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Poa riphaea, an endangered stenoendemic species in the Hrubý Jeseník Mts (Eastern Sudetes)

Poa riphaea – ohrožený stenoendemit Hrubého Jeseníku (Východní Sudety)

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The taxonomy, nomenclature, geographic distribution, karyology, morphology and isozyme variation in *Poa riphaea*, a supposed endemic species in central Europe, were studied. We especially focused on resolving the long-standing uncertainty about its relationship with *P. laxa* by assessing morphological and isozyme data. Attention was also paid to the morphological differention between *P. riphaea* and *P. nemoralis* from the highest parts of the Hrubý Jeseník Mts. Our isozyme analysis did not reveal any within-population genetic variability in the last remaining population of *P. riphaea* at the summit of Mt Petrovy kameny. The reasons for the variability in its morphology are discussed in the context of environmental conditions. The octoploid chromosome number of *P. riphaea* has been, probably, for the first time, reliably determined to be 2n = 56. We also present a map of the species' historical and recent distribution. In addition to the sole recent locality at Mt Petrovy kameny, we have confirmed two historical localities (Tabulové skály rock and Velká Kotlina glacial cirque). We have selected a neotype for the name *P. riphaea*.

Keywords: chromosome number, distribution, flora of central Europe, Hrubý Jeseník Mts, isozymes, intra-population variability, morphometrics, *Poa*, typification

Introduction

Poa riphaea (Asch. et Graebn.) Fritsch of the *P. glauca* Vahl s.l. complex (*Poa* sect. *Stenopoa* Dumort.) is considered to be a stenoendemic species in the Hrubý Jeseník Mts (Eastern Sudetes Mts, Czech Republic), where a small declining population is restricted to a single recently found location on the summit of Mt Petrovy kameny (Holub 1999). For a long time, its taxonomic position was rather controversial. Ascherson & Graebner (1900) described *P. riphaea* as an intraspecific taxon of *P. laxa* Haenke, which belongs to section *Oreinos* Asch. et Graebn. Soon afterwards, Fritsch (1909) first elevated *P. riphaea* to species level, but most authors in the first half of the 20th century thought that these two species were closely related. Laus (1927) even wrote about a sympatric occurrence of *P. riphaea* and *P. laxa* at Petrovy kameny rock. Although Ascherson & Graebner (1900) knew *P. riphaea* only from the Hrubý Jeseník Mts, later authors (Rouy 1913, Stojanov & Stefanov 1923, Jirásek 1934) reported similar plants in other European mountain regions (e.g. in France, Balkans and Western Carpathians). In the Flora Europaea Edmondson (1980) mentions *P. riphaea* as a synonym of *P. laxa*. But there is another different taxonomical concept, which places *P. riphaea* in the *P. glauca* s.l complex. This treatment was accepted by 19th century authors who identified plants of *P. riphaea* as taxa presently included in the synonymy of *P. glauca* [e.g. *P. aspera* Gaudin (Wimmer et Grabowski

1827), *P. caesia* Sm. (e.g. Fiek 1881, Oborny 1883) or even as *P. nemoralis* var. *glauca* Wimm. (Wimmer 1840)]. Nannfeldt (1935), in his monograph devoted to the *P. laxa* s.l. complex, rejected a close relationship between *P. riphaea* and *P. laxa.* He determined plants from the Hrubý Jeseník Mts as *P. glauca*. Detailed morphological and anatomical studies, which clearly separate *P. riphaea* and *P. laxa*, were published by Chrtek and Jirásek (Jirásek & Chrtek 1963, Chrtek & Jirásek 1966). These authors also identified *P. riphaea* recorded from places other than the Hrubý Jeseník Mts as *P. cenisia* subsp. *contracta* Nyár. or abnormal specimens of *P. laxa.* They consider *P. riphaea* to be an endemic microspecies of the *P. glauca* s.l. complex. Compared to the relatively robust results of morphological and anatomical studies those of molecular studies are rather ambiguous. Stoneberg-Holt et al. (2004) studied the relationships between predominantly central-European species of the genus *Poa* by sequencing the *trn*L intron and *trn*L-F intergenic spacer in cpDNA. They also included in their study material of *P. riphaea*, *P. laxa*, *P. glauca* s. str. and two endemic taxa belonging to the *P. glauca* s.l. complex, which were described in the last decade of the 20th century from the Western Carpathians (Bernátová & Májovský 1997, Bernátová et al. 1999). They detected very little differentiation between the sections *Stenopoa* and *Oreinos.* In their study, *P. riphaea* shared the same haplotype with *P. laxa* and *P. glauca* and was very similar to other Carpathian endemic taxa. Gillespie et al. (2007) sequenced a longer region of cpDNA, the *trn*T-*trn*F spacer, which includes the region previously studied. These authors analysed a larger number of taxa collected worldwide, including the species included in the previous study except for *P. laxa*, which was replaced by a very closely related North-American species, *P. fernaldiana* Nannf. Sequence data from this study supported a close affinity of *P. riphaea* with *P. glauca*, contrary to Stoneberg-Holt et al. (2004), who suggested a possible close relationship between *P. laxa* and *P. riphaea*. Both studies, however, were primarily aimed at elucidating the phylogenetic structure of the genus *Poa,* and resolution at the level of the sections *Oreinos* and *Stenopoa* was very problematic. In order to determine the relationships among the species of these sections we need more sensitive methods than the sequencing of the above-mentioned cpDNA region.

There are no reliable reports of the chromosome numbers of *P. riphaea*. Holub (1999) described this species as “a polyploid grass”. Dostál (1989) reports chromosome counts of 2n = 42, 44, 49, 56 without mentioning the source. Within the *P. glauca* s.l. complex the sympatric occurrence of two or three cytotypes in one population is reported in Norway (Engelskjøn 1979) and Switzerland (Duckert-Henriod & Favarger 1987), but these reports are for abundant and extensive populations growing at localities with very rugged topography. Considering the very restricted distribution and small number of extant specimens of *P. riphaea*, the accuracy of Dostál’s numbers is very dubious.

Another interesting topic is the historical distribution of *P. riphaea* in the Hrubý Jeseník Mts. Already Wimmer & Grabowski (1827), who reported this species for the first time, mention its occurrence at three localities: the summit of Mt Petrovy kameny, Mt Praděd and the summit of Mt Keprník. The number of localities recorded for *P. riphaea* increased during the 19th and 20th centuries to include the following: Velká Kotlina glacial cirque, small rocks on the left side of the road from Švýcárna (Schweizerei) chalet to the town of Kouty nad Desnou (Winkelsdorf), Mt Výrovka (Uhuštýn) and Medvědí hřbet ridge (Wimmer 1840, Fiek 1881, Oborny 1883, Formánek 1892). By contrast, Podpěra (1926) states that the only confirmed locality for *P. riphaea* is at the summit of Mt Petrovy kameny. Jirásek & Chrtek (1963) also only confirm this locality. However, Dostál (1989) lists several localities, and Holub (1999) stresses the necessity to search other suitable localities for this species in the subalpine zone of the Hrubý Jeseník Mts.

The only population of *P. riphaea* has experienced a constant decline over the last decades (Holub 1999, Kavalcová 2003). *Poa riphaea* is included among the species in the Czech Republic that are critically endangered (Procházka 2001). The current population is monitored regularly, and there are plans to strengthen it by sowing seed collected in situ (Kavalcová 2003).

Considering the facts and problems mentioned above, we can outline several areas of interest for us to study. Morphological and isozyme analyses provide a detailed insight into the intrapopulation variability of *P. riphaea,* which might be crucial for the protection of this critically endangered endemic species. The other objective of our study was to estimate the chromosome number of this species. To explore the possible relationship between *P. laxa* and *P. riphaea*, we compared morphological, karyological and isozyme data and examined the published morphological diagnostic characters. Because of the high frequency with which *P. riphaea* is confused with *P. nemoralis*, samples of mountain populations *P. nemoralis* from subalpine rocks on the Hrubý Jeseník Mts were also morphologically analysed. Finally, we attempted to ascertain the historical distribution and recent status of the localities reported for *P. riphaea* in the Hrubý Jeseník Mts.

Materials and methods

Plant material

The material included in the isozyme analysis consisted of 18 samples of *P. riphaea* collected at Petrovy kameny tor and one cultivated plant of *P. riphaea* (this plant was also used for counting the chromosome number). The material was complemented by one sample of *P. pratensis* L. (Petrovy kameny), which was mentioned by Chrtek (2002) as possibly misidentified as *P. riphaea*, and *P. babiogorensis* Bernátová, Májovský et Obuch (a stenoendemic species belonging to the *P. glauca* s.l. complex collected from Mt Babia hora, W Carpathians, locality Sokolica). A parallel study was done on *P. laxa* (Hoták et al. 2007), so the zymograms of this species were compared with those we recorded. Altogether, 101 samples of *P. laxa* from 12 populations in the Krkonoše Mts and 31 samples of *P. laxa* from eight populations in the Western Carpathians (populations from the Low Tatras and Mt Babia hora) were analysed in this study.

For the purposes of the morphological analyses, 59 samples of *P. riphaea* were used (55 samples from Petrovy kameny, four from cultivation two of which were from the experimental garden of the Institute of Botany in Průhonice and two from the grass collection of OSEVA PRO Ltd, Czech Republic). Regarding the threatened population of *P. riphaea*, only a single stem with a panicle was taken from every specimen sampled at Petrovy kameny (the material was collected after flowering). In the morphological analyses, we compared this material with a collection of *P. laxa* (66 samples in total: 57 from the Krkonoše Mts and nine from the Western Carpathians) and mountain populations of *P. nemoralis* from the Hrubý Jeseník Mts (14 samples from Mt Keprník and Tabulové skály rock). The samples for isozyme and morphological analyses were collected throughout the entire population; each sample corresponded to a single plant.

Chromosomes were counted in two specimens of *P. riphaea* cultivated from seeds collected at Mt Petrovy kameny. Before the counting, the specimens were cultivated in the experimental garden of the Institute of Botany in Průhonice. Voucher herbarium specimens are preserved at PRC.

Isozyme analysis

Isozyme analyses to determine genetic variability were carried out at the Isozyme Laboratory of the Institute of Botany in Průhonice. The methodology of tissue preparation, electrophoresis and staining followed Vallejos (1983) and Soltis & Soltis (1989) with several modifications (Kaplan et al. 2002). During tissue preparation, the so-called 'Luzula' extraction buffer system was used. Electrophoresis on non-denaturing polyacrylamide gels was carried out in a Hoefer vertical unit. Following methodical optimization, five isozyme systems were chosen for the final analysis: 6-phosphogluconate dehydrogenase (6PGDH, EC 1.1.1.44), alcohol dehydrogenase (ADH, EC 1.1.1.1), leucine aminopeptidase (LAP, EC 3.4.11.1), esterase (EST, EC 3.1.1.-) and superoxide dismutase (SOD, EC 1.15.1.1). If two or more different loci were present on a gel (EST, SOD), the most anodally migrating locus was assigned the number '1'. It was not possible to carry out an allelic interpretation because of the low within-population genetic variability and presence of high levels of polyploidy.

Morphometric analysis

Morphometric analyses focused on evaluating the morphological variability of *P. riphaea* and key characters that can be used to separate this species from *P. laxa* and *P. nemoralis*. In all, 29 morphological characters and their ratios were measured (Appendix 1). Published characters that distinguish between *P. riphaea* and *P. laxa* were also included (Jirásek & Chrtek 1963, Chrtek & Jirásek 1966, Chrtek 2002). Other characters included followed Brysting et al. (1997) or were chosen based on our own preliminary morphometric analysis. Morphometric data were analysed using the statistical package SAS 9.1 (SAS Institute 2004), employing the procedures UNIVARIATE, CORR, PRINCOM, CANDISC and DISCRIM. Principal component analysis (PCA) was performed to visualize the variability present in the dataset and evaluate the contribution of individual characters. Canonical and classificatory discriminant analyses (the non-parametric k-nearest neighbour method with cross-validation) were used to review key diagnostic characters separating *P. riphaea* from *P. laxa* and *P. nemoralis,* respectively, and their contribution to the separation of the these species. Individual plants were used as operational taxonomic units. Attention was also paid to several morphological characters that were not measured (e.g. overall habit of plants).

Chromosome counts

Chromosome numbers were determined at the mitotic metaphase in somatic cells of root tips. The numbers were counted in cells of at least three different root tips of each specimen. The material was pre-treated with a saturated solution of p-dichlorobenzene for three hours, then fixed in a 3:1 mixture of 96% ethanol and acetic acid (Carnoy) and stained using lacto-propionic orcein. Chromosomes were counted under a Carl Zeiss Jena NU microscope equipped with an Olympus Camedia C-2000 Z camera.

Historical and recent distribution of Poa riphaea

Our study of the historical and recent distribution of *P. riphaea* in the Hrubý Jeseník Mts is based on an analysis of literture records (Wimmer & Grabowski 1827, Wimmer 1840, Fiek 1881, Oborny 1883, Formánek 1892, Podpěra 1926) and examination of specimens in the following herbaria: B, BRA, BRNM, BRNU, GLM, OL, OP, OVMB, PR, PRC, W, WRSL and WU (abbreviations follow Holmgren et al. 1990). During the course of the research, we visited most of the localities previously reported (Petrovy kameny rock, Mt Keprník, Tabulové skály rock, Velká Kotlina glacial cirque, rocks in vicinity of Švýcárna chalet, Mt Výrovka and Medvědí hřbet ridge).

Results

Isozyme analysis

All samples of *P. riphaea* (18 from Mt Petrovy kameny and one from a cultivated plant) had the same phenotype at all seven loci of five isozyme systems. At the inter-specific level, the phenotypes of *P. riphaea* differed from those of the other species studied. The one exception was the locus SOD-1, which was very similar to the phenotype of some *P. laxa* samples marked as phenotype SOD-1 B (Hoták et al. 2007). On the other hand, the 6-PGDH phenotypes of *P. laxa* and *P. babiogorensis* were nearly identical to each other but quite different from this isozyme system in *P. riphaea*. Compared to other species, phenotypes of *P. pratensis* from Mt Petrovy kameny were unique at all loci.

Morphometric analysis

The high morphological within-population variability of *P. riphaea* was predominantly for characters greatly affected by the environment (length and width of panicle, number of spikelets in the panicle, lengths of the longest branch at 1st and 2nd node). These characters contributed most significantly to the first axis of the principal component analysis. As to the characters that are little affected by the environment, there was high variability in the length of the ligule and of the line of hairs on the middle vein of the lemma. The morphological analysis revealed no significant difference between cultivated plants of *P. riphaea* and those collected in the field.

At the inter-specific level, the results of our morphometric analysis of *P. riphaea*, *P. nemoralis* and *P. laxa* correspond with the results of previous morphometric studies (Jirásek & Chrtek 1963, Chrtek & Jirásek 1966). On the ordination diagram of the PCA of all the samples of *P. riphaea* and *P. laxa* measured (Fig. 1), both species formed distinct groups. A subsequent discrimination analysis yielded a similar output (Fig. 2). The characters that correlated most strongly with the canonical axis, were the length of the ligule, lengths of the longest branch at the 1st and 2nd node, and the ratio between the length of the line of hairs on the marginal vein of the lemma and the length of the lemma (the absolute values of their total canonical structure exceeded 0.74). The first and third characters were confirmed as diagnostic characters. Despite their relatively high variability, lengths

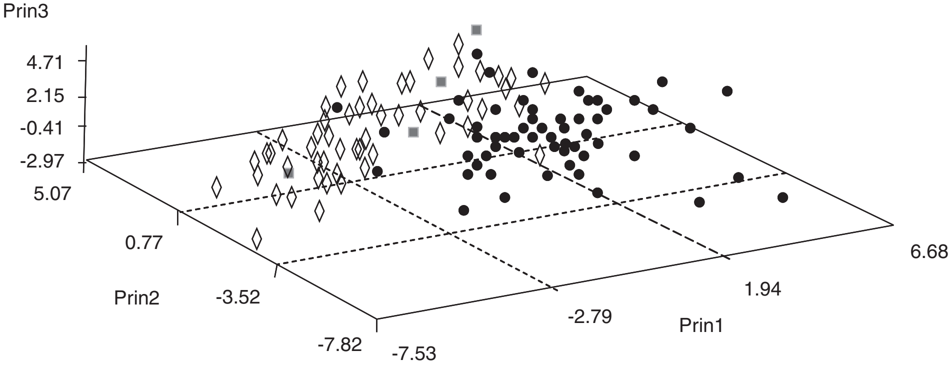

Fig. 1. – Ordination diagram of the PCA analysis of ◊ all the samples of *Poa riphaea* collected, ■ cultivated plants of *P. riphaea* and ● *P. laxa*. The first three components account for 32.7, 14.2 and 10.2% of the variation.

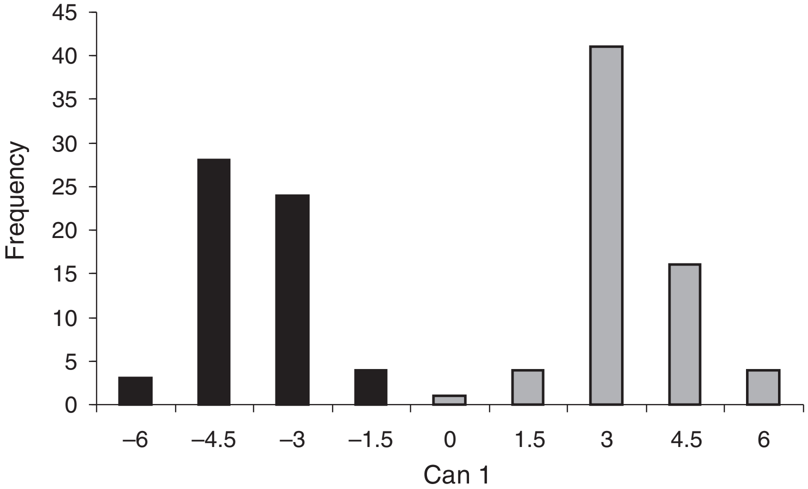

Fig. 2. – Histogram of the canonical discriminant analysis of ■ *Poa riphaea* and ■ *P. laxa*.

of the longest branch at the 1st and 2nd node turned out to be new characters separating the two species. Of the other previously published distinguishing characters (Chrtek 2002), the absolute value of 0.5 was exceeded by the length of the panicle. By contrast, width of the panicle and the ratio between the sheath and blade of the uppermost culm leaf were rather problematic characters.

The populations of *P. nemoralis* from the Hrubý Jeseník Mts were clearly separated from *P. riphaea*. Both species formed distinct groups in the ordination diagram of the PCA (Fig. 3) and in the output of the discriminant analysis (Fig. 4). Characters that were most strongly correlated with canonical axis, were length of ligule, length of the longest branch at the 2nd node and length of the blade of the uppermost culm leaf (the absolute values of

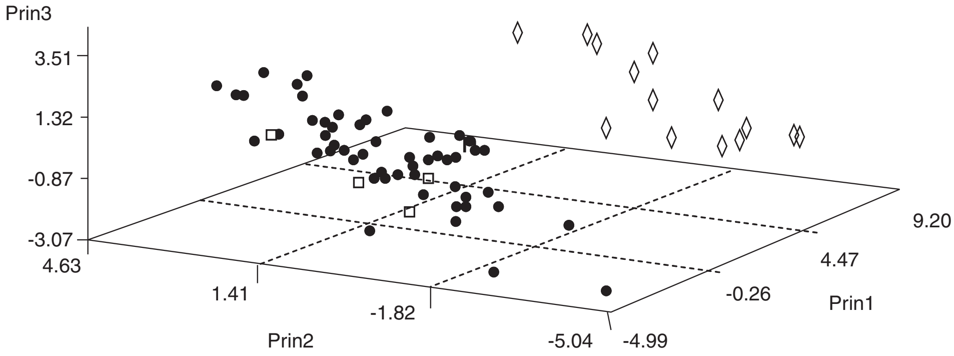

Fig. 3. – Ordination diagram of the PCA analysis of ● *Poa riphaea* from Petrovy kameny, □ cultivated plants of *P. riphaea* and ◊ *P. nemoralis*. The first three components account for 38.1, 18.8 and 6.7% of the variation.

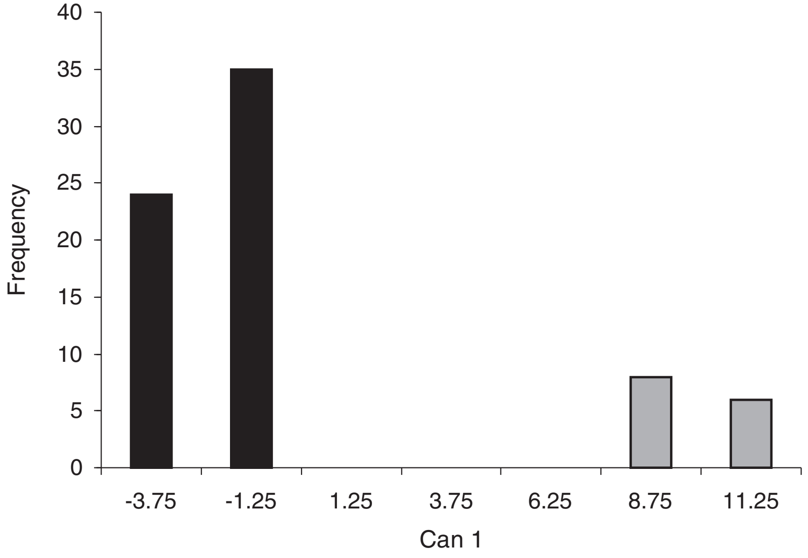

Fig. 4. – Histogram of the canonical discriminant analysis of ■ *Poa riphaea* and ■ *P. nemoralis*.

their total canonical structure exceeded 0.8). However, the other 12 characters exceeded the absolute value of 0.5. Some of them, e.g. number of branches at the 1st (lowest) and 2nd panicle node, ratio between length of the line of hairs on the vein between central and marginal veins of lemma and length of lemma, are reported as diagnostic characters in previous studies (Chrtek & Jirásek 1966, Chrtek 2002). The statistics of the above-mentioned characters are presented in Table 1.

Morphological separation of all three species was confirmed by K-nearest neighbours non-parametric classificatory discriminant analysis (k = 10), which correctly classified all the plants of *P. riphaea*, *P. laxa* and *P. nemoralis*.

Table 1. – Results of descriptive data analysis of the most important characters and problematic characters, respectively, separating the species *Poa laxa* (PL), *P. riphaea* (PR) and mountain populations of *P. nemoralis* from the Hrubý Jeseník Mts (PN). LL – length of ligule, LB1 – length of the longest branch at 1st node of panicle, LB2 – length of the longest branch at 2nd node of panicle, NB1 – number of branches of 1st (lowest) panicle node, NB2 number of branches of 2nd panicle node, RLM – ratio between the length of the line of hairs on the marginal vein of the lemma and length of the lemma, RLV – ratio between length of line of hairs on vein between central and marginal veins of lemma and length of lemma, LP – length of the panicle, WP – width of the panicle, LBL – length of blade of uppermost culm leaf, RSB – ratio between blade and sheath of the uppermost culm leaf (all length and width values in mm). Important characters for separation of *P. riphaea* and *P. laxa* are LL, LB1, LB2, RLM and LP, important characters for separation of *P. riphaea* and *P. nemoralis* are LL, LB1, LB2, NB1, NB2, RLV, LBL and RSB, problematic characters for separation of *P. riphaea* and *P. laxa* are WP and RSB.

Character	Species	Mean	Median	Standard deviation	Percentile	
					10%	90%
LL	PL	3.9	3.9	0.5	3.2	4.5
	PR	2.3	2.3	0.3	1.9	2.7
	PN	0.4	0.4	0.07	0.3	0.5
LB1	PL	19	19.5	6	12	26
	PR	8.1	8	4	4	14
	PN	18.7	17.5	5.7	13	28
LB2	PL	15.9	15.5	4.7	9	22
	PR	6.5	6	2.9	3	11
	PN	18	17	3.9	13	22
NB1	PL	1,9	2	0.7	1	3
	PR	1.6	2	0.6	1	2
	PN	2.8	3	1	2	4
NB2	PL	1.8	2	0.6	1	2
	PR	1.8	2	0.5	1	2
	PN	3.3	3	0.9	2	5
RLM	PL	0.4	0.4	0.07	0.3	0.7
	PR	0.5	0.5	0.06	0.5	0.6
	PN	0.5	0.5	0.03	0.5	0.5
RLV	PL	0.07	0	0.1	0	0.2
	PR	0.3	0.4	0.2	0	0.5
	PN	0	0	0	0	0
LP	PL	47.9	47.5	8.5	38	62
	PR	34.8	34	10.1	21	48
	PN	52.7	50	10	42	67
WP	PL	8	7	3.6	4	13
	PR	8.1	5	6.7	2	20
	PN	9.2	9.7	3.8	5	15
LBL	PL	36.3	36	12.3	21	54
	PR	29.9	29.5	9.1	22	43
	PN	60.9	59	10.7	52	78
RSB	PL	0.9	0.9	0.3	0.7	1.4
	PR	1.1	1	0.4	0.7	1.8
	PN	1.9	1.8	0.3	1.4	2.3

Chromosome number

The chromosome number 2n = 56 was estimated for both cultivated plants of *P. riphaea* (counted by Z. Hoták and V. Jarolímová). This number corresponds to the octoploid level. To our knowledge, it is the first verified record for this species.

Historical and recent distribution of Poa riphaea

Although the recent occurrence of *P. riphaea* was confirmed only at the tor of Mt Petrovy kameny, there are literary records of as many as seven different localities in the Hrubý Jeseník Mts (Petrovy kameny, Keprník, Výrovka, rocks in vicinity of the road from Švýcárna chalet, Medvědí hřbet, Praděd, Velká Kotlina; see e.g. Jirásek & Chrtek 1963). In total, 112 herbarium specimens of *P. riphaea* were revised (Appendix 2). Besides a very rich collection of specimens from Mt Petrovy kameny (96) there were specimens from two other localities. Six specimens came from the Tabulové skály rock on the slope of Mt Praděd and nine from the Velká Kotlina glacial cirque. The oldest specimens from all three localities are dated the end of the 19th century (Winkler 1867 B, WRSL, WU 'an Felsenspalten der Petersteins im Mährischen Gesenke', Oborny 1882 PRC 'Tafelsteine', Rieger 1891 OP 'Felsen in Gr. Kessel'). The most recent exactly dated specimen, which was probably from the Tabulové skály rock, was collected in 1900 (Schäfer 1900 GLM). The last specimen from Velká Kotlina was collected in 1961 [Pokluda 1961 BRNM 'Hrubý Jeseník: Velká Kotlina: na skalách při jihozáp. exp., cca 1300 m n.m. (ve štěrbinách)']. There is material from the population at Petrovy kameny, which documents its continuous occurrence up to the present (Peš 1992 OP). One cultivated specimen came from Olomouc botanical garden (Otruba 1941 OLM). The specimens of *P. riphaea* were labelled as *P. laxa* var. *riphaea* (Asch. et Graebn.) Polívka, *P. laxa* subsp. *riphaea* (Asch. et Graebn.) Hegi, *P. caesia*, *P. glauca* or even as *P. alpina* L. and *P. supina* Schrad. On the other hand, a few specimens labelled as *P. riphaea* were misidentified (e.g. '*P. riphaea*, Velká Kotlina' 1971 Moravcová OVMB as *P. alpina*).

Our field research confirms the occurrence of *P. riphaea* at Mt Petrovy kameny, where the population consisted of ca 110 specimens (counted by Z. Hoták in 2004). No other population was found at Tabulové skály rock and the Velká Kotlina glacial cirque.

Discussion

Intrapopulation variability

The genetic homogeneity recorded for the only extant population of *P. riphaea* was inconsistent with the morphological heterogeneity of the plant material collected. However, this variability was restricted to characters greatly affected by the environment. These characters also showed a high degree of reciprocal correlation although the values for the correlations did not exceed the limits for exclusion from the analysis (correlation coefficients did not exceed the value 0.95). Despite the limited number of individuals, they occur in a wide range of microhabitats in terms of their exposure to humidity and different soil conditions. These factors apparently influence the habit of the plants.

The literary record in Laus (1927) of the co-occurrence of *P. laxa* and *P. riphaea* at Mt Petrovy kameny can be attributed to the morphological plasticity of *P. riphaea*. Some plants of *P. riphaea* that grow in shady fissures morphologically resemble *P. laxa*. They have lax panicles and lack the typical glaucous colouration, but characters on their lemmas and ligules are characteristic of *P. riphaea*. The supposition, moreover, that these plants are hybrids between *P. riphaea* and *P. nemoralis* (V. Kavalcová, pers. comm.) is untenable. They lack any intermediate morphological characters except for a long lax panicle and long leaf blades. Furthermore, their isozyme patterns are identical to those of *P. riphaea*.

The results of our isozyme analyses, which detected genetic homogeneity, cast doubt on the existence of several chromosome numbers within *P. riphaea* (Dostál 1989), even though we counted the chromosome numbers of only two cultivated plants. Dostál's counts were probably taken from records of *P. glauca* in central Europe, e.g. 2n = 42, 49, 56 (Duckert-Henriod & Favarger 1987) for Swiss populations.

During its existence the restricted population of *P. riphaea* at Mt Petrovy kameny could have undergone fluctuations in size resulting in loss of genetic variability. Nevertheless, it is probable that the main reason for the genetic homogeneity of *P. riphaea* is its breeding system. Very low or undetectable genetic variability is typical of agamospermy, which is the prevailing breeding system in the *P. glauca* s.l. complex (Pálsson 1986, Kelley et al. 2009). Considering the above facts, it is possible that the present population of *P. riphaea* could be a clone of one plant.

Differentiation between Poa riphaea and other species

Our results are in accordance with the conclusions of previous studies (Jirásek & Chrtek 1963, Chrtek & Jirásek 1966). *Poa riphaea* is a species distinct from *P. laxa* both genetically and morphologically. Chromosome numbers of the two species also differ (*P. laxa*: 2n = 28; Duckert-Henriod & Favarger 1987, according to a summary of records for various localities throughout the distribution of this species). Most of the key characters separating these species were confirmed (e.g. length of ligule, length of panicle), and new distinguishing characters were found (lengths of the longest branch at 1st and 2nd node). The material studied did not allow us to assess some important anatomical and morphological characters such as length and shape of anthers, shape of endodermis wall cells. Their significance is indisputable because they are not environmentally dependent. Nevertheless, some published key characters (Chrtek 2002) are subject to environmental influence (e.g. ratio between sheath and blade of the uppermost culm leaf) or phenology (width of panicle), for that reason their use is quite limited. During the flowering phase panicle branches turn outwards and a panicle is relatively broad, after this phase the panicle becomes compressed, therefore lengths of the longest branches of the 1st and 2nd nodes seem to be a more useful equivalent character. Some distinguishing characters that were observed but not measured (colouration, shape of branches, stems and panicles) were also problematic for plants growing in extreme conditions. Uncritical use of these characters could have caused the misinterpretations mentioned in the previous part of the discussion. Also populations of *P. nemoralis* from Mt Keprník and the Tabulové skály rock differ from *P. riphaea*. Although their habit and slightly glaucous colouration can be similar to that of *P. riphaea*, morphological analysis clearly separated these two species and confirm the results of a previous study (Chrtek & Jirásek 1966).

Poa babiogorensis and *P. pratensis* were also included in the isozyme analysis. The genetic divergence recorded for *P. babiogorensis* is in accordance with the morphological and ecological differentiation of the Carpathian endemic species belonging to the *P. glauca* s.l. complex (Bernátová et al. 1999). However, this problem needs to be studied in detail. The isozyme pattern of *P. pratensis* is completely different from that of *P. riphaea*, which confirms the high genetic divergence recorded between *P. pratensis* and the section *Stenopoa* (Gillespie & Soreng 2005).

What was the historical occurrence of Poa riphaea in the Hrubý Jeseník Mts?

Reported localities of *P. riphaea* can be divided into two main groups: localities below the timberline that are rather dubious and those above the timberline with a possibility of at least historical occurrence. The first group comprises three localities in the central part of the Hrubý Jeseník Mts (rocks in the vicinity of the road from Švýcárna chalet, Medvědí hřbet ridge, Mt Výrovka, ca 1100–1261 m a.s.l.). The habitats at all these localities are relatively small rocks covered by primary mountain forest. There are no subalpine plant species there. Moreover, there are no herbarium specimens for these localities, and our field research did not confirm the occurrence of *P. riphaea* there. The authors of these records could have mistaken *P. nemoralis* for *P. riphaea,* but we also did not find *P. nemoralis* there. The probability that *P. riphaea* occurred at these localities is obviously very low.

The second group consists of localities above the timberline in the subalpine zone of the Hrubý Jeseník Mts (Petrovy kameny, Velká Kotlina, Tabulové skály, Keprník, ca 1300–1460 m a.s.l.). In the case of the Velká Kotlina glacial cirque, the timberline is lowered by avalanches. Many other high-mountain plant species are also found at these localities. In this group, the locality with the least reliable historical occurrence of *P. riphaea* is Mt Keprník. Despite the very old literature records (Wimmer & Grabowski 1827, Wimmer 1840), all herbarium specimens for this locality found during this study evidently belonged to a mountain ecotype of *P. nemoralis*. During our field research, also a recent occurrence of *P. nemoralis* was confirmed at the summit of Keprník. Considering these facts, the remote location of this locality from other localities and taxonomical problems in the early stage of the research on this species, the misidentification with *P. nemoralis* is also the most likely explanation for Mt Keprník locality.

In contrast to the previous locality, there are herbarium specimens of *P. riphaea* for the next three localities. Although it is possible that in some cases the plants of *P. riphaea* collected from Mt Petrovy kameny could be mixed with other plant material from the Tabulové skály rock or the Velká Kotlina glacial cirque, these two localities are confirmed by several collectors and, e.g. Oborny vouched for two localities. At the Tabulové skály rock on the side of Mt Praděd, there is still a small population of *P. nemoralis*, but the oldest herbarium specimens for this locality belong to *P. riphaea* (however, later specimens, e.g. Korb 1935 W, belong to *P. nemoralis*). The character of this locality is very similar to the only recent locality at Mt Petrovy kameny and the historical occurrence of this species at this locality is very likely. The disappearance of this local population was probably connected with stone mining at this locality for the construction of the first lookout tower on the summit of Mt Praděd at the beginning of the 20th century. The occurrence in the Velká Kotlina cirque poses a similar problem. The last specimens for this locality are dated 1960s. Since then, despite very detailed research (Jeník et al. 1983a, b and our own research) *P. riphaea* has not been found there again. However, considering the total area of the cirque and its vertical structure, its presence there cannot be ruled out.

Poa riphaea is richly represented in herbarium collections, which shows that the only current population at Mt Petrovy kameny is only a fragment of a once much larger population. The decline is thought to be due to a combination of previously intensive tourism, which was restricted in 1984, dry summers in past decades and probably also air pollution (Kavalcová 2003). It is very likely, however, that inconsiderate sampling of herbarium material started the decline as early as the first half of the 20th century. Moreover, the vulnerable biotope of moss terraces suffered considerable disturbance, which could have intensified the effect of the above-mentioned risk factors.

Our research indicates that *P. riphaea* used to have a small distribution area in the central part of the Hrubý Jeseník Mts, which was restricted to a few rocky localities (Petrovy kameny rocks, Tabulové skály rocks, Velká Kotlina glacial cirque) in the subalpine zone. This distribution dwindled to the point that today only a single locality remains. The former distribution was probably a remnant of a broader area occupied by the *P. glauca* s.l. group in central Europe during glacial times. Currently, this group, including the Carpathian endemic species and populations of *P. glauca* s. str. in the Eastern Alps, has a disjunct distribution and is restricted to isolated, relict localities (Bernátová et al. 1999, Niklfeld pers. comm.).

Identification key

This identification key for *Poa riphaea*, *P. laxa*, mountain populations of *P. nemoralis* and *P. pratensis* from Hrubý Jeseník Mts is based on anatomical and morphological data from the present paper and previous studies ((Jirásek & Chrtek 1963, Chrtek & Jirásek 1966, Chrtek 2002). Brief comments on the distribution of these species on subalpine rocks in Hrubý Jeseník Mts are attached.

1a Number of branches at the 1st and 2nd node of panicle 3–5 (–7). (If only 2 branches are present, then ligule is shorter than 0.7 mm) 2

1b Number of branches at the 1st and 2nd node of panicle 1–2 3

2a Ligule shorter than 0.7 mm. – Plants variable in colouration, usually slightly glaucous; leaf blades 1.5–2.5 mm broad; lemma at base sparsely lanate. Several localities in the subalpine belt of the Hrubý Jeseník Mts (Keprník, Tabulové skály rock, Velká Kotlina glacial cirque, ? Petrovy kameny rock) .... ***P. nemoralis*** L.

2b Ligule 1–2 mm long. – Plants dark green; leaf blades 2–4 mm broad; lemma at base densely lanate. Few plants at Petrovy kameny rock .... ***P. pratensis*** L. s. str.

3a Ligule 3–4,5 mm long; panicle branches smooth, the longest branch of the 1st node of the panicle 12–26 mm long; anthers 1–1.4 (–1.6) mm long; root epidermal cell walls differ in thickness. – Plants forming loose tufts; stems often arch-shaped, soft; leaf blades green to bluish green; panicles weak, pendulous, ca 3–6 (–8) cm long; spikelets with 3–5 florets, usually with violet colouration; lemma at base lanate. In the Czech Republic only in the Krkonoše Mts .... ***P. laxa*** Haenke

3b Ligule 1.9–2.7 mm long; panicle branches scabrous, the longest branch of the 1st node of the panicle 4–14 mm long; anthers 2–2.4 mm long; root epidermal cell walls of equal thickness. – Plants forming dense tufts; stems usually erect, rigid; leaf blades dark or greyish green; panicles dense, usually erect (rarely pendulous), ca 2–5 cm long; spikelets with 2–3 (–4) florets, usually dirty yellow-green without distinctive violet colouration; lemma at base sparsely lanate or sometimes not lanate. Recently only at Petrovy kameny rock .... ***P. riphaea*** (Asch. et Graebn.) Fritsch

Typification of *Poa riphaea*

Poa riphaea (Asch. et Graebn.) Fritsch, Exkursionsfl. Oesterreich. 65 (1909).

Basionym: *Poa laxa* IV. *riphaea* Asch. et Graebn., Syn. Mitteleur. Fl. 2(1): 400–401 (1900).

Ascherson and Graebner did not designate a type specimen of *P. riphaea* (Ascherson et Graebner 1900). The original material was probably in Ascherson's collection, which was deposited at the Botanical Museum in Berlin-Dahlem (B). The original material could not be found during a visit by one of the authors of this study (J. Štěpánek) in December 2009. It was probably destroyed by fire during a bombing raid on the night of March 12, 1943 (Vogt, the curator of the herbarium, pers. comm.). For this reason, we designate below a neotype for *P. riphaea*:

Neotype (neotypus hoc loco selectus): '*Poa laxa* Haenke v. *riphaea* Aschers., skály Petrštýnu v Jeseníku,' ['*Poa laxa* Haenke v. *riphaea* Aschers., the Petrštýn rocks (Petrovy kameny) in the Jeseník Mts.'] 16 Jul 1937, leg. J. Otruba (herb. PRC 451530).

Synonyms:
≡ *P. laxa* subsp. *riphaea* (Asch. et Graebn.) Hegi, Ill. Fl. Mitt.-Eur. 1: 312 (1908).
≡ *P. laxa* var. *riphaea* (Asch. et Graebn.) Polívka, Klíč k úplné květeně zemí Koruny české 1: 758 (1912).
– *P. aspera* sensu Wimm. et Grab. p. p., Fl. Siles. 1: 74 (1827), non Gaudin (1811).
– *P. nemoralis* var. *glauca* sensu Wimm. p. p., Fl. Schles. 427 (1841), non Gaudin (1811).
– *P. caesia* p.p. sensu auct. flor. e Sudetis (Hrubý Jeseník) (e.g. Fiek 1881, Oborny 1881, Formánek 1892), non Smith (1800).

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Souhrn

V příspěvku jsou shrnuty výsledky studia lipnice jesenické (*Poa riphaea*) – endemického druhu Hrubého Jeseníku, v rámci něhož byly získány poznatky o vnitropopulační variabilitě, počtu chromozómů, a historickém rozšíření druhu. Pozornost byla věnována i problematice udávané příbuznosti k lipnici plihé (*P. laxa*). Rovněž byla provedena typifikace jména *P. riphaea* a vybrán neotyp. Podle výsledků isoenzymové analýzy nebyla u studovaného druhu zjištěna žádná genetická vnitropopulační variabilita, zaznamenaná morfologická variabilita byla diskutována ve vztahu k podmínkám prostředí lokality. Mezi druhy *P. riphaea* a *P. laxa* byla zjištěna karyologická a genetická divergence, potvrzena byla rovněž velká část morfologických znaků udávaných k jejich odlišení. S ohledem na časté záměny *P. riphaea* s horskými ekotypy *P. nemoralis* z nejvyšších partií Hrubého Jeseníku byly přezkoumány i morfologické znaky odlišující tyto dva druhy; i mezi nimi byla prokázána jasná diferenciace. Poprvé byl pro druh *P. riphaea* stanoven počet chromozómů: 2n = 56 (oktoploidie). Rozbor současného a historického rozšíření druhu *P. riphaea* v Hrubém Jeseníku byl proveden na základě studia literárních údajů, herbářových dokladů a vlastního terénního výzkumu. Kromě jediné existující lokality Petrovy kameny byl historický výskyt potvrzen na dalších dvou lokalitách (Tabulové skály, Velká Kotlina). Věrohodnost dalších literárních údajů o výskytu tohoto druhu byla rozebrána v diskusi.

Klíč k určení druhů *Poa riphaea*, *P. laxa*, *P. pratensis* a horských populací *P. nemoralis* z Hrubého Jeseníku

1a Větévky dolních dvou pater laty vyrůstající po 3–5 (–7). (Jsou-li přítomny pouze 2 větévky, pak jazýček kratší než 0,7 mm) 2
1b Větévky dolních dvou pater laty vyrůstající po 1–2 3
2a Jazýček kratší než 0,7 mm. – Zbarvení rostlin proměnlivé, rostliny obvykle nasivělé; čepele listů 1,5–2,5 mm široké; plucha na bázi s řídkou huninkou chlupů. Několik lokalit v subalpínském pásmu Hrubého Jeseníku (Keprník, Tabulové skály, Velká Kotlina, ? Petrovy kameny) .... ***P. nemoralis*** L.
2b Jazýček 1–2 mm dlouhý. – Rostliny tmavě zelené; listové čepele 2–4 mm široké; plucha na bázi s bohatou huninkou. Ojedinělé rostliny rostoucí na Petrových kamenech .... ***P. pratensis*** L. s. str.
3a Jazýček 3–4,5 mm dlouhý; větévky laty hladké, nejdelší větévka spodního patra laty 12–26 mm dlouhá; prašníky 1–1,4 (–1,6) mm dlouhé; stěny buněk kořenové endodermis nestejně silné. – Rostliny řídce trsnaté; stébla často obloukovitě prohnutá, měkká; čepele listů zelené až modrozelené; lata řídká, na vrcholu převislá, ca 3–6 (–8) cm long; klásky 3–5květé, zpravidla fialově naběhlé; plucha na bázi s huninkou vláknitých chlupů. V České republice pouze v Krkonoších .... ***P. laxa*** Haenke

3b Jazýček 1,9–2,7 mm dlouhý; větévky laty drsné, nejdelší větévka spodního patra laty 4–14 mm dlouhá; prašníky 2–2,4 mm dlouhé; stěny buněk kořenové endodermis stejně silné. – Rostliny hustě trsnaté; stébla obvykle přímá, tuhá; čepele listů tmavě zelené až šedozelené; lata hustá, obvykle přímá (vzácně na vrcholu převislá), ca 2–5 cm dlouhá; klásky 2–3 (–4)květé, obvykle špinavě žluté bez výrazného fialového nádechu; plucha na bázi s řídkou huninkou nebo vzácněji bez ní. V současnosti pouze Petrovy kameny
.... ***P. riphaea*** (Asch. et Graebn.) Fritsch

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Appendix 1. – List of measured characters for morphological analyses. For measurement of spikelet and spikelet parts (glumes, lemma, rachilla etc.) characters the lowest spikelet from the longest branch at the 1st (lowest) node was used.

1. number of culm leaves, 2. length of blade of uppermost culm leaf (mm), 3. length of sheath of the uppermost culm leaf (mm), 4. ratio between blade and sheath of the uppermost culm leaf, 5. length of ligule (mm), 6. length of panicle (mm), 7. width of panicle (mm), 8. length of 1st (lowest) internode of panicle (mm), 9. length of internode under panicle (mm), 10. number of panicle nodes, 11. number of branches of 1st (lowest) panicle node, 12. number of branches of 2nd panicle node, 13. number of branches of 3rd panicle node, 14. length of the longest branch at 1st node of panicle (mm), 15. length of the longest branch at 2nd node of panicle (mm), 16. number of spikelets of panicle, 17. number of spikelets of branches at 1st node, 18. number of spikelets of branches at 2nd node, 19. number of spikelets of branches at 3rd node, 20. length of spikelet (mm), 21. number of flowers in spikelet, 22. length of upper glume (mm), 23. length of lower glume (mm), 24. ratio between lengths of upper and lower glume, 25. length of lemma of lowest flower (mm), 26. length of lowest rachilla of lowest flower (mm), 27. ratio between length of haired line on central vein of lemma and length of lemma, 28. ratio between length of haired line on marginal vein of lemma and length of lemma, 29. ratio between length of haired line on vein between central and marginal veins of lemma and length of lemma.

Appendix 2. – List of revised herbarium vouchers of *P. riphaea* (both Czech and German names of the localities are mentioned; in parentheses the number of duplicates in the herbarium collection is reported).

Hrubý Jeseník Mts (Gesenke). – Petrovy kameny rock (Petersteine): Winkler 1867 B, WRSL, WU (2); Bachmann 1872 WU; Oborny 1882 PRC, 1886 BRNU, WU; Callier, Hirte & Scholz 1893 B, GLM, PRC, WRSL, WU; Teuber 1903 BRNU, BRNM, W, 1905 BRNM; Rothe 1903 BRNU, Podpěra 1906 BRNU; Laus 1906, 1907 (2), 1908, 1910, 1930 BRNU, 1907 (2), 1908 (2), 1933 BRNM, 1906, 1910, 1929 OLM, 1929 (2), 1935 OP, 1929, 1933 PR, 1911, 1924, 1929 (2), 1930, 1933 PRC, 1907, 1930 W, 1907 WU; Dvořák 1912 PRC, 1946 BRA; Skřivánek 1912, 1953 BRNM (2), 1955 BRA; Suza 1912 BRNM, BRNU; Weber 1926 OLM, 1934 BRNM, 1935 B, W; Kruber 1927 B; sine auct. 1927? PRC; Leneček 1928, 1934 PRC; O. & E. Behr 1931 W; Prinz 1931 PR; Laus & Weber 1932 BRNM; Thenius 1932, 1936, sine dat. BRNU; Schmeja 1934 OP, Otruba 1934, 1937 OLM, 1937 PRC; sine auct. 1934 PRC, Korb 1935 W (2); Preis 1935 PRC; Krajina 1946 PRC; Pospíšil 1946 BRNM (2); Šmarda 1947 BRNM (3); Deyl 1947, 1966, 1967 PR; Černoch 1954 BRNM; Duda & Krkavec 1958 OP; Pokluda 1959 BRNM (2), OP, 1961, 1963 BRA; Unar 1969 BRNU; Peš 1992 OP; Baenitz sine dat. GLM; Žižka sine dat. PRC. – **Tabulové skály rock (Tafelsteine) and Mt Praděd (Altvater):** Oborny 1882 PRC (2); Freyn 1883 BRNM; Hora 1889 PRC; Schäfer 1900 GLM; Prinz sine dat. PR. – **Velká Kotlina glacial cirque (Grosser Kessel):** Rieger 1891 OP; sine coll. 1915 BRNM; Dostál 1947 PR (2); Deyl 1947, 1952; Pokluda 1961 BRNM (3).
Cultivation. – Olomouc – botanical garden: Otruba 1941 OLM