The effect of serpentine on morphological variation in the *Galium pumilum* group (*Rubiaceae*)

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ABSTRACT: A total of 16 populations of taxa from the *Galium pumilum* group were examined for 14 morphological characters to asses the impact of serpentine habitats on their morphological variation. Univariate and multivariate statistical procedures were applied on a set of selected characters. The results of statistical analyses revealed notable differences in the morphology of serpentine and non-serpentine populations of *G. pumilum*. Significant differences were ascertained between a set of vegetative characters, while the variables of the generative parts of the plants showed conspicuous similarities. However, the ranges of variability in all the morphological characters of both ecotypes overlapped considerably. In contrast, serpentine populations of *G. valdepilosum* are not markedly different from non-serpentine ones. In *G. valdepilosum*, there are less contrasting characters of some environmental factors acting on serpentine and non-serpentine sites. This fact could be responsible for the morphological similarities among populations of *G. valdepilosum*. Both investigated taxa could be included within the group of species which are tolerant of ultramafic soil. As serpentine populations of *G. pumilum* show specific ecotypic responses to serpentine soil, the results of both karyological and morphological analyses indicate that serpentine and non-serpentine populations are probably not genetically isolated from each other.

KEYWORDS: *Galium pumilum* group, morphology, serpentine

Introduction

The patterns of variation among populations may reflect ecogenetic adaptation by natural selection to current ecological conditions. Variation within species may be influenced by two forces, that is ecogenesis (natural selection for current ecological conditions) and phylogenesis (past, historical events, including the effects of genetic drift and selectively neutral mutation, THORPE & al. 1994). Due to the unique properties of serpentine habitats, serpentine stimulates plant variation at all hierarchic levels - from the individual to the species. Conventional wisdom has it that azonal habitats, like those of ultramafic soils, are more stressful than nearby habitats on zonal soils. Therefore plants on ultramafic soils might be expected to show important differences in growth rates (KRUCKEBERG 1992). Serpentine rocks and their soils are characterized by toxic quantities of heavy metals particularly nickel and chromium, low nutrient levels, a high Mg/Ca ratio, drought and large temperature fluctuations, all of which lead to vegetation stress. Hence, it is to be expected that populations growing on such soil type must be adapted in various level to these special edaphic conditions.

Many studies dealing with the impact of serpentine habitats on plant variation have been published (e.g. COBON & MURRAY 1983, DENTON 1979, KRUCKEBERG 1984, 1986, MAYER & SOLTIS 1994, ŠTĚPÁNKOVÁ 1996, WESTERBERGH & SAURA 1992, WESTERBERGH & RUNE 1996). Today, the amount of land contamined with heavy metals has dramatically increased due to mining, smelting, and other industrial activities. Hence the questions on heavy metal tolerance in plants are still topical (e.g. BROWN & al. 1995, ERNST & al. 1992, SCHAT & TEN BOOKUM 1992, SCHAT & KALFF 1992).

The *Galium pumilum* group is well known for its intricate morphological and chromosomal variation. Morphological variation seems to be particularly pronounced in high polyploids, hexa- or octoploids, that are widely distributed throughout Europe, while the diploids and the tetraploids prevail in South and Central Europe, often distributed in small and isolated areas. Several factors acting interactively must be invoked to explain the very complicated pattern of variability within the *G. pumilum* group. The most important ones can be summarized as follows: polyploidy, hybridization and phenetic plasticity.

The major work leading to the elucidation of the taxonomic and evolutionary relationships in the genus *Galium* L. sect. *Leptogalium* LANGE was done by EHRENDORFER (e.g. 1949, 1953, 1956, 1962). There are several studies on the taxonomic revision of this section in particular parts of Europe, e.g. Germany (WÖRZ 1995), Poland (KUCOWA 1962), Slovakia (ŠIPOŠOVÁ 1987). The comprehensive study on the cytogeography of this group was done by KRENDL (1993).

Despite the work of EHRENDORFER (1956), who revealed the ecological specialization of particular members of the *G. pumilum* group, there is a lack of detailed studies focusing on the problems of adaptation to such different environments as these represented serpentine and non-serpentine habitats. As the first step in understanding the processes of evolutionary divergence caused by ecological, namely edaphic conditions, the morphology of the two representatives of the *G. pumilum* group were studied.

To clarify the role of serpentine within the processes of morphological differentiation, two questions were considered:

1. how within- and between-population variations contribute to the overall variability of *Galium pumilum* MURRAY and *G. valdepilosum* HEINR. BRAUN,

2. whether possible differences in morphological variation between populations are related to their occurrence on and off serpentine habitats.

Material and methods

Sites and sampling. This study is entirely based on material collected in the field. Sixteen populations of *Galium pumilum* and *G. valdepilosum*, originating from localities in the Czech Republic, were sampled in 1992-1996. The individuals were chosen at random within each locality. The list of localities are given in Tab. 1. Serpentine sites are relatively small and isolated from each other. The characteristics of the soils are in good agreement with those generally assumed for ultramafic soil. The ratio of Ca/Mg is low and ranged from 0.36-3.99. In contrast the concentration of heavy metals in the soil is high. The concentration of Ni ranged from 4.82 µg/g to 6.39µg/g, Cr 0.06-8.25 µg/g and Co 0.08-1.30 µg/g . More details on the chemical analysis of the soils from sampled localities are presented in the paper by KRAHULCOVÁ & ŠTĚPÁNKOVÁ (1997). Non-serpentine localities were selected in a wide range of habitats. The populations were collected on basiphylous substrates as well as from silicate.

Measurements. Fourteen selected morphological characters, listed in Tab. 2, were measured on 480 individuals. From each individual the longest leaf was taken for measurements. Roughness of the leaf margin and density of hairness was scored (see Tab. 2). Plant height was measured from the node where the stem emerges from the ground. All characters were measured on dry plants, only corolla size was measured after boiling the corolla.

Statistical analysis. Univariate and multivariate statistical procedures were applied to the set of selected traits. The multivariate technique Canonical discriminant analysis (CDA) was performed in order to examine the pattern of overall morphological variation among all of the populations simultaneously. Univariate statistical analyses (basic description statistics, analysis of variance - ANOVA) were used to asses the contribution of each attribute to the differences among populations.

Results

Galium pumilum MURRAY

In Tab. 3 the numerical characteristic of the 14 evaluated morphological characters are presented. The results obtained from the Tukey test (ANOVA) show clearly, that from the overall set of characters, just two can be considered as unsuitable for distinguishing between morphology of serpentine and non-serpentine populations. Detailed morphological analysis reveals that, in relation to non-serpentine populations, the plants growing on serpentine soil are characterized by the following features: smaller plant height, shorter internodes, less divergently branched inflorescences, wider leaves, stem more pubescent at the base, leaves less rough at the margins. However, it is necessary to point out that the differences between serpentine and non-serpentine populations, resulting from statistical analyses, are very weak. There is great variation

Tab. 1. - List of the localities of the populations of *Galium pumilum* s. l.

No.	Locality	Coordinates	Altitude (m a.s.l.)
Galium pumilum MURRAY, non-serpentine populations			
1.	W Bohemia, on the slope above the road Vodná - Hlinky; Štěpánková 1995	50°06'30"N 12°51'40"E	550
2.	N Bohemia, České středohoří Mts, the edge of a quarry 1.1 km NE of Prackovice; Štěpánková 1995	50°34'30"N 14°01'00"E	250
3.	E Bohemia, pine wood 2 km NW of Polná; Štěpánková 1995	49°30'15"N 15°41'10"E	510
4.	C Moravia, the edge of the wood near a fishpond 0.8 km S of Jedovnice; Štěpánková 1995	49°20'15"N 16°45'20"E	470
Galium pumilum MURRAY, serpentine populations			
5.	W Bohemia, the edge of the wood N of Mnichov; Štěpánková 1995	50°03'15"N 12°47'30"E	650
6.	E Bohemia, serpentine rocks 0.5 km SE of Věžná - railway station; Štěpánková 1995	49°26'50"N 16°16'30"E	390
7.	E Bohemia, serpentine rocks 1 km SE of Šlapanov; Skála and al. 1992	49°32'00"N 15°40'20"E	500
8.	E Bohemia, serpentine rocks 1.7 km S of Staré Ransko; Štěpánková 1996	49°39'50"N 15°49'30"E	642
Galium valdepilosum HEINR. BRAUN, non-serpentine populations			
9.	N Bohemia, České středohoří Mts, N foothill of Boreč Mt, 0.5 km SW of Režný Újezd; Štěpánková 1995	50°31'00"N 13°59'30"E	420
10.	C Bohemia, S slopes above Želivka river, 1.7 km NW of Nesměřice; Štěpánková and Chrtek 1995	49°44'00"N 15°00'45"E	290
11.	S Bohemia, a rocky slope on the left bank of Křemžský potok brook, 2.3 km E of Holubov; Štěpánková and Chrtek 1996	48°53'30"N 14°21'30"E	490
12.	S Bohemia, W slope on the right bank of Vltava river, 0.6 km W of Zlatá Koruna; Štěpánková 1996	48°51'15"N 14°22'30"E	490
Galium valdepilosum HEINR. BRAUN, serpentine populations			
13.	C Bohemia, serpentine rocks on SW slope above Sedlický potok, highway bridge, 2.3 km NW of Bernartice; Štěpánková 1995	49°41'15"N 15°06'10"-20"E	380
14.	C Bohemia, pine wood on W slope above Sedlický potok, N of highway bridge, 2.5 km NW of Bernartice; Štěpánková, Skála and Krahulcová 1994	49°41'15"N 15°06'10"E	380
15.	S Bohemia, pine wood on the left slope above Křemžský potok brook, 1 km E of Holubov; Štěpánková and Chrtek 1994	48°53'30"N 14°20'30"E	490
16.	S Bohemia, pine wood on the left slope above Křemžský potok brook, ca. 600 m E of Holubov; Štěpánková and Chrtek 1994	48°53'20"N 14°20'30"E	480

Tab. 2. Characters investigated on the plants of *Galium pumilum* and *G. valdepilosum* from the population described in Tab. 1. (Number of observations per populations 30)

Character	Abbreviation	Measurement scale
Corolla size	cor	mm
Fruit length	frl	mm
Branch length	branch	mm
Number of leaves and leaf-like stipules per whorl	numbl	-
Plant height	planth	mm
Inflorescence length	infle	mm
Internode length	nodel	mm
Leaf length	leavl	mm
Leaf width	leavw	mm
Leaf roughness	roughl	0-1-2 (smooth to rough)
Stem hairness	hairs	0-1-2 (glabrous to dense hirsute)
Ratio of the plant height / inflorescence length	plin	-
Ratio of the leaf length / leaf width	ll	-
Ratio of the inflorescence length / branch length	inbr	-

Tab. 3. Numeric parametrs of 14 characters measured on the individuals from serpentine and non-serpentine sites of the species *Galium pumilum* and *G. valdepilosum*. Values in the table are: means ± s.d., HG – homogeneous group resulting from Tukey test, rows not showing the same letter are different at P<0.05. For abbreviations of the characters see Tab. 2.

Character	*Galium pumilum*			*Galium valdepilosum*		
	serp.	non-serp.	HG	serp.	non-serp.	HG
cor	3.72 ± 0.10	3.74 ± 0.15	a a	3.58 ± 0.10	3.55 ± 0.12	a a
frl	1.31 ± 0.05	1.34 ± 0.04	a a	1.33 ± 0.02	1.34 ± 0.02	a a
nodel	41.12 ± 7.59	64.83 ± 14.52	a b	38.00 ± 8.14	37.36 ± 6.17	a a
numbl	7.61 ± 0.75	7.28 ± 0.75	a b	6.57 ± 0.82	6.62 ± 0.68	a a
planth	257.62 ± 46.99	329.62 ± 49.12	a b	203.40 ± 45.90	200.60 ± 33.50	a a
branch	52.37 ± 12.39	73.44 ± 22.58	a b	63.23 ± 25.07	61.44 ± 12.92	a a
infle	128.85 ± 25.38	160.20 ± 55.11	a b	115.24 ± 42.00	109.40 ± 28.22	a a
leavl	16.37 ± 3.03	15.03 ± 3.10	a b	16.09 ± 2.42	16.26 ± 2.07	a a
leavw	1.66 ± 0.17	1.31 ± 0.19	a b	1.51 ± 0.24	1.48 ± 0.19	a a
roughl	5.25 ± 2.20	7.00 ± 1.18	a b	5.09 ± 1.70	5.57 ± 1.72	a b
hairs	0.59 ± 0.67	0.12 ± 0.32	a b	1.42 ± 0.83	1.33 ± 0.83	a a
inbr	2.51 ± 0.49	2.26 ± 0.85	a b	1.86 ± 0.42	1.80 ± 0.39	a a
plin	2.04 ± 0.43	2.27 ± 0.74	a b	1.89 ± 0.49	1.93 ± 0.49	a a
ll	9.89 ± 1.78	11.53 ± 2.02	a b	10.79 ± 1.73	11.08 ± 1.75	a a

apparent both within and between the populations at each site for all the morphological attributes, and the ranges of the attributes overlap considerably between sites. In addition, the analysis of variance ANOVA revealed that intrapopulation variation represents the main source of overall variability, while the proportion of interpopulation variation is also equally low in the species concerned.

Galium valdepilosum HEINR. BRAUN

For this study it seems that ploidy variation affects the morphology of *G. valdepilosum* more than serpentine. While the populations of *G. pumilum* examined were homogeneous in chromosome number, belonging to octoploid (2n=88) cytotype only, within *G. valdepilosum* two cytotypes were found in the Czech Republic (KRAHULCOVÁ & ŠTĚPÁNKOVÁ 1997): diploid 2n=22 and tetraploid 2n=44. The distribution area of the diploid populations is restricted to the region of SW Moravia, from where their occurrence continues into Lower Austria, whereas the tetraploids in the studied area have a wider distribution in Bohemia, extending into eastern Bavaria .

There are considerable differences in morphology between diploid and tetraploid cytotypes. The most pronounced dissimilarities are expressed in the size of the corolla and length of fruit.

To discover the effect of serpentine on the differentiation of populations of *G. valdepilosum*, only one cytotype was statistically processed. The tetraploid populations were chosen because there was an inadequate number of samples of diploids although both cytotypes occur on serpentine and non-serpentine sites.

For this taxon, the statistical processing of the data set gives a rather different picture of variation in comparison with *G. pumilum*. Taking the results of analysis of variance ANOVA, it can be concluded that there only is one character - leaf roughness which distinguishes populations of serpentine from non-serpentine sites. There are no statistically significant differences in other characters between populations growing on and off serpentine soils. Similarly to *G. pumilum*, the sample sets of *G. valdepilosum* showed a higher proportion of within population variability than between population variability.

Discriminant analysis

Canonical discriminant analysis (CDA) was used to reveal the pattern of morphological variation between serpentine and non-serpentine populations belonging to *G. pumilum* and *G. valdepilosum*.

The discriminant scatter diagram (Fig. 1) provides some insight into the morphological distinctiveness of *Galium pumilum* populations growing on and off serpentine soils. Particular populations were used as a classification factor. The plot shows the population centroid and the distribution pattern of population data plotted on the basis of the two (out of seven) most discriminating functions. These discriminant functions accounted for 98.1% of the variability among populations. As the group

34

Character	Axis 1	Character	Axis 2	Character	Axis 1	Character	Axis 2
infle	1.61	ll	2.36	infle	-1.05	infle	1.35
leavw	-1.09	leavl	-1.57	roughl	0.86	inbr	-0.72
plin	0.86	leavw	1.17	ll	0.61	hairs	0.64
ll	-0.69	planth	-0.46	branch	0.59	branch	-0.64
planth	-0.63	branch	0.36	hairs	0.57	leavw	0.63
inbr	-0.51	plin	0.31	inbr	0.33	roughl	-0.45

separation is relatively weak, two major clusters can be distinguished. Group centroids of serpentine populations are in the first, group centroids of non-serpentine populations are combined in the second. The values of standardized coefficient show that variables contributing most to the discriminant power of the function are the length of inflorescence and width of leaves (Tab. 4). As expected, using serpentine and non-serpentine ecotypes as the classification factor, the length of inflorescence and width of leaves are most effective in the disccriminating proces as well.

The discriminant diagram in Fig. 2 illustrates group centroids and the distribution pattern ascertained for *Galium valdepilosum* populations. As was already mentioned above, to detect the impact of serpentine on morphological divergence only tetraploid cytotype was included within the set of attributes. It is evident from Fig. 2 that populations of *G. valdepilosum* posses a rather different pattern of morphological variation. This is in accordance with the results of univariate statistical procedures. There is no group of serpentine populations clearly separated from all other populations on non-serpentine soils. The plot is made on the basis of the two most discriminating functions which accounted for 84.9% of the variability among the populations. Of the total 14 canonical variates the 1st-7th are significant at the 95% level. The values of standardized coefficient are summarized in Tab. 5. The variables contributing most to the discriminant ability of discriminant functions are the length of inflorescence and leaf roughness. If the serpentine and non-serpentine ecotypes were used as the classification factor, the different variables - length of branch and ratio inflorescence length/length of branch contributed most effectively to the discriminat function.

Discussion

In the present study, notable differences were found in the morphology of serpentine and non-serpentine populations of *G. pumilum*. Indeed, a unique character related to habitat type is found in the populations of *G. pumilum* growing on serpentine. However,
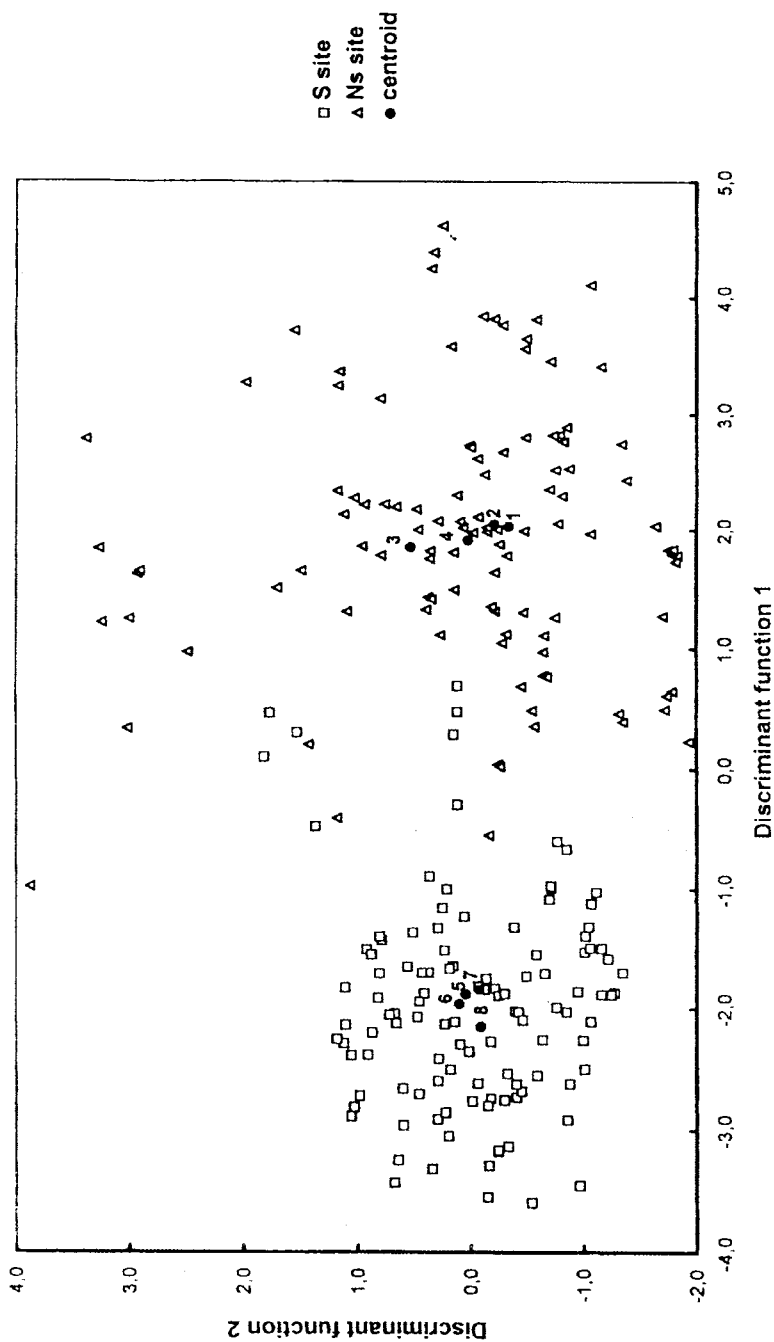
Fig. 1. Scatter diagram of CDA of the eight populations of *Galium pumilum* based on 14 measured characters (see Tab. 2). The populations' class means (centroids) are marked by numbers refering to those given in the Tab.1. NS site - non-serpentine sites, S - serpentine sites.
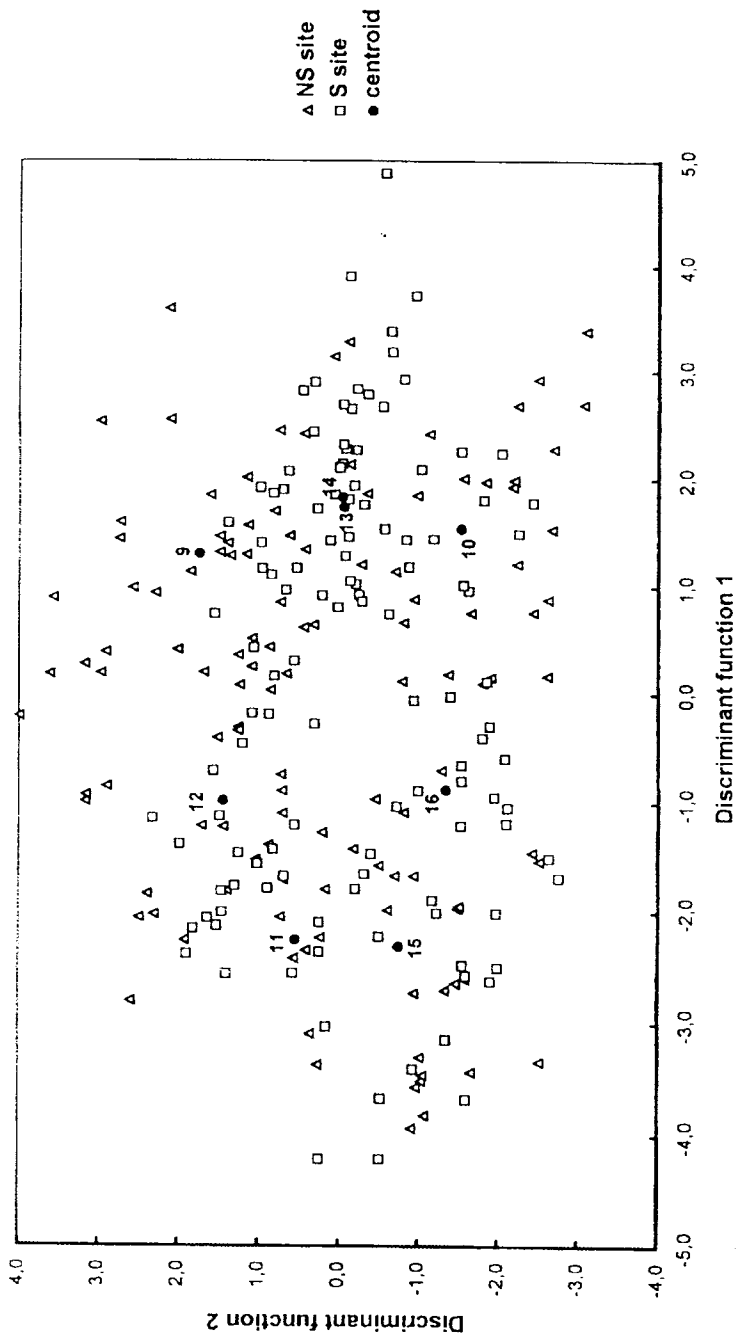
Fig. 2. Scatter diagram of CDA of the eight populations of *Galium valdepilosum* based on 14 measured characters (see Tab. 2). The populations' class means (centroids) are marked by numbers refering to those given in the Tab.1. NS site - non-serpentine sites, S - serpentine sites.

the ranges of variability in all the morphological characters of both ecotypes overlap considerably. It is necessary to point out, that considerable differences were ascertained between the vegetative set of characters, while the variability of the generative parts of the plants showed conspicuous similarity. In contrast, serpentine populations of *G. valdepilosum* are not markedly different from non-serpentine ones.

To explain a cause for the differences in morphological variation between serpentine and non-serpentine populations of *G. pumilum* and *G. valdepilosum*, different ecological factors for both species must be invoked, besides additional factors. In *G. pumilum*, the ecological differences between serpentine and non-serpentine sites are much more clearly expressed. The environmental, especially edaphic conditions of serpentine sites are quite different than those of non-serpentines ones. There is often a tendency for *G. pumilum* to grow on habitats of a mesic character (oligotrophic meadows or a range of woodland on deep brown earths), rarely on outcrops with skeletal soils derived from basiphylous or silicate substrata.

Unlike *G. pumilum*, most of the non-serpentine populations of *G. valdepilosum* show a rather narrow ecological amplitude. They were gathered on xeric and strongly exposed bedrocks with skeletal, base-rich or, more rarely, silicate soils. Hence, less contrasting characters of some environmental factors, acting both on and off serpentine habitats, could be responsible for the resemblance in morphology detected within the population set of *G. valdepilosum*. In addition, the other aspect must be stressed to explain the pattern of morphological variation of *G. pumilum* and *G. valdepilosum* in relation to serpentine. There is an absence of spatial isolation between serpentine and non-serpentine samples. The neighbouring, non-serpentine populations grow only a short distance from the closest serpentine ones and there is, therefore, a possibility for gene flow between particular populations in both directions. This gene connection could be responsible for buffering the effect of serpentine stress on morphological variation.

Floras on ultramafic soils can be strikingly unusual (KRUCKEBERG 1992). According to him there are three types of floristic elements in relation to serpentine: 1) serpentine endemics (e.g. *Streptanthus glandulosus* HOOK., *Alyssum bertolonii* DESV., *Cerastium alsinifolium* TAUSCH), 2) local or regional indicator species (e.g. *Cheilanthes marantae* (L.) DESV. on the serpentine of south Moravia, *Rhododendron lapponicum* (L.) WAHLENB. on the serpentine of Newfoundland and on Mt. Albert), and 3) bodenvag species, taxa widespread on serpentine and non-serpentine habitats (e.g. *Oberna behen* (L.) IKONNIKOV, *Achillea millefolium* L., *Arenaria serpyllifolia* L., *Thymus praecox* OPIZ).

Both taxa investigated could be included within the bodenvag species group, which are tolerant of ultramafic soils. As serpentine populations of *G. pumilum* show specific ecotypic responses to serpentine soil, the results of both karyological (KRAHULCOVÁ & ŠTĚPÁNKOVÁ 1997) and morphological analyses indicate that serpentine and non-serpentine populations are probably not genetically isolated from each other.

Acknowledgements

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