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Seasonal variation in *Melampyrum nemorosum*

Sezónní variabilita druhu *Melampyrum nemorosum*

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Dedicated to the memory of Josef Holub for his support of young botanists

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Variation of *Melampyrum nemorosum* was studied. Eleven morphological characters usually described as seasonal and considered to be significant for infraspecific division of the species were measured. It was found that some of the characters change markedly during the flowering period in the same population. The number of internodes has been believed to be the most important character, although it is one of the most variable. The present study does not support the traditional distinction of three seasonal taxa in *M. nemorosum*, as only two population groups could have been distinguished. The early-flowering populations occur in meadows and flower in May and in the first half of June. The late-flowering populations occur predominantly in forests and shrubs and flower from the beginning of June until September. These two groups differ primarily in the total number and length of internodes. Differences in the number of branches and that of flowering branches are frequent but less constant across different biotopes. No differences in the number of intercalary internodes between the both population groups were found. Seasonal types of *M. nemorosum* can be taxonomically treated at the level of variety. The variety *nemorosum* should be reserved for late populations of the species. The epitype of the name of this variety is established, because the lectotype of *M. nemorosum* is a fragmentary plant which is impossible to determine with certainty. For nomenclatural reasons, the early populations are described in the present papers as a new var. *praecox*.

Keywords: *Melampyrum nemorosum*, *Scrophulariaceae*, seasonal variation, multivariate analysis, morphometrics, taxonomy, nomenclature, Central Europe

Introduction

The genus *Melampyrum* is highly variable in terms of morphological characters. An important aspect of variation of many species is the so-called seasonal variation. This terms refers to the situation when different populations of one species flower in different periods of the year. Seasonal variation occurs in many genera of several families of flowering plants. Many species exhibiting seasonal variation are hemiparasitic annuals of the family *Scrophulariaceae*.

The phenomenon was first described in the 19th century as "seasonal dimorphism" (Wettstein 1895, 1899, 1900), characterized by two different variants occurring in a single species, distinguished by so-called seasonal characters. In groups exhibiting this type of variation, the most important seasonal characters are number of internodes and that of intercalary internodes (i. e. internodes between the uppermost branches and the lowest flowers of the terminal inflorescence), number of branches and that of flowering branches, leaf and bract width and length, and flowering period. Later, it was found that many species produce more than two variants and occurrence of some of these variants is related to specific habitat factors (Sterneck 1901, Ronniger 1911, Soó 1926-1927). Therefore, the phenomenon is now called "pseudoseasonal polymorphism" and the individual variants are called "ecotypic variants" or "ecotypes". The most important ecotypes are aestival (early-flowering, with few internodes, one intercalary internode, and few short branches), autumnal (late-flowering, with many internodes, some intercalary internode, and many flowering branches), monticol or montane (flowering in the middle of the season, mainly in the mountains, morphologically intermediate between the former two), and segetal (in cornfields, morphologically between the aestival and autumnal types). Four basic hypotheses have been formulated to explain the origin of seasonal variation, but none of them seems to be satisfactory. Mowing of meadows may be a reason for the development of early-flowering variants (Wettstein 1895, 1900, Sterneck 1901, Ronniger 1911). These variants must flower and set seed before the mowing in spring. Another hypothesis explained the origin of early-flowering variants by the influence of short growing period during the Ice Age, i.e. without the influence of humans (Schwarz 1935, Smejkal 1963, Bolliger 1989). Another opinion suggested that the ecotypes are mere adaptations to the habitat conditions (Heinricher 1898, 1902, 1903, Semler 1904). However, it is highly probable that ecotypic variation is caused by the interplay of numerous abiotic and biotic factors (Soó 1926–1927, Yeo 1968, Karlsson 1974, 1976). Recently, this opinion has been largely advocated (Zopfi 1991, 1993a, 1993b). Zopfi (1995) hypothesized that the differentiation of basic ecotypes in *Rhinanthus glacialis* occurred during the prehistoric period and was conditioned by differences in edaphic factors and climate in different altitudes. However, he assumed that the originating of present ecotypes is, in historical terms, a very young process which is responsible for differentiation at a finer scale and coincides with the existence of human-made grassland habitats.

So far, most authors studying intraspecific taxonomy in *Melampyrum* focused directly on pseudoseasonal variation within the genus. The pseudoseasonal variants were traditionally evaluated as subspecies. Numerous variants have been described in various species of *Melampyrum*. However, new variants were often described in rather schematic way on the basis of individual herbarium specimes and did not reflect natural variation within the given species.

Since the work of Ronniger (1911), three seasonal taxa have been traditionally distinguished in *M. nemorosum* according to the theory of seasonal variability (Soó 1926–1927, Soó & Webb 1972, Garcke 1972, Hartl 1974, Rothmaler 1994), i. e. the aestival type *Melampyrum nemorosum* subsp. *moravicum* H. Braun, autumnal type *Melampyrum nemorosum* subsp. *nemorosum*, and montane type *M. nemorosum* subsp. *silesiacum* Ronn. All three taxa were reported from the Czech Republic (Braun 1884, Ronniger 1911, Domin 1936, Dostál 1948–1950, 1982, 1989). The aim of the present study was to describe and evaluate overall intraspecific variation of *M. nemorosum* with focus on Central Europe. Special attention was paid to the "seasonal variation" in order to determine whether and how many "seasonal" taxa can be distinguished. The selection of localities followed this purpose.

Material and methods

Collation of data

The terms “population” and “population sample” are used to reflect that some populations were studied repeatedly using several population samples. About 2000 plants of *Melampyrum nemorosum* were studied in 74 population samples (consisting of 20–30 plants each). The samples were taken from 35 populations from the Czech Republic, 7 from Slovakia, 1 from Austria and 1 from Sweden (see Appendix 1 for the list of localities in which the samples were collected). Seven populations were studied repeatedly over a growing period or in the course of different growing periods. One population cultivated from seeds was also included. The voucher specimens are deposited in the author’s private herbarium and in PRC.

Eleven characters usually described as seasonal and considered to be significant in the infraspecific division of the species were measured in each plant: stem height (**S**, in cm) and the number of internodes (**I**) – both between the node with cotyledones and the node with the lowest flowers of the terminal inflorescence; number of intercalary internodes (**II**) – between the uppermost branches and the lowermost flowers; number of branches – respective branch pairs (**B**); flowering branches – respective flowering branch pairs (**FB**), leaf width (**LW**), leaf length (**LL**) and distance of the widest part of leaf from leaf base (**LD**) – all measuered on a leaf from the central part of stem (in mm); bract width (**BW**), length (**BL**) and distance of the widest part of bract from its base (**BD**) – all measured on the lowest bract (in mm).

Herbarium material from the following collections was studied: BRA, BRNM, BRNU, CB, CHOM, HR, LI, LIM, LIT, MJ, NJM, OMP, PRC, PR, SAV, SLO, WU, ZMT, private collections of Václav Chán, Rudolf Kurka, Zdeněk Skála, Jiří Sladký, and particularly that of Vojtěch Žíla.

Statistical analysis

Data were transformed to achieve normality. Logarithmic transformation ($\log_{10}$) was used for characters related to the size (S, LW, LL, LD, BW, BL, BD), and root transformation for the others (I, II, B, FB). Missing measurements (particularly the size of defoliated leaves) were omitted from the respective analyses, except of RDA where they were substituted by the mean value of the character calculated for the respective population sample. Substituted values never represented more than 25% of the population sample.

The change in observed characters in the course of the vegetation period was evaluated by t-test and RDA (redundancy analysis; Lepš 1996, ter Braak & Prentice 1988). Time was used as an explanatory variable, coded on the basis of calendar date. The month was expressed by hundreds (May 0, June 100, July 200, August 300, September 400) and the days were transformed into the decimal system so that the progress was fluent. In the case of repeated observations carried out in the same population in two years, the particular years were used as covariables. Correlation matrices of the characters were used for computation and the results were tested by using Monte Carlo permutation test. RDA analyses were carried out using CANOCO 3.12 (ter Braak 1988), CANODRAW 3.0 (Šmilauer 1992), and CANOPOST 1.0 (ter Braak & Šmilauer 1998) software.

The principal component analysis performed on the character correlation matrix was used as the ordination method for individual population samples characterized by the mean value of the observed characters. PCA was carried out using the SYN-TAX 5.02 package (Podani 1994).

Linear discrimination analysis was used to test the separation of *M. nemorosum* populations; STATISTICA 5 package was used.

Results

Variation in studied characters of one population during the flowering period

Repeated measurements of the same populations during a single growing period showed a remarkable change in some of the measured characters. Plants with "earlier characters" started to flower early and as the vegetation period proceeded, "later" plants flowered and gradually prevailed changing the mean character value of the whole population. Such pattern of development was observed in 6 localities.

Four localities were observed repeatedly for 2–3 years and in another locality, two populations from different habitats (hazel scrub vs. grassy balk) were also observed separately. Of the resulting 14 cases observed in total, an increase in average number of internodes over the flowering period was recorded, in 13 cases being statistically significant ($p < 0.05$, Table 1, Fig. 1). The most distinct change was found in the number of internodes. Internode number usually varied around 4, more rarely up to 6 and exceptionally exceeded 7. Mean internode number usually increased by one during the flowering period. In particular plants, an increase by two internodes was also exceptionally recorded.

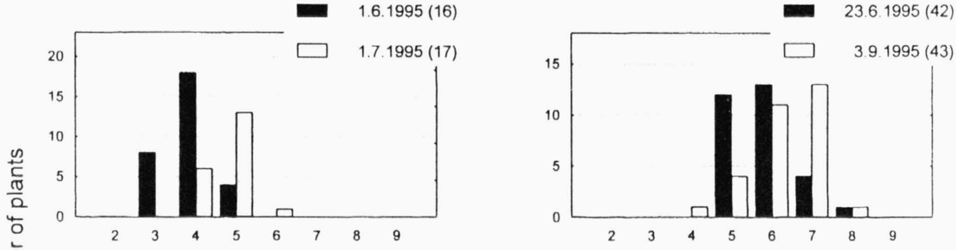
Other characters changed much less. The number of intercalary internodes changed only slightly compared to the total number of internodes and the increase was statistically significant in 3 cases only (Table 1). Number of intercalary internodes in all populations ranged between 0–4, the most common number being 1 or 2.

The mean number of branches increased significantly in 4 cases and decreased in 1 case during the flowering period. The range (expressed as a difference between minimum and maximum number) of branches in members of a single population is usually 4, but the values up to 6 were also recorded. The mean number of flowering branches increased significantly in 4 cases and decreased in 2 cases in the course of the flowering period. The range in the number of flowering branches may exceed 6 and is bigger in populations with a higher number of internodes (i. e. the late ones). The stem length elongated in 12 cases, and the difference was statistically significant in 7 of them. No trends over time were found in the leaf and bract dimensions.

The pattern of changes in *M. nemorosum* is documented by RDA analysis performed on one of the populations (Fig. 2). Although the time (1st canonical axis) explained less than 10% of the total variation in data set, Monte Carlo permutation test was highly significant in almost all the cases studied. This is because in individual populations only the number of internodes is closely correlated with time (proportion of the variation explained usually ranges between 10–25%), while other characters exhibit variation not correlated with time. The within-populational variation uncorrelated with time is, however, rather unimportant in terms of the studied problem.

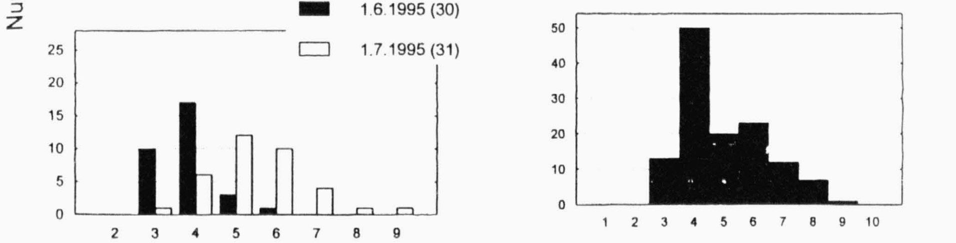
Table 1. – Changes of number of internodes and interkalary internodes in the course of the flowering period in selected populations. Significant differences are shown in bold.

Locality (sample no.)	Number of internodes				Number of interkalary internodes			
	Beginning of flowering	End of flowering	F	p	Beginning of flowering	End of flowering	F	p
Přední louky 1994 (3–4)	3.0 ± 0.52	4.3 ± 1.32	28.26	< **0.001**	1.2 ± 0.48	1.4 ± 0.82	1.03	0.315
Přední louky 1995 (5–6)	3.3 ± 0.83	4.0 ± 0.77	13.53	< **0.001**	1.4 ± 0.72	1.5 ± 0.65	1.40	0.240
Přední louky 1996 (7–8)	2.9 ± 0.63	3.5 ± 0.73	13.12	**0.001**	1.2 ± 0.43	1.2 ± 0.57	0.02	0.900
Porážky 1994 (14–15)	3.9 ± 0.52	4.7 ± 1.18	10.24	**0.002**	1.6 ± 0.67	1.6 ± 0.81	0.09	0.763
Porážky 1995 (16–17)	3.9 ± 0.63	4.7 ± 0.55	25.40	< **0.001**	1.6 ± 0.68	1.4 ± 0.68	1.15	0.288
Porážky 1996 (18–19)	3.7 ± 0.55	4.8 ± 1.01	26.16	< **0.001**	1.2 ± 0.50	1.7 ± 0.75	5.68	**0.021**
Závišín 1994 (40–41)	5.8 ± 0.75	6.0 ± 0.76	1.04	0.313	1.5 ± 0.51	1.4 ± 0.49	1.67	0.200
Závišín 1995 (42–43)	5.8 ± 0.81	6.3 ± 0.88	5.14	**0.027**	1.2 ± 0.43	1.4 ± 0.49	1.25	0.267
Závišín 1996 (44–45)	5.5 ± 0.76	6.2 ± 0.77	7.20	**0.011**	1.5 ± 0.61	1.5 ± 0.51	0.01	0.947
Suchovská doubrava (65–66)	6.7 ± 1.11	7.4 ± 0.68	5.71	**0.021**	1.8 ± 0.59	1.7 ± 0.73	0.70	0.406
Kazivec 1995 (30–31)	3.8 ± 0.73	5.5 ± 1.25	44.36	< **0.001**	1.1 ± 0.34	1.1 ± 0.24	1.01	0.318
Kazivec 1996 (32–33)	4.0 ± 0.37	6.5 ± 1.04	170.08	< **0.001**	1.0 ± 0.18	1.6 ± 0.56	32.64	< **0.001**
Studená – hazel scrub (57–59)	5.9 ± 0.64	6.7 ± 0.70	12.58	**0.001**	1.1 ± 0.35	1.4 ± 0.63	2.00	0.169
Studená – grassy balk (58–60)	5.5 ± 0.92	6.3 ± 0.72	7.19	**0.012**	1.2 ± 0.41	1.8 ± 0.56	11.40	**0.002**



a) Porážky (early population)

b) Závišín (late population)



c) Kazivec (mixed population)

d) Kazivec (30-33)

Fig. 1. – Changes in the frequency distribution of internodes in the course of the flowering period shown for selected populations (a–c). Frequency distribution of the number of internodes in the population sample no. 30–33 from the locality Kazivec (d).

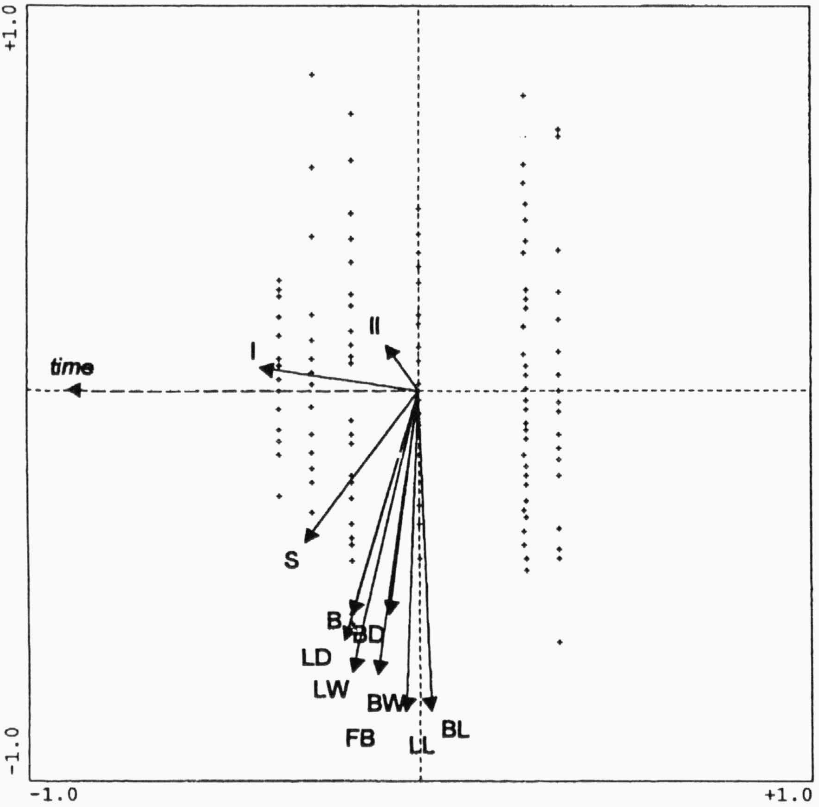


Fig. 2. – RDA analysis of population samples recorded at the beginning and the end of the flowering period in the locality Přední louky. Explanatory character: time, covariables: years. Total variation explained by the first canonical axis: 3.6% (I – 16.2%, S – 8.7%, LD – 3.5%, LW – 2.9%, B – 2.9%, FB – 1.2%, BW – 1.1%, II – 0.7%, BD – 0.6%, LL – 0.1%, BL – 0.1%), Monte Carlo permutation test: F = 8.61, p <0.01. See Methods and Table 2 for character codes.

Correlation between the characters studied

The strongest correlation (Pearson correlation coefficients, $\alpha < 0.01$) was found between the number of internodes and the number of branches (r = 0.67), number of branches and that of flowering branches (r = 0.72) and between various leaf and bract dimensions (LW–LD: r = 0.67, LW–LL: r = 0.75, LW–BW: r = 0.67, LD–LL: r = 0.74, LL–BW: r = 0.60, LL–BL: r = 0.69, BW–BL: r = 0.66). The pattern of correlation between characters did not change in the course of the flowering period.

Analysis of among-population variation

Given the character of variation in observed characters, PCA was used to analyse the relationship among the population samples. The first 3 axes explained 87.6% of total variation, of which the first axis accounted for 58.3%, the second one for 21.1%, and the third

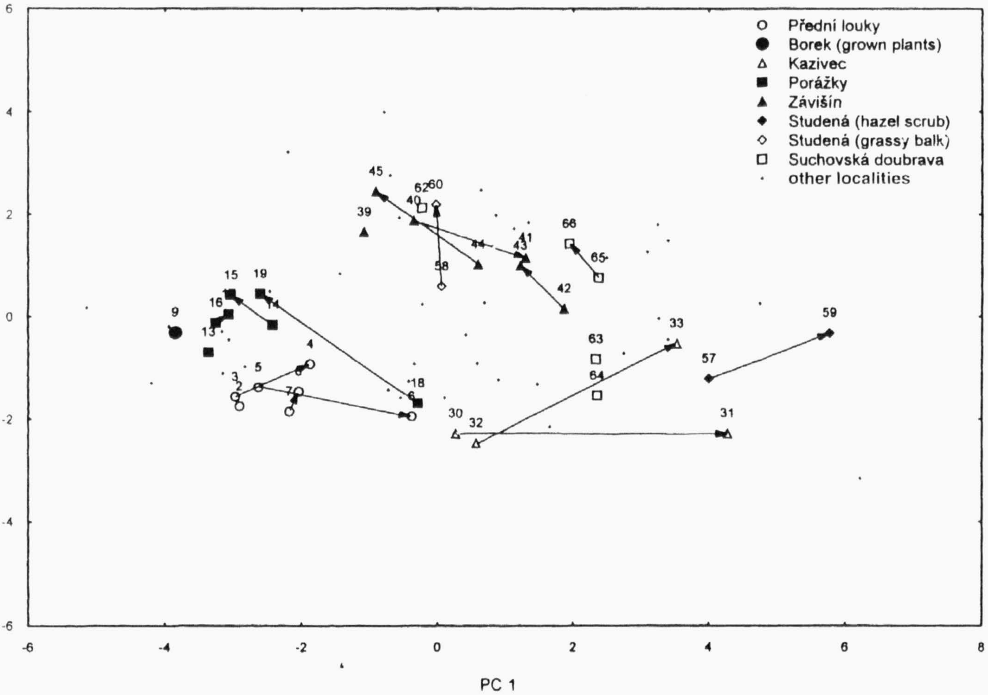


Fig. 3. – Principal component analysis of population samples of *Melampyrum nemorosum*. Particular localities are indicated by using different symbols. Arrows point from the position of the sample at beginning of the flowering season to that at its end. See text for explanation.

axis for 8.2%. If the origin of samples and direction of their development over time are taken into account, two population groups can be distinguished represented by two arms of a "horse-shoe" (Fig. 3). A population can be found at different positions during the growing season but always within one of the arms. The described pattern reflects well the field experience. Populations, which begin to flower very early (during May), usually in meadows, are situated within one horse-shoe arm while the other arm is formed predominantly by scrub and forest populations which begin to flower later (during June). Other characters were correlated with the first PCA axis, with an exception of the number of intercalary internodes, which was correlated with the second and third axes. The number of internodes and bract length was more closely correlated with the second axis (Fig. 4a, b).

The above results imply that two groups of populations can be distinguished in the material studied. They can be termed as "early" and "late" ones. However, it is difficult to draw a distinct line between these two groups since there is no apparent gap between both. The solution can be indicated by using population samples from the locality Kazivec (no. 30–33, see Appendix 1) which represent a transition between early and late populations because plants of both types grow there together. This is obvious from a very high range of values of some characters (compared to other populations), particularly of the number of internodes (compare Fig. 1c, d with 1a, b; Table 1), number of branches and leaf width recorded in the locality during the flowering period. In addition, this population grows at the

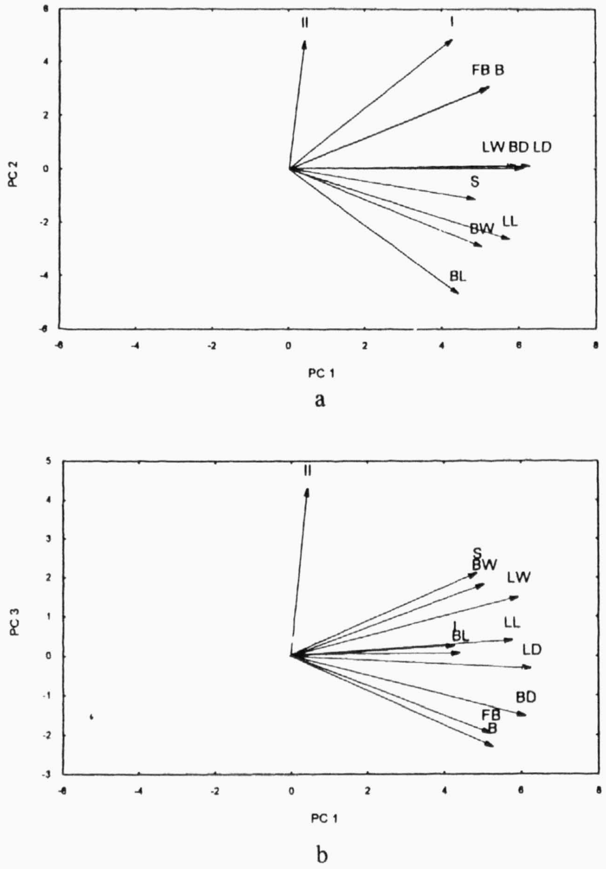


Fig. 4. – Character vector plot from principal component analysis: PC1, PC2 (a), PC1, PC3 (b). See Methods and Table 2 for character codes.

forest edge, in contact with early populations of the meadows and late populations of nearby oak forest. The Kazivec population starts to flower at the same time as the early populations do. However, when flowering is over in the early populations, further plants still start to flower in Kazivec. Consequently, the first measurements in the season are close to early populations, whereas the samples from the later period clearly belong to the late populations (Fig. 3). To avoid dividing population samples from one locality between both groups, the Kazivec locality is ranked to the late populations (Fig. 5).

Discriminant analysis

Differences between both population groups were investigated by using the discriminant analysis. The distribution of individual plants along the canonical discrimination axis (Fig. 6) supports, despite some overlap, the suggested division of the studied material into two groups. Canonical correlation coefficient (expressing the measure of relation between discriminating function and the distribution of objects into groups) equals 0.809. The total ca-

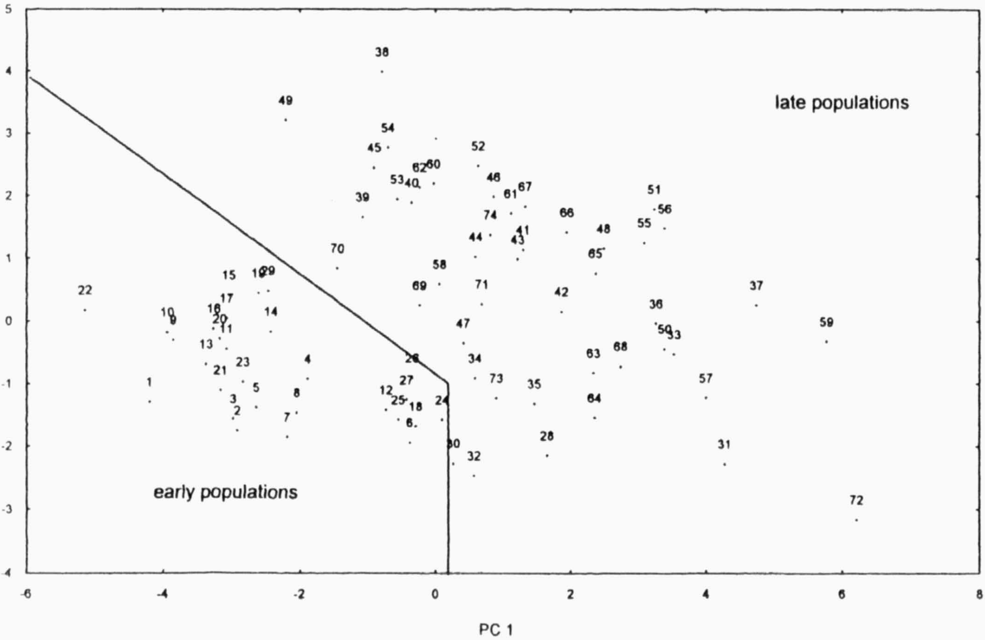


Fig. 5. – Principal component analysis of population samples of *Melampyrum nemorosum*. Distribution of particular samples in the two groups (early vs. late type of populations).

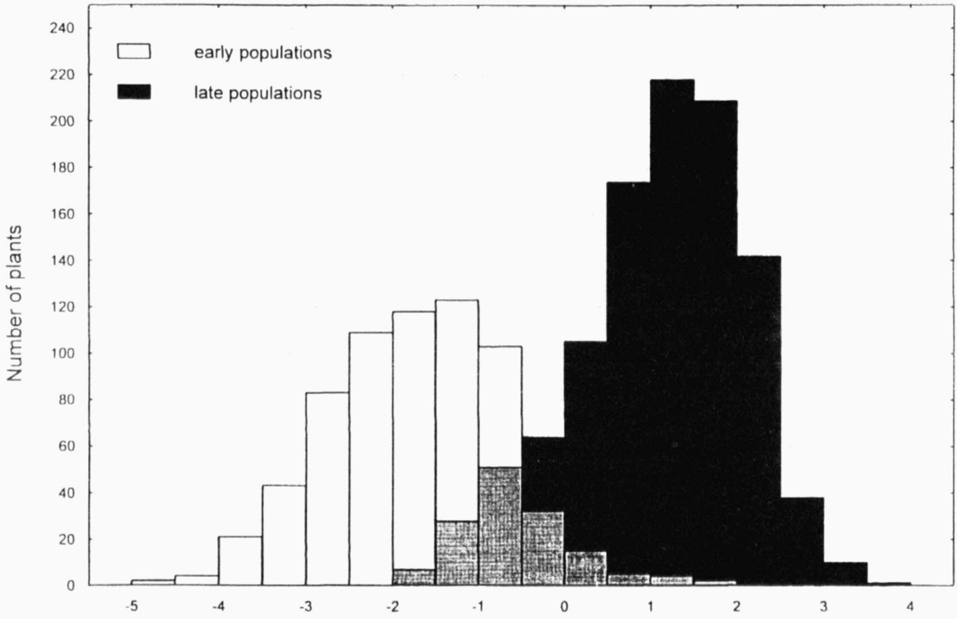


Fig. 6. – Canonical discriminant analysis of plants of *Melampyrum nemorosum*. Frequency distribution of specimens along the canonical variable. Overlap between both populations is shown in grey colour.

Table 2. – Factor structure coefficiens and standardized coefficients from discriminant analysis of early and late populations of *Melampyrum nemorosum*. See Methods for detailed explanation of measured characteristics.

Character	Factor structure coefficiens	Standardized coefficients
Stem length (S)	0.211	–0.346
Number of internodes (I)	0.724	0.826
Number of intercalary internodes (II)	0.061	–0.193
Number of branches (B)	0.671	0.206
Number of flowering branches (FB)	0.592	0.206
Leaf width (LW)	0.409	0.124
Leaf distance (LD)	0.446	0.259
Leaf length (LL)	0.260	0.080
Bract width (BW)	0.112	–0.045
Bract distance (BD)	0.312	0.146
Bract length (BL)	0.048	–0.004

Table 3. – Classification matrix of *Melampyrum nemorosum* plants tested by posterior probabilities method.

Populations	Number of plants to early group	Number of piants to late group	Correct (%)
Early	612	53	92.0
Late	92	955	91.2
Total	704	1008	91.5

nonical structure (i.e. correlations between the canonical variable and original characters) and standardized canonical coefficients, which document the relative magnitude of contribution of the original variables into a canonical function, are presented in Table 2. The characters best correlated with the canonical axis were the number of internodes, number of branches and that of flowering branches, and to a lesser extent also the leaf width and the distance of the widest part to leaf and bract base. The number of internodes nevertheless contributes most to the division into the groups, and its information is unique, not present in any other character. In branches and flowering branches, the information is to a great extent identical, and thus the standardized coefficients equal about half of the structure coefficients. The same holds for some of the leaf and bract dimensions.

The classification function was calculated for both populations groups. The data used for the composition of the classification function were reversely tested by this function and the values of so-called posterior probabilities were obtained (Table 3).

The classification of whole populations samples, which were a priori excluded from the composition of the classification function, showed that the majority of incorrectly identified plants were concentrated in a small number of population samples (Table 4). This method is much more suitable for testing the classification function than the posterior probabilities. Population samples with higher proportion of incorrectly classified plants mainly belong to those situated in "the turning point of the horseshoe" in the PCA diagram (Fig. 3). Although this results to a large extent from the used method, it is possible to conduct the analysis of these population samples. They mostly belong either to early popula-

Table 4. – Correctly and incorrectly classified plants in individual population samples of *Melampyrum nemorosum*, which were a priori excluded from the composition of the classification function. Population samples with less than 80% of correctly classified plants are shown in bold.

Early populations			
	Number of plants		
Sample no.	Correct	Incorrect	Correctly classified (%)
1	18	0	100.0
2	30	0	100.0
3	30	0	100.0
4	18	1	94.7
5	29	0	100.0
6	24	2	92.3
7	29	0	100.0
8	11	2	84.6
9	14	0	100.0
10	28	1	96.6
11	18	1	94.7
12	12	8	60.0
13	29	0	100.0
14	30	0	100.0
15	12	0	100.0
16	28	1	96.6
17	11	0	100.0
18	27	2	93.1
19	9	3	75.0
20	26	0	100.0
21	27	0	100.0
22	28	0	100.0
23	29	0	100.0
24	21	8	72.4
25	25	2	92.6
26	14	0	100.0
27	25	4	86.2
29	17	11	60.7
Total	619	46	93.1

Late populations			
	Number of plants		
Sample no.	Correct	Incorrect	Correctly classified (%)
28	10	20	**33.3**
30	7	24	**22.6**
31	26	4	86.7
32	5	16	**23.8**
33	26	0	100.0
34	13	13	**50.0**
35	11	9	**55.0**
36	15	0	100.0
37	16	0	100.0
38	29	0	100.0
39	22	0	100.0
40	30	0	100.0
41	21	1	95.5
42	30	0	100.0
43	29	0	100.0
44	20	0	100.0
45	16	0	100.0
46	22	0	100.0
47	24	6	80.0
48	22	0	100.0
49	30	0	100.0
50	29	1	96.7
51	20	0	100.0
52	24	0	100.0
53	18	0	100.0
54	30	0	100.0
55	30	0	100.0
56	20	0	100.0
57	15	0	100.0
58	15	0	100.0
59	10	0	100.0
60	10	0	100.0
61	29	0	100.0
62	24	0	100.0
63	22	4	84.6
64	20	10	**66.7**
65	28	1	96.6
66	16	0	100.0
67	27	1	96.4
68	16	0	100.0
69	12	0	100.0
70	23	3	88.5
71	23	0	100.0
72	14	1	93.3
73	16	3	84.2
74	15	0	100.0
Total	930	117	88.8

Pooled data for all populations

Correct no.	Incorrerct no.	Correctly classified (%)
1549	163	90.5

tions collected exceptionally late, when the majority of plants already finished flowering (sample no. 8,19, 27) or to extraordinarily early collected specimens of the late population, when majority of plants have not flowered yet (samples no. 47, 64, 70). In these cases the number of incorrectly classified plants is not too high. Relatively higher proportion of incorrectly classified plants in samples no. 12 and 24 can be, to some extent, caused by an atypical habitat for the early, originally meadow populations (small forest and margin of hazel scrub). A higher number of incorrectly classified plants yielded the classification of sample no. 29, which, however, undoubtedly consists of both early and late plants as documented by the frequency distribution of internode numbers exhibiting clear maxima of 3 and 6 internodes. The situation was similar in Kazivec, where plants from the population samples collected in the beginning of flowering period (no. 30 and 32) are predominantly classified incorrectly. The same is probably true for the locality Babinské louky (sample no. 28). At present, the locality is seriously damaged and rest of the *M. nemorosum* population occurs there. The population sample was collected at the edge of the meadows, already in contact with the late populations, which abundantly occur in nearly bushes. Apparently the prevailing very early plants of the late type were involved in the population from Zděchov (sample no. 34), although the influence of early plants recorded nearby cannot be excluded.

Differentiation of early and late populations

In almost all characters studied (with an exception of the number of internodes), the values measured in late populations strongly overlap with those obtained for early populations (Table 5), although their frequency distributions differ. Some derived characters – particularly the mean length of the internode – are sometimes suitable for determination and can be used for this purpose in addition to the characters used in the distriminant analysis.

The complete results are available in Štech (1998).

Table 5. – Overview of selected characters measured in early and late populations of *Melampyrum nemorosum*. Mixed and uncertain population samples (no. 28–35) were omitted.

	Early populations				Late populations			
Character	Mean	S. D.	Minimum	Maximum	Mean	S. D.	Minimum	Maximum
Stem length (S)	17.83	4.51	5.5	35.0	20.19	5.18	5.0	50.0
Number of internodes (I)	3.70	0.92	1.0	8.0	6.26	1.09	3.0	11.0
Number of intercalary internodes (II)	1.41	0.64	0.0	4.0	1.56	0.64	1.0	4.0
Number of branches (B)	2.53	1.01	0.0	6.0	4.82	1.05	1.0	8.0
Number of flowering branches (FB)	0.87	0.81	0.0	4.0	2.83	1.28	0.0	7.0
Leaf width (LW)	9.65	3.38	3.0	25.0	14.64	5.35	4.5	32.5
Leaf distance (LD)	9.93	3.48	1.0	28.0	15.16	4.80	1.0	32.5
Leaf length (LL)	43.56	10.25	16.0	80.0	51.32	13.46	14.0	100.0
Bract width (BW)	16.01	4.08	5.0	32.0	17.08	5.21	6.0	35.0
Bract distance (BD)	8.05	4.38	0.0	26.0	12.67	4.97	0.0	32.0
Bract length (BL)	49.03	10.94	21.0	83.0	49.26	12.85	1.0	101.0

Discussion

No study dealing in detail with variation of seasonal characters in *Melampyrum nemorosum* has been available so far. Ronniger (1911) first published the descriptions of three subspecies recognized on the basis of the seasonal variation theory:

Aestival type – *M. n.* subsp. *moravicum* (H. Braun) Ronn.: "Internodien wenige, die untersten sehr gestreckt, Kotyledonen zur Blütezeit meist vorhanden und frisch. Stengel meist einfach, oder mit wenigen, steil nach aufwärts gerichteten Ästen; mittlere Stengelblätter länglich-lanzettlich, selten mehr als 10 mm breit".

Monticol type – *M. n.* subsp. *silesiacum* subsp. nova: "Pflanze verzweigt (1–4 Astpaare); Interkalarblattpaare fehlend; Internodien ziemlich zahlreich; mittlere Stengelblätter länglich-lanzettlich, an der Basis am breitesten; Kotyledonen zur Blütezeit gewöhnlich verwelkt oder abgefallen".

Autumnal type – *M. n.* subsp. *nemorosum* – "Internodien zahlreich, die unteren nicht gestreckt; Kotyledonen zur Blütezeit fast stets verwelkt oder abgefallen; Pflanze sparrig verzweigt, zwischen der obersten Verzweigung und dem untersten Blütenpaar sind an der Hauptachse Interkalarblattpaare eingeschaltet. Mittlere Stengelblätter eiförmig oder eilänglich, 15–35 mm breit".

Soó (1926–1927) characterized the subspecies by ranking of the node on which the inflorescence starts and by the number of intercalary leaf pairs. His values are easy to transform into the numbers of stem and intercalary internodes; he gives 2–4 (–5) internodes and 0–1 interkalary internodes for subsp. *moravicum*, and corresponding values of 5–6 and 1 (–2) for subsp. *silesiacum*, 7–9 and 3–5 for subsp. *nemorosum*, respectively.

The discriminating characters introduced by Ronniger and completed by Soó have been accepted with minor corrections (or sometimes inaccuracies) in later works of other authors. However, this study brings an evidence that only two groups, i. e. the early and late types, can be distinguished. The number of internodes recorded during the whole flowering period was 2–5 in early populations and 5–8 in late populations. This means that a taxon with 5–6 internodes cannot be distinguished; this number does not even cover variation within a single population. The number of intercalary internodes is very similar in both early and late populations (plants with 1–2 intercalary internodes strongly prevail). This holds true also for populations with more than 6 internodes, which contradicts the data from the literature.

It is absolutely impossible to distinguish taxa according to the presence of either one or more intercalary internodes. Absence of intercalary internodes is rare and occurs in very short plants without branches; such a feature cannot be obviously used to characterize a taxon.

On the other hand, the number of intercalary internodes strongly correlates with the total number of internodes, especially in the late populations. Some plants with very high number of internodes thus have also exceptionally high number of intercalary internodes, and these values have been probably regarded as typical of the autumnal type. Plants indicated by Ronniger and his successors as subsp. *silesiacum* mostly represent very early plants of the late type, with internode number lower than population mean during full flowering. Their branches usually do not flower yet, point upward, and tend to have rather broad leaves and preserved cotyledons. This habit, however, quickly changes as the branches lengthen, start to flower and stop pointing so markedly upwards. Cotyledons, and somewhat fleshy leaves often as well, quickly fall off. Very typical plants of this type occurred for instance in the population samples 47 and 68 in the mid-June. I was not unfortunately able to revise type specimens of *M. n.* subsp. *silesiacum*. Ronninger gives two

Table 6. – Frequency distribution of the number of branches and that of flowering branches in early (n = 765 plants) and late populations (n = 1007 plants) in the material studied.

	Branches total									Flowering branches							
Number of branch pairs	0	1	2	3	4	5	6	7	8	0	1	2	3	4	5	6	7
Early (%)	1.8	14.0	31.6	36.3	14.8	1.3	0.1			37.1	41.4	19.3	1.6	0.5			
Late (%)		0.2	1.3	9.7	23.5	40.0	21.6	3.4	0.2	2.6	12.2	26.3	31.3	18.1	7.0	2.2	0.3

Table 7. – Frequency distribution of the number of internodes and that of intercalary internodes given for the taxa of *M. nemorosum* in Poland (based on the data from Jasiewicz 1958).

Taxa	Number of internodes							Number of specimens	Number of intercalary internodes			Number of specimens
	3	4	5	6	7	8	9		0–1	2	3	
subsp. *moravicum* (%)	23	47	29	1				91	94	6		89
subsp. *silesiacum* (%)		1	5	18	38	33	5	359	55	44	1	357

localities from Silesia and one from Thüringen in the protologue. I do not know the situation in Thüringen but it is almost certain that in Silesia, only late populations are found. I revised several plants which were determined by Ronniger as *M. nemorosum* subsp. *silesiacum* and these were indeed late plants in the very beginning of flowering. Such plants occur in a number of populations of the late *M. nemorosum*, and it is definitely not possible to evaluate them as an independent taxon. On the other hand, it cannot be excluded that later plants of early populations could have been, although very rarely, also classified here. They have a number of internodes exceeding mean value within the population, they have already branches, often even flowering at that time (more than reported for subsp. *moravicum* in Ronniger's description, Table 6), and their cotyledons are already fallen off.

Some authors never accepted the division into three taxa or distinguished only two of them. Jasiewicz (1958) reports only *M. n.* subsp. *moravicum* and *M. n.* subsp. *silesiacum* from the whole Poland. Based on the study of herbarium material, he presented the percentage of internode number produced before the onset of flowering and the percentage of intercalary leaf pairs. His values were transformed into the number of stem and intercalary internodes (Table 7). Although the number of intercalary internodes is lower than usually reported for *M. n.* subsp. *nemorosum*, the total numbers of stem internodes correspond rather to the values reported for this type than for *M. n.* subsp. *silesiacum*. The percentage of internodes fairly well matches the numbers obtained in the present study for both early and late populations (Table 8).

Tsvelev (1981) gives 3–5 internodes and 2–4 intercalary internodes for *M. nemorosum* subsp. *nemorosum*, and (1–) 2–3 internodes and 0–1 intercalary internodes for subsp. *moravicum*. He also questioned the existence of subsp. *silesiacum* by pointing out that the differences between subsp. *nemorosum* and subsp. *silesiacum* are very indistinct in the European part of the former USSR.

Table 8. – Frequency distribution of the number of internodes and that of intercalary internodes in early (n = 765 plants) and late populations (n = 1007) in the material studied.

	Number of internodes											Number of intercalary internodes			
Population	1	2	3	4	5	6	7	8	9	10	11	0–1	2	3	4
Early (%)	0.3	5.5	38.7	38.7	14.6	0.9	1.2	0.1				63.5	31.0	5.1	0.4
Late (%)			0.4	4.1	19.6	37.2	25.9	11	1.5	0.0	0.1	51.5	42.1	5.6	0.8

As far as the other seasonal characters are concerned, particularly the number of branches and that of flowering branches, these are even more variable than the number of internodes (Table 6). Summary data indicate that the early type has usually more branches than reported (most frequently 2–3 branch pairs). Moreover, one pair of flowering branches is usually developed. The common number of branches in the late populations ranges from 3 to 6, i. e. well within the range of both the values given for *M. n.* subsp. *nemorosum* and subsp. *silesiacum*. This can be considered as another evidence that it is not possible to distinguish these two types.

The oblique or horizontal position of branches and the presence of cotyledones are even more influenced by environmental conditions than the numbers themselves. These features usually change in the course of flowering even on the same plant.

Taxonomic conclusions

The investigated populations are differentiated into two morphologically quite distinct groups, which are linked by a limited number of transitions. In Central Europe, and with a great probability also elsewhere (Ganeshin 1916), both groups differ in their ecological requirements. The early populations almost exclusively occur in a specific type of meadows, relatively rich in nutrients, usually once mown and extraordinarily rich in species. The late populations are most common in deciduous forests, scrub and their edges. The properties of the populations are genetically fixed and not conditioned by the habitat type. The experimental sowing, although not very successful, yielded a small population of early plants, grown under completely different climatic and ecological conditions, which still corresponded to the original type even after several years of independent reproductions. The sample of this population was included in the statistical analysis under no. 9 and the seed used for sowing came from the population sample no. 4.

In the investigated material, it is undoubtedly possible to distinguish only two quite well differentiated infraspecific taxa from the viewpoint of the seasonal variability. To adopt a suitable taxonomic category for these taxa is relatively difficult task. It is important to take into account the following points:

(1) Both taxa are not entirely homogeneus units. Every population is to some extent different and probably adapted to environmental conditions by its seasonal character. The internode number recorded in two near, very similar localities of early types of *M. nemorosum* in various stages of the flowering period and in different seasons is compared in Fig. 7. Both populations are similar at the first sight, but there are obviously constant differences in the number of internodes. This internal heterogeneity concerns both early and late populations.

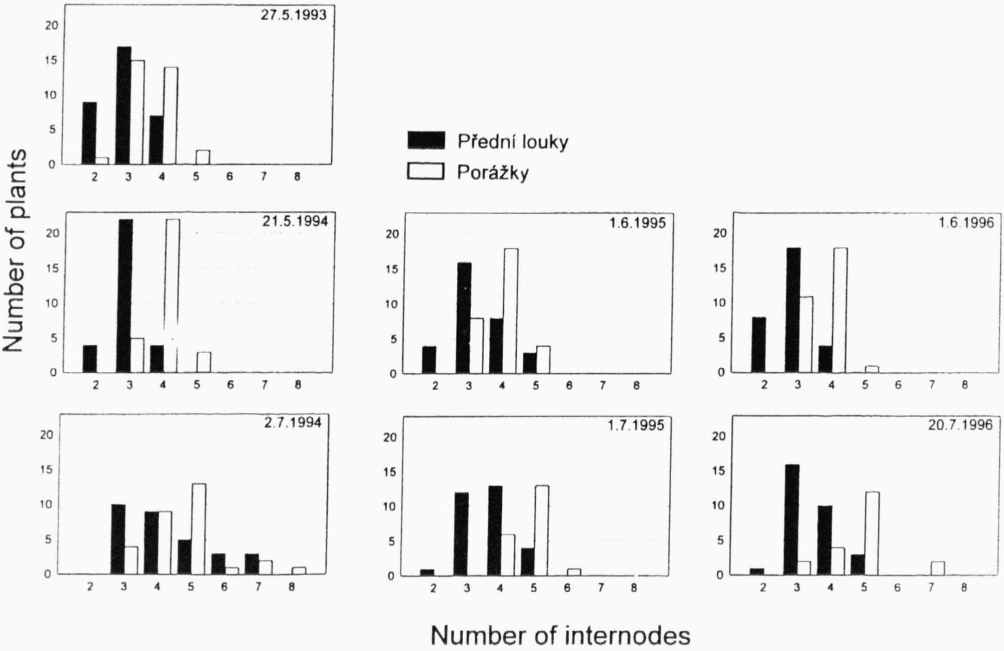


Fig. 7. – Development of the number of internodes recorded in two populations samples of the early type of *Melampyrum nemorosum* in the course of four years.

(2) Although the early type of populations is probably much more frequent in some regions (northern Europe in particular), it is scattered throughout the whole distribution area of the late type.

(3) The differentiation of the populations occurred in the polytopic way, and it is highly probable that populations of the same phenological type do not have common origin.

In addition to the previous arguments, another important, although indirect evidence of polytopic origin of particular phenotypes is available. Similar types do occur not only in very closely related plants differing only in calyx indumentum (they are sometimes treated as a separate species *M. polonicum*) but also in a number of other more or less related species and even in some related genera. In genus *Melampyrum*, the reason for this can be very closely associated with the mode of reproduction. Like other species, *M. nemorosum* is pollinated by various representatives of insects (*Hymenoptera*), namely bumble-bees (*Bombus*). Because of rather long corolla tube, it is often penetrated by bumble-bees on the base which can have an important effect on the genetic structure of populations and consequently it can speed up micro-evolutionary processes. This topic, however, requires further study.

The seasonal types have been most commonly and traditionally evaluated as subspecies (Ronniger 1911, Soó 1926–1927, Dostál 1948–1950, 1989, Rothmaler 1994). Provided that we do not want to create a completely independent category of ecotype as used by Soó and Webb (1972) it seems much more appropriate to evaluate both types, on the basis of the above mentioned assumptions, in the rank of varieties. This treatment is not novel (Beck 1893, Hartl 1974). Moreover, this solution makes it possible to differentiate the geographical variability, playing an important role in *M. nemorosum* agg., from the seasonal variability that has almost no geographical pattern.

Nomenclature

The nomenclature within the group studied is not simple. It is very suitable to designate the most common late type of populations as *M. n.* var. *nemorosum*. Recently Fischer lectotypified the name *M. nemorosum* by the specimen no 76.3 (LINN) with the annotation "... agrees very well with the typical *M. nemorosum* s. str. (or subsp. *nemorosum*) and therefore chosen here as lectotype" (Fischer 1997). He probably based his choice on the fact that the plant from the cited specimen has 2 intercalary internodes and according to the descriptions it corresponds quite well to *M. n.* subsp. *nemorosum*. Unfortunately this is not completely true and the mentioned plant is not complete, so that it is not obvious what was the total number of internodes. In addition to the intercalary internodes, it has only a part of the first internode beneath the uppermost pair of branches. As the internodes are quite long, it cannot be completely excluded that the plant belongs to the early type. Nobody is probably able to recognize it from the selected lectotype. In this case, the choice of an epitype is considered the most appropriate solution enabled by the Tokyo Code (Greuter et al. 1995, Article 9.7.) and it should be unequivocally chosen from plants of the late type (see below).

The situation in plants of the early type is much more complicated. Braun (1884) described a new species, *M. moravicum*. All later authors (Beck 1893, Ronniger 1911, Soó 1926–1927, Soó & Webb 1972, Hartl 1974) used this name for describing the early populations. Although the short branches and their numbers are emphasized in the Braun's description, the number of internodes is not mentioned there and it is not therefore obvious at all that the early type is described indeed. This would be completely irrelevant if the type really belonged to the early population. All circumstances, however, indicate that Braun had only an extraordinarily poorly branched and small plants of the late type of *M. nemorosum*.

One specimen containing four plants, collected by Bubela on 19 August 1883 near the town of Vsetín and annotated as *M. subalpinum* Juratzka (p. var.) is deposited in PRC. Braun's letter to Bubela entitled "*Melampyrum nemorosum, subalpinum*, var. *moravicum* mihi" is enclosed to the specimen. In the letter Braun asked Bubela for a specimen of this form. He described the plant as a new species *M. moravicum* already in 1884 stating in his description that the plant was found by his friend J. Bubela in the meadows near Vsetín. It is probable that Braun received from Bubela one plant, which he kept and described after then as a new species. It is thus very probable that the four plants represent isotypes. Effort to find the holotype has not been successful until now. No specimen labelled *M. moravicum* by Braun was found in the herbarium of Naturhistorisches Museum Wien (W) where most of the Braun's specimens should be deposited (according to the curator E. Vitek). If no specimen labelled *M. moravicum* by Braun was found, it will be necessary to lectotypify this name by one of the four above mentioned plants.

All plants from this herbarium sheet come from a population which can be unambiguously assigned to the late type. The plants are relatively small, little branched, they probably grew in a very unfavourable site or had no suitable host plants. Such plants occasionally occur even in normal populations of *M. nemorosum*. Another evidence that no early type has ever grown in the type locality of *M. moravicum* is the copious number of exsiccates collected by Bubela in the surrounding of Vsetín, often annotated as locus classicus (Fl. Exs. Austro-Hung., no 1397 – Fl. Exs. Reipubl. Bohem. Slov., no 469 – Schultz Herb. Norm., no 2243), and located in a number of herbaria. No plants of these exsiccates can be considered as belonging to early populations. Some of them have only 3 internodes but if other characters are taken into account, it is necessary to consider them as earlier plants of the late type populations.

Although all later authors used the basionym *M. moravicum* H. Braun for the early populations, it is not possible to use this name (Article 7.4. of the Tokyo Code), because its type belongs to var. *nemorosum* and therefore can only be listed among the synonyms of var. *nemorosum*. The only other name used for early populations was *M. nemorosum* subsp. *zingeri* Ganeshin (Ganeshin 1916). Ganeshin described the new subspecies from wet meadows in the surrounding of St. Petersburg. He distinguished this subspecies from the early Central European populations ("*M. moravicum*") by narrow leaves (2–5 mm) and bracts (4–14 mm). Such plants, however, can be found in our populations as well; Ganeshin's plants represent probably merely the marginal variation of early populations. Already Tsvelev questioned this taxon by pointing out that it is not possible to distinguish it from the Czech plants named *M. moravicum* (Tsvelev 1981). Czerepanov also considered subsp. *zingeri* as a mere synonym of subsp. *moravicum* (Czerepanov 1981). This complicated situation can be solved in the following ways:

(1) It is possible to propose the name *M. moravicum* for conservation (Art. 14.9). It is nevertheless questionable whether the name is generally widespread and used. Some authors, aware of considerable taxonomic confusion, avoid the infraspecific classification referring to the necessity of further studies of infraspecific taxa (Adler et al. 1994, Ehrendorfer & Gutermann 1973).

(2) The second possibility is to use the Ganeshin's name and combine it into the rank of a variety. Ganeshin, however, clearly excluded the major part of all early populations from his subspecies. Therefore I do not consider this possibility appropriate.

(3) Probably the most appropriate solution is the description of the early type of populations in *M. nemorosum* using a new name. This is made possible by the fact that no valid name exists for this taxon in the varietal rank (cf. Article 11.2 of the Tokyo Code). This solution is further supported by the need of partly altered delimitation of early and late populations because Ronniger delimited the early type ("subsp. *moravicum*") on the basis of three seasonal taxa.

New delimitation of the seasonal taxa

Melampyrum nemorosum L. var. *nemorosum*

Syn.: *Melampyrum nemorosum* subsp. *genuinum* Čelak. Prodr. Fl. Böhm. 335, 1873 nom. inval. – *M. moravicum* H. Braun Oesterr. Bot. Z. 34: 422, 1884. – *M. nemorosum* var. *subsimplex* Uechtr. Jber. Schles. Ges. Vaterl. Cult. 63: 233, 1886. – *M. nemorosum* subsp. *decrescens* Čelak. fil. Věstn. Král. Čes. Společ. Nauk, cl. 2, 1887(5): 117. – *M. nemorosum* subsp. *silesiacum* Ronniger Vierteljahrsschr. Naturforsch. Ges. Zürich 55: 312, 1911.

Internodia (inter cotyledones et initium inflorescentiae) numerosa (≥ 5, rarius minus initio temporis florendi populationis), foliis breviora. Rami plerumque longi, floriferi, suberecti vel patentes (raro rami breves, erecti - sub conditionibus non benignis). Folia caulina 10 mm latiora, solum sub conditionibus non benignis angustiora.
Floret VI – IX, in silvis, dumetis, raro in pratis.
Lectotypus: LINN. 760.3 (Fischer 1997).
Epitypus: Specimen no. 953/a in PRC, Bohemia centralis, pagus Čelákovice, in silva frondosa situ septentrionali ab pago (1.5 km), M. Štech, 18. 8. 1994, hoc loco designatus.
Exsiccata: Exs. Torun., no. 235. – Fl. Exs. Austro-Hung., no. 624, 1397, 2601. – Fl. Exs. Reipubl. Bohem. Slov., no. 270, 469. – Fl. Lituan. Exs., no. 76. – Fl. Siles. Exs., no. 117, 121, 122, 123, 124. – Petrak Fl. Bohem. Morav. Exs., no. 682. – Schultz Herb. Norm., no. 2243. – Tausch Herb. Fl. Bohem., no. 1199, 1200.

Variability: A highly variable taxon, namely in terms of leaf width, number of internodes, bract colour and calyx indumentum. The number of internodes mostly 5–10, plants with only 3–4 internodes occur in some localities at the beginning of the growing period, approaching the other variety; many plants, however, usually posses broader leaves. If plants of both varieties occur together, it is often impossible to assign individual plants to the respective variety. The leaf width seems to be strongly related to environmental conditions: plants from dry, sunny and unfavourable sites obviously tend to produce narrow leaves, while plants from wet nutrient-rich sites produce rather broad leaves.
Distribution: This type prevails throughout the whole distribution area of the species.

Melampyrum nemorosum L. var. *praecox* Štech var. nova

Syn.: *Melampyrum nemorosum* subsp. *moravicum* auct. non H. Braun 1884. – *Melampyrum nemorosum* subsp. *zingeri* Ganeschin Tr. Bot. Muz. Imp. Akad. Nauk 16: 124, 1916.

Internodia (inter cotyledones et initium inflorescentiae) 2–4, rarius plus (sub finem temporis florendi populationis), foliis pariter longa vel longiora. Rami plerumque breviores, rarius 1–2 paria floriferi, suberecti. Folia caulina 15 mm angustiora et saepissime 5–10 mm lata.
Floret V–VI (–VII), in pratis.
Holotypus: Specimen no. 953/b in PRC, first plant from the left, Moravia orientalis, montes Bílé Karpaty, pagus Suchovské mlýny, in pratis Přední louky situ boreo-orientalis ab pago (1.9 km), M. Štech, 21. 5. 1994.
Exsiccata: Fl. Exs. Reipubl. Social. Čechoslov., no. 1557 (ut *M. nemorosum* subsp. *moravicum*). – Hayek Fl. Stir. Exs., no. 246 (ut *M. moravicum*). – Herb. Fl. Ross., no. 2560 (ut *M. n.* subsp. *zingeri*).

Variability: Much less variable compared to var. *nemorosum*. The number of internodes usually ranges from 2 to 4, rarely to 5 (such plants resemble var. *nemorosum*).
Distribution: Scattered throughout the distribution range of the species, it is probably more common in southern Scandinavia.
Distribution in the Czech Republic: The variety is documented from Babinské louky meadows in the České Středohoří hills, where only the last remnants of the populations survive. One locality was documented from Jiřice near Mělník in the past but the taxon is extinct there now. In Moravia, the variety was reliably documented only from the Bílé Karpaty Mts where it grows scattered, and from the adjacent areas of the Carpathian Mesophyticum. For the list of revised herbarium specimens belonging to this variety see Appendix 2.

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Souhrn

Práce se zabývá variabilitou druhu *Melampyrum nemorosum* ve střední Evropě. Zvláštní pozornost byla věnována tzv. sezónní proměnlivosti, která je obvykle považována za významnou při vnitrodruhovém členění. Bylo sledováno 11 znaků (délka lodyhy, počet lodyžních a interkalárních článků, celkový počet párů větví a počet kvetoucích párů větví, délka a šířka listu ze středu lodyhy a vzdálenost nejširšího místa od jeho báze a stejné 3 rozměry u nejspodnějšího listenu v květenství) ve více než 40 populacích. Opakovaná měření v průběhu jedné vegetační sezóny prokázala, že některé znaky se v průběhu kvetení populací mění. Nejvýrazněji v průběhu kvetení jedné populace může vzrůstat počet lodyžních článků, přesto je tento znak nejvhodnější k rozlišení vnitrodruhových typů. Studie nepotvrdila tradiční členění druhu *M. nemorosum* do 3 vnitrodruhových taxonů. Bylo zjištěno, že lze rozlišit pouze 2 typy. Časný typ má obvykle 2–4 dlouhé lodyžní články a pouze 1–3 krátké větve, roste na květnatých loukách a kvete již v průběhu května a června. V České republice se v současné době dobře zachované populace tohoto typu vyskytují pouze v Bílých Karpatech a v přiléhajících oblastech Karpatského mezofytika. Běžně rozšířený, později kvetoucí typ, který se vyskytuje především v lesích a křovinách, má zpravidla 5 a více lodyžních článků a bývá více větven. Pro taxonomické hodnocení obou typů je nejvhodnější kategorie variety. Pozdní typ představuje nominátní varietu a časný typ je nově popsán jako var. *praecox*, protože dosud běžně používané jméno *M. moravicum* se vztahuje rovněž na pozdní typ rostlin.

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Appendix 1. – List of localities of population samples.

Early type of populations. **Czech Republic**: **1**. SE Moravia, Bílé Karpaty Mts, Radějov: Čertoryje nature reserve, ca 6 km E of the village, 430 m a. s. l., 4. 6. 1995; **2**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: meadows Přední louky ca 1.9 km ENE of the village, 480 m a. s. l., 27. 5. 1993; **3**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: meadows Přední louky ca 1.9 km ENE of the village, 480 m a. s. l., 21. 5. 1994; **4**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: meadows Přední louky ca 1.9 km ENE of the village, 480 m a. s. l., 2. 7. 1994; **5**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: meadows Přední louky ca 1.9 km ENE of the village, 480 m a. s. l., 1. 6. 1995; **6**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: meadows Přední louky ca 1.9 km ENE of the village, 480 m a. s. l., 1. 7. 1995; **7**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: meadows Přední louky ca 1.9 km ENE of the village, 480 m a. s. l., 1. 6. 1996; **8**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: meadows Přední louky ca 1.9 km ENE of the village, 480 m a. s. l., 20. 7. 1996; **9**. S Bohemia, Budějovická pánev basin: Borek near České Budějovice – shrubby slope near the village (grown plants – seeds obtained from the pop. sample no. 4), 430 m a. s. l., 10. 6. 1996; **10**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: meadows Přední louky ca 2.25 km NE of the village, 480 m a. s. l., 1. 6. 1995; **11**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: meadows Přední louky ca 2.6 km NE of the village, 510 m a. s. l., 1. 6. 1995; **12**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: forest edge ca 2.6 km NE of the village, 510 m a. s. l., 1. 6. 1995; **13**. SE Moravia, Bílé Karpaty Mts, Vápenky: meadow near the Porážky nature reserve ca 1.3 km NW the village, 600 m a. s. l., 27. 5. 1993; **14**. SE Moravia, Bílé Karpaty Mts, Vápenky: meadow near the Porážky nature reserve ca 1.3 km NW the village, 600 m a. s. l., 21. 5. 1994; **15**. SE Moravia, Bílé Karpaty Mts, Vápenky: meadow near the Porážky nature reserve ca 1.3 km NW the village, 600 m a. s. l., 2. 7. 1994; **16**. SE Moravia, Bílé Karpaty Mts, Vápenky: meadow near the Porážky nature reserve ca 1.3 km NW the village, 600 m a. s. l., 1. 6. 1995; **17**. SE Moravia, Bílé Karpaty Mts, Vápenky: meadow near the Porážky nature reserve ca 1.3 km NW the village, 600 m a. s. l., 1. 7. 1995; **18**. SE Moravia, Bílé Karpaty Mts, Vápenky: meadow near the Porážky nature reserve ca 1.3 km NW the village, 600 m a. s. l., 1. 6. 1996; **19**. SE Moravia, Bílé Karpaty Mts, Vápenky: meadow near the Porážky nature reserve ca 1.3 km NW the village, 600 m a. s. l., 20. 7. 1996; **20**. SE Moravia, Bílé Karpaty Mts, Javorník nad Veličkou: Machová nature reserve ca 1.6 km ESE of the railway station Vrbovce, 480 m a. s. l., 1. 6. 1996; **21**. E Moravia, Bílé Karpaty Mts, Brumov-Bylnice: Pod Horou nature reserve, ca 3 km E of Brumov, 540 m a. s. l., 4. 6. 1995; **22**. SE Moravia, Bílé Karpaty Mts, Brumov-Bylnice: Šumlatová nature reserve ca 3.4 km E(N)E of Brumov, 580 m a. s. l., 4. 6. 1995. **Slovakia**: **23**. West Slovakia, Bílé Karpaty Mts, Vrbovce: meadows on the Tri kopce hill ca 4.75 km NNW of the village, 500 m a. s. l., 31. 5. 1995; **24**. Central Slovakia, Kremnické vrchy Mts, Kremnické Bane: meadows ca 0.25 km NNE of railway station Kremnické Baně, 860 m a. s. l., 15. 6. 1996; **25**. Central Slovakia, Kremnické vrchy Mts, Kremnické Bane: meadows ca 1 km E of railway station Kremnické Bane, 800 m a. s. l., 15. 6. 1996; **26**. Central Slovakia, Kremnické vrchy Mts, Kremnica: meadows on the Kremnický štít hill ca 1.6 km SE of railway station Kremnica, 880 m a. s. l., 10. 7. 1997. **Sweden: 27.** Upsalla: town park, in the grass, 50 m a. s. l., 20. 7. 1995.

Mixed and uncertain populations. **Czech Republic**: **28**. NW Bohemia, České středohoří hills, Čeřeniště: meadows Babinské louky ca 1 km SE of the village, 540 m a. s. l., 14. 6. 1995; **29**. E Moravia, Bílé Karpaty Mts, Brumov-Bylnice: edge of the reserve Pod Horou ca 2.8 km E of the Brumov, 540 m a. s. l., 4. 6. 1995; **30**. SE Moravia, Bílé Karpaty Mts, Kazivec: forest edge above the stream Kazivec ca 2.25 km NE of the village Suchovské mlýny, 480 m a. s. l., 1. 6. 1995; **31**. SE Moravia, Bílé Karpaty Mts, Kazivec: forest edge above the stream Kazivec ca 2.25 km NE of the village Suchovské mlýny; 480 m a. s. l., 1. 7. 1995; **32**. SE Moravia, Bílé Karpaty Mts, Kazivec: forest edge above the stream Kazivec ca 2.25 km NE of the village Suchovské mlýny, 480 m a. s. l., 1. 6. 1996; **33**. SE Moravia, Bílé Karpaty Mts, Kazivec: forest edge above the stream Kazivec ca 2.25 km NE of the village Suchovské mlýny, 480 m a. s. l., 20. 7. 1996; **34**. East Moravia, Javorníky Mts, Zděchov: path margin ca 1.7 km WSW of the village, 500 m a. s. l., 13. 6. 1996. **Slovakia: 35**. Central Slovakia: Chočské vrchy Mts, Lúčky: path margin ca 2.9 km WSW of the village, 840 m a. s. l., 14. 7. 1997.

Late type of populations. **Czech Republic**: **36**. Central Bohemia, Bohemian Karst, Srbsko: forest edge ca 2 km ENE of the village, 300 m a. s. l., 19. 7. 1996; **37**. Central Bohemia, Elbe basin, Čelákovice: forest ca 1.5 km NNE of the village, 175 m a. s. l., 18. 8. 1994; **38**. S Moravia, Hodonín region: forest Dúbrava near the village Zbrod, 170 m a. s. l., 4. 8. 1993; **39**. S Bohemia, Blatná region, Závišín: forest ca 2.5 km S of the village, 465 m a. s. l., 28. 9. 1993; **40**. S Bohemia, Blatná region, Závišín: forest ca 2.5 km S of the village, 465 m a. s. l., 22. 7. 1994; **41**. S Bohemia, Blatná region, Závišín: forest ca 2.5 km S of the village, 465 m a. s. l., 22. 8. 1994; **42**. S Bohemia, Blatná region, Závišín: forest ca 2.5 km S of the village, 465 m a. s. l., 23. 6. 1995; **43**. S Bohemia, Blatná region, Závišín: forest ca 2.5 km S of the village, 465 m a. s. l., 3. 9. 1995; **44**. S Bohemia, Blatná region, Závišín: forest ca 2.5 km S of the village, 465 m a. s. l., 18. 7. 1996; **45**. S Bohemia, Blatná region, Závišín: forest ca 2.5 km S of the village, 465 m a. s. l., 21. 8. 1996; **46**. S Bohemia, Blatná region,, Závišín: forest margin near railway station Závišín, 470 m a. s. l., 28. 9. 1993; **47**. S Bohemia, Blatná region, Závišín: forest ca 2.4 km S of railway station Závišín, 460 m a. s. l., 23. 6. 1995; **48**. S Bohemia, Šumava foothills, Krejčovice: along path ca 700 m N of the village, 720 m a. s. l., 5. 8. 1995; **49**. S Bohemia, Šumava foothills, Krejčovice: wet meadow ca 700 m N of the village Krejčovice, 720 m a. s. l., 5. 8. 1995; **50**. S Bohemia, Šumava foothills, Jáma: roadside ca 750 m NE of the village, 700 m a. s. l., 26. 6. 1995; **51**. S Bohemia, Šumava foothills, Smědeč: forest margin ca 1.5 km SSE of the village, 670 m a. s. l., 14. 8. 1996; **52**. S Bohemia, Šumava foothills, Český Krumlov: forest margin in the Vyšenské kopce nature reserve, ca 900 m NW of the town, 490 m a. s. l., 14. 8. 1993; **53**. S Bohemia, Šumava foothills, Vyšší Brod: slope near road at the south margin of the town, 610 m a. s. l., 16. 7. 1993; **54**. S Bohemia, Šumava foothills, Branná: roadside ca 800 m S of the village, 515 m a. s. l., 7. 8. 1994; **55**. NE Bohemia, Stará Paka, Krkonoše foothills: forest ca 750 m ENE of the railway station Stará Paka, 470 m a. s. l., 15. 8. 1994; **56**. E Bohemia, Dolní Poorličí basin, Bědovice: forest ca 500 m NNW of the village, 250 m a. s. l., 6. 9. 1996; **57**. W Moravia, Českomoravská vrchovina highlands, Studená: hazel scrubs ca 1.6 km N of the village, 675 m a. s. l., 26. 6. 1997; **58**. W Moravia, Českomoravská vrchovina highlands, Studená: grassland ca 1.6 km N of the village, 675 m a. s. l., 26. 6. 1997; **59**. W Moravia, Českomoravská vrchovina highlands, Studená: hazel scrubs ca 1.6 km N of the village, 675 m a. s. l., 16. 9. 1997; **60**. W Moravia, Českomoravská vrchovina highlands, Studená: grassland ca 1.6 km N of the village, 675 m a. s. l., 16. 9. 1997; **61**. S Moravia, Ždánický les Mts, Ždánice: forest margin ca 3.2 km N of the village, 410 m a. s. l., 7. 8. 1993; **62**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: forest Suchovská doubrava ca 1.8 km ENE of the village, 480 m a. s. l., 7. 8. 1993; **63**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: forest Suchovská doubrava ca 1.8 km ENE of the village, 480 m a. s. l., 2. 7. 1994; **64**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: forest Suchovská doubrava ca 1.8 km ENE of the village, 480 m a. s. l., 1. 7. 1995; **65**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: forest Suchovská doubrava ca 1.8 km ENE of the village, 480 m a. s. l., 20. 7. 1996; **66**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: forest Suchovská doubrava ca 1.8 km ENE of the village, 480 m a. s. l., 25. 9. 1996; **67**. SE Moravia, Bílé Karpaty Mts, Suchovské mlýny: forest Lipinka ca 3.2 km NNE of the village, 490 m a. s. l., 6. 8. 1993; **68**. SE Moravia, Zlínské vrchy Mts, Zlín: forest margin ca 750 m SSE of the railway station Zlín-Příluky, 310 m a. s. l., 11. 6. 1993; **69**. E Moravia, Vsetínská kotlina basin, Semetín: forest edge ca 200 m W of the village, 390 m a. s. l., 12. 6. 1993; **70**. E Moravia, Vsetínská kotlina basin, Semetín: forest edge ca 200 m W of the village, 390 m a. s. l., 1. 7. 1994; **71**. E Moravia, Vsetínská kotlina basin, Ratiboř: meadows edge near solitude Nivka ca 2 km SE of the village, 430 m a. s. l., 1. 7. 1994. **Slovakia: 72**. Central part, Kremnické vrchy Mts, Kremnica: path margin ca 650 m SE of railway station Kremnica, 690 m a. s. l., 10. 7. 1997; **73**. Central part, Tatry Mts foothills, Vavrišovo: forest margin E of the village, 700 m a. s. l., 16. 7. 1997. **Austria: 74.** NW part, Mühlviertel, Bad Leonfelden: path margin E of the village, 930 m a. s. l., 13. 7. 1996

Appendix 2. – List of revised herbarium specimens of *Melampyrum nemorosum* var. *praecox*.

Czech Republic: **Elbe Basin:** Grasige Au bei Jiřice bei Elbe, 25. 5. 1923, G. Beck, PRC. **Bílé Karpaty Mts:** Bílé Karpaty, louky u Radějova, 31. 5. 1967, S. Ondráčková, ZMT. – Bílé Karpaty, Radějov: Čertoryje, 13. 6. 1963, Unarová, MJ. – Radějov u Strážnice: Lučina, křoviny v úd. potoka Járkovce, 350 m n. m., 6. 6. 1975, Elsnerová, MJ. – Bílé Karpaty, Čertoryje, 400 m n. m., 22. 6. 1970, Dostál, PR. – Bílé Karpaty: v údolí Járkovce, 410 m n. m., 8. 6. 1946, Šmarda, BRNM. – Bílé Karpaty, Olšice za Radějovem, 420 m n. m., 27. 5. 1953, Dvořák, BRNM. – Louky u Radějova, 31. 5. 1967, Kubát, LIT. – Radějov: Radějovské louky, 31. 5. 1967, Belicová, HR. – Tvarožná Lhota: Vojšické louky, 350 m n. m., 8. 6. 1946, MJ. – Radějov: Čertoryje, 2. 6. 1967, ?, MJ. – Bílé Karpaty, loco Čertoryje prope Kněždub, 1. 6. 1973, F. Weber, PR. – Uherský Brod, Příhazy: SZ svah Kyjanice, 600 m n. m., 30. 5. 1943, Pospíšil, BRNM. – Uher. Brod, Příhazy: horská louka na SZ svahu Kyjanice, 600 m n. m., PRC. – Velká nad Veličkou: „Háj", 13. 6. 1953, Černoch, BRNM. – Vápenky: Porážky, 23. 5. 1968, ?, Jihlava. – Bílé Karpaty, Vrbovce: coll. Machová, 9. 6. 1949, Deyl, PR. – Bílé Karpaty, na louce na SV svahu Lesné (696 m), 1. 8. 1944, Šourek, BRA. – Bílé Karpaty, rezervace Lesná pod Javořinou, 24. 5. 1961, Elsnerová, Unar, MJ. – Lesná pod Velkou Javořinou, 25. 5. 1967, Unar, BRNU. – Bílé Karpaty: Lesná supra Korytná, 26. 6. 1956, Skřivánek, BRNM. – Bílé Karpaty: náhorní louky „Lesná" nad obcí Korytnou, 13. 8. 1944, V. Skřivánek, Herb. Kůrka. – východní svah Lesné, 1. 8. 1944, Šourek, PR. – Bílé Karpaty, Vápenice: při žluté značce z Mikulčina vrchu, 8. 6. 1967, Unar, BRNU. – Bílé Karpaty, Sidonie: louky při cestě na Biely vrch, SV obce, 650 m n. m. 4. 6. 1981, MJ. – Bílé Karpaty, Nedašov: Hrušova dolina, na louce, 550 m n. m., 26. 5. 1981, Elsnerová, MJ. – Nedašov: louka mezi list. lesy předělená pruhem křovin, Hrušová dolina, ?, MJ. – Nedašov: CHÚ „Kaňoury", křov. stráň ca 4 km V obce, na J úklonech Vysočky, 640 m n. m., 5. 6. 1984, Elsnerová, MJ. – Bílé Karpaty, Brumov: louky nad Hodňovským údolím, hojně, 620 m n. m., ?, MJ. – okres Bylnice, Sv. Štefan: na vlhkej lúčke sev. svahu, 400 m n. m. 28. 5. 1954, Grebenščíková, SAV. – in silvis et pratis prope vicum Sv. Štěpán procul stationem Vlárský průsmyk, 31. 5. 1954, Deyl, PR. – Bylnice: in pratis loco dicto „Tratihušt" supra Sv. Sidonic?, 26. 5. 1947, Skřivánek, BRNM. – Bylnice: V svah Tratihoště, 680 m n. m., 26. 5. 1947, Šmarda, BRNM. – Bylnice: stráň vrchu Pláňava ca

0.5 km JZ od žel. zast., 6. 6. 1975, Elsnerová, Jihlava. – Brumov: na horské louce na severním svahu trig. 707 Tratihušť, 26. 5. 1947, Šourek, PR. – Starý Hrozenkov: v lese nad Krásnovským mlýnem, 1931, Podpěra, BRNU. – **České středohoří hills:** Č. Středohoří, Luka nad Babinou, 7. 6. 1903, Domin, PRC. – Babínské louky v Českém Středohoří, 6. 6. 1925, V. Krajina, PRC. – Č. Středohoří: Orchidejové louky u Babiny, 2. 6. 1925, Sillinger, PR. – **Vsetínská kotlina basin:** Hovězí: louka na Slepcově, 10. 6. 1923, G. Říčan, BRNU. – **Hostýnské vrchy Mts:** Polomsko pr. Rajnochovice, 15. 6. 1922, Podpěra, BRNU – **Javorníky Mts:** Javorníky „Kubíčci" in convalle Mísné p. Zděchov, 540 m n. m., 16. 6. 1967, Dvořáková, BRNU. – Javorníky, in nemore convallis Mísné, loco Kubíčci dicto, 530 m n. m., Smejkal, BRNU. – Fl. Exs. Reipubl. social. Čechoslov., no 1557, Moravia orient., montes Javorníky: in silva mixta convallis „Mísné" (loco Kubíčci dicto) prope pagum Zděchov haud procul ab oppidulo Hovězí, 580 m n. m., 17. 6. 1967, Dvořáková, Smejkal, BRNU, PR, PRC, WU. – Vsacké hory: Johanová u Kovolů v křoví, 600 m n. m., 6. 1934, G. Říčan, BRNU. – Vsacký Cáb, 6. 1940, ?, BRNM.

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