005; [www.pralesy.cz/](http://www.pralesy.cz/)). Due to the high variability of natural plant communities, the requirements for forest type homogeneity in ecologically distinctive localities might lead to the definition of additional PNV units; at an ecologically less distinctive site, production or soil conditions might lead to the same. By intersection of these three layers, a range of new, seemingly homogeneous units would result, but that would feature numerous and unacceptably broad mutual transitions. Thus, the observed development of vegetation variability in units of the system is also a consequence of its primarily applied function, which is landscape classification for use in future planning. The classification of extreme sites with no possible economic (forestry) use was deliberately simplified during the construction of the ANONYMOUS (1971/1976) PNV system. These extreme sites also highlight a failure of some basic mechanisms of the whole system construction (vegetation zonality, etc.). We consider the applied use of the system of PNV in (forest) management planning to be the main reason for its future existence and the main concern in its further development.

The demarcation of additional PNV units by dividing the existing ones would be rather counter-productive with respect to the focus of the system. Instead, the classification should be simplified and more lucid. In our opinion, the need for a more accurate characterization of units which are homogeneous in terms of production, site and phytocoenosis is overestimated. Such a step would neither reflect the characteristics of actual ecosystems nor be necessary for the application of a PNV system in forest management planning and nature conservation. A number of other systems do not assume homogeneity in the units used (HAASE 1989; BUČEK, LACINA 2002), but rather specify an acceptable measure of heterogeneity and clearly declare which ecosystem components are of key significance in the classification. In our opinion, a suitable hierarchical unit for the application of the system in the landscape and for further development is the forest type series (FTS) (or an analogous unit like ST which merge FTs according to their

real ecological affinity). This aggregated unit can be more objectively defined in the landscape, and is justified with respect to both forest management and practical nature conservation.

The criterion of objectivity in landscape classification should be of key importance for the future development of the system. The structure of individual relevés, as well as the resulting map of actual vegetation in the Mramor locality, suggests that the differentiation of actual plant communities is lower than in the PNV, even when considering aggregated PNV units (FTS etc.). In light of the procedure of deriving the PNV map from actual vegetation, the opposite could rather have been anticipated. The question thus arises whether the PNV map was created objectively, and whether the PNV mapping criteria were realistic and accurate. Potential geobiocoenoses are differentiated at a higher spatial level than those actually present. Compared with the development of actual vegetation, less variable factors should be taken into account in the construction of potential natural vegetation (for example, the important effect of historic and current management is absent). The strongest competing tree species in the PNV types also have a wider ecological rank than the dominants of the actual or reconstructed communities (see e.g. JANSSEN, SIEBERT 1991; HÄRDITLE 1995; CHYTRÝ 1998). Criteria used in the PNV classification differentiate actual ecological environmental gradients; but, then there arises a question how these criteria reflect the composition of potential plant communities. In just one example – how can Forest Types 2B9, 2W1 and 2W3 be mutually differentiated? With respect to permanent ecological site characteristics, these Forest Types considerably overlap (ŠAMONIL 2007a,b) and the “differential” taxa as mentioned in the name of these FTs are almost universally present in the locality (*Galium odoratum*, *Mercurialis perennis*, *Alliaria petiolata*, see Tables 1, 2). In future, the applicability of individual classification criteria should be tested.

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## Variabilita rostlinných společenstev v rámci jednotek potenciální vegetace: případová studie z Českého krasu

**ABSTRAKT:** Na lokalitě Mramor byla na podkladu mapy potenciální přirozené vegetace (PNV) studována vegetace aktuální. S použitím stratifikovaného náhodného výběru bylo na ploše 106,4 ha zaznamenáno 188 fytocenologických snímků. Porovnán byl průběh variability vegetace v rámci celé lokality s variabilitou uvnitř vymezených jednotek PNV. Stratifikace lokality podle jednotek PNV jen částečně pokrývala hlavní směry variability vegetace. Na ekologicky vyhraněných stanovištích vedla stratifikace k nedostatečnému pokrytí reálné variability. Naopak v místech, kde byl ekologický gradient relativně krátký, bylo území „přesnímkováno“. Variabilita rostlinných společenstev v rámci jednotek potenciální vegetace byla vysoká. Výsledky studie naznačují, že potřeba reálného vymezení produkčně, stanovištně a fytocenologicky homogenních jednotek PNV může být přeceněna. Tato představa neodpovídá vlastnostem skutečných ekosystémů a není ani nezbytná pro uplatnění systému PNV v lesnickém plánování a v praxi ochrany přírody. Vhodnou jednotkou pro aplikaci systému v krajině a jeho rozvoj se zdá být například soubor lesních typů.

**Klíčová slova:** klasifikace vegetace; variabilita vegetace; potenciální přírodní vegetace; dubové lesy; Český kras

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