

Changes of seasonal characters in populations of *Melampyrum sylvaticum* along an altitudinal gradient^{*)}

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Melampyrum sylvaticum agg. represents a critical taxonomic group. Many infraspecific taxa have been described based on so-called seasonal characters. This study analyzes the variation of seasonal characters in the populations along a steep altitudinal gradient. The most important seasonal characters are the same at the level of the individual plant. Despite clear differentiation at the population level, any delimitation of taxa based on mere seasonal characters seems to be artificial and groundless.

ŠTECH M., 2012: Veränderung saisonaler Merkmale in Populationen von *Melampyrum sylvaticum* entlang eines Höhengradienten.

Melampyrum sylvaticum agg. ist ein kritischer taxonomischer Komplex. Auf Grund so genannter saisonaler Merkmale sind bereits viele infraspezifische Taxa beschrieben worden. Eine Analyse der saisonalen Veränderlichkeit in Populationen entlang eines steilen Höhengradienten ergab, dass die wichtigsten saisonalen Merkmale auf Ebene der Einzelpflanze durchgehend gleich sind. Obwohl auf Populationsebene eine deutliche Differenzierung festgestellt wurde, scheint eine Abgrenzung von Taxa nur auf Grund saisonaler Merkmale künstlich und ist daher ungerechtfertigt.

Keywords: *Melampyrum sylvaticum*, seasonal variation, infraspecific taxa.

Introduction

The hemiparasitic genus *Melampyrum* represents one of the most variable European genera at the infraspecific level. Two most important sources of this variation are a) genetic differentiation of populations due to enormous microspeciation rate and b) strong phenotypic plasticity due to large ecological amplitude of species, inclusive an influence of the host plants on the morphology of the parasitic plant.

An important aspect of genetically fixed infraspecific variation is a seasonal or pseudo-seasonal variation. This term refers to the situation when different populations of one species flower in different periods of the year (e.g. WETTSTEIN 1895, Soó 1926–1927). This phenomenon is known in many hemiparasitic annuals of the family *Orobanchaceae* (former tribus *Rhinantheae* of family *Scrophulariaceae* and in some other annuals (e.g. *Gentianella*, *Gentianaceae* – RÖNNIGER 1911, ZOPFI 1991). Some morphological characters are in correlation with the flowering period – so called seasonal characters. The most important of these characters are the total number of internodes (internodes between the node with cotyledones and the node with lowest flowers of the terminal inflorescences) and the number of intercalary internodes (i.e. internodes between uppermost branches and lowest flowers of the terminal internodes). Length of internodes, number of branches, flowering branches and their position represent other seasonal characters. Many infraspecific taxa have been described and distinguished traditionally on the basis of these characters. The late flowering types with many internodes and intercalary internodes and many branches are named as autumnal types, the early flowering types with a small number of internodes, intercalary internodes and branches are termed as aestival or vernal types. Morphologically intermediate types are named as montane (usually occurring in mountains) or segetal (occurring in fields) types (e.g. Soó & WEBB 1972).

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However the seasonal variation is more complex and unique in each particular species of the genus *Melampyrum*. The phenomenon is called “pseudoseasonal polymorphism” now because of the evidence of an important role of specific habitat factors at seasonal type origin (Soó 1926–1927, KARLSSON 1974, 1976, ZOPFI 1993a). The pseudoseasonal types were classified in the different taxonomic ranks in the past – in the genus *Melampyrum* most usually as subspecies (e.g. RONNIGER 1911, Soó 1926–1927) or as a special category “ecotype” (Soó & WEBB 1972).

The basic seasonal types are more pronounced in species with different ecological requirements. For example the aestival and autumnal types of *Melampyrum nemorosum* occurring as forest species as like as meadow species in Central Europe are good to distinguish (ŠTECH 2000a). On the other hand the complex pattern of seasonal type with vague delimitation is representative for mostly forest species like *Melampyrum sylvaticum* or *M. pratense*. The *Melampyrum sylvaticum* can be assigned to the boreal-montane element of the European flora (MEUSEL et al 1978). It predominantly occurs in mountain and boreal spruce and pine forests (DALRYMPLE 2007). An altitudinal range of its occurrence is large in Central Europe (ŠTECH 2000b, ŠTECH & DRÁBKOVÁ 2005). Supposed occurrence of infraspecific taxa along altitudinal gradient is not distributed uniformly (RONNIGER 1911). The aim of this study is to describe a variation of seasonal characters in populations *Melampyrum sylvaticum* along an altitudinal gradient and to compare this variation with formal infraspecific taxa described on the basis of these characters.

Material and methods

Four populations of *Melampyrum sylvaticum* were chosen along a steep altitudinal gradient near Lake Halstatt in Upper Austria: 1) Bad Goisern: forest around parking area in the most western part of the village of Ramsau, 650 m a. s. l., – 2) Bad Goisern: forest along the path in the lower part of the glacial cirque at the eastern slope of the Hoch Kalmberg mount ca 2.5 km ESE of the Goiserer Hütte chalet, 800 m a. s. l. – 3) Bad Goisern: forest along the path in the lower part of the glacial cirque at the ENE slope of the Hoch Kalmberg mount ca 2 km ESE of the Goiserer Hütte chalet, 900 m a. s. l. – 4) Bad Goisern: forest ca 0.5 km W of the Goiserer Hütte chalet, 1500 m a. s. l. Samples of all populations were collected in one day (23.7.1997). *Melampyrum sylvaticum* is common in this region and an occurrence is more or less continual in an appropriate habitat along the whole gradient. Five morphological characters called as seasonal and considered to be significant in the infraspecific division of the species were measured in 20 plants from each population: 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 inflorescences; number of intercalary internodes (II) – between the node with uppermost branches and the node with lowermost flowers; number of nodes with branches (B) and flowering branches (FB).

Analysis of Variance (ANOVA) was used to data analyse and Scheffé’s post hoc test to identify which populations showed significant difference in the main seasonal characters. Data were transformed to achieve normality. Logarithmic transformation (\log_{10}) was used for the character S and root transformation for the others (I, II, B, FB). Statistica 10 package was used for analysis (STATSOFT INC. 1984–2011).

Results

All measured seasonal characters change along altitudinal gradient. They take lower average values from lower altitude to higher one (Tab. 1). The most obvious and regular is a dependence of the total number of internodes on the altitude (Fig. 1). All studied populations differ significantly in this character (Tab. 2). The changes of seasonal characters are continuous and the values of particular characters dominating in a population are usually present in the altitudinal neighboring ones too (Fig. 2, 3). Variation in particular seasonal characters is completely continuous at the plant level (Fig. 4, 5), while populations are constituted from a limited part of this continuous pattern (Fig. 5).

Tab. 1: Average values of measured characters in particular populations along the altitudinal gradient. – Tab. 1: Durchschnittswerte der saisonalen Merkmale in Einzelpopulationen entlang eines Höhengradienten.

Character	Altitude of population (m a. s. l.)			
	650	800	900	1500
S	13.98	10.81	10.24	6.74
I	6.30	4.95	4.25	2.40
II	1.90	1.60	1.20	1.00
B	3.90	3.50	3.20	1.70
FB	2.20	2.50	1.95	0.65

Tab. 2: Results of the Scheffé's post hoc test used to determine significant differences between populations from different altitudes (* = $p < 0.05$, *** = $p < 0.01$). – Tab. 2: Resultate von Scheffé's post hoc Test angewandt auf die Bestimmung der signifikanten Unterschiede zwischen Populationen aus verschiedener Höhe (* = $p < 0.05$, *** = $p < 0.01$).

	Character	Altitude of population (m a. s. l.)			
		650	800	900	1500
650	S	-	*	***	***
	I	-	***	***	***
	II	-	n.s.	***	***
	B	-	n.s.	n.s.	***
	FB	-		n.s.	***
800	S		-	n.s.	***
	I		-	*	***
	II		-	n.s.	***
	B		-	n.s.	***
	FB		-	n.s.	***
900	S			-	***
	I			-	***
	II			-	n.s.
	B			-	***
	FB			-	***

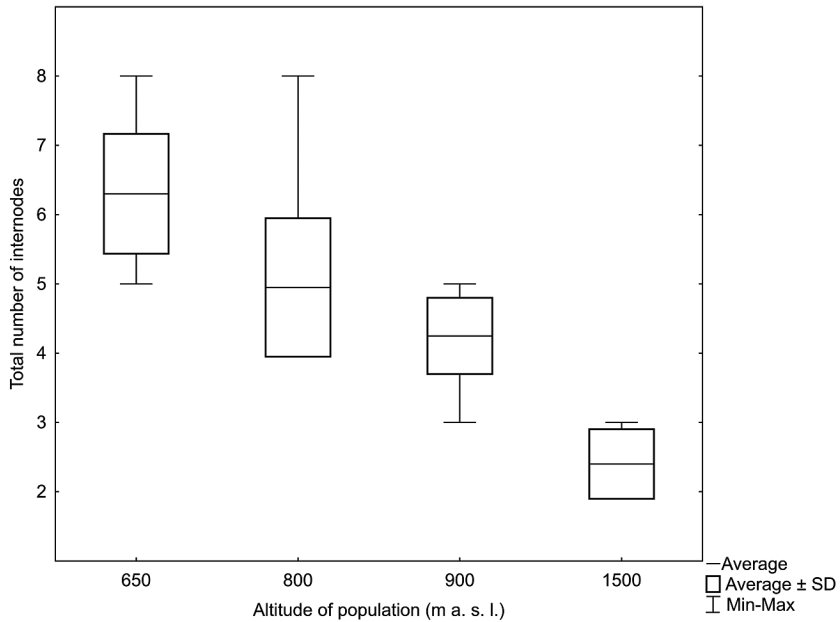


Fig. 1: Basic statistical parameters of total number of internodes in particular populations along the altitudinal gradient. – Abb. 1: Statistische Grundparameter für die Internodiengesamtzahl in Einzelpopulationen entlang eines Höhengradienten.

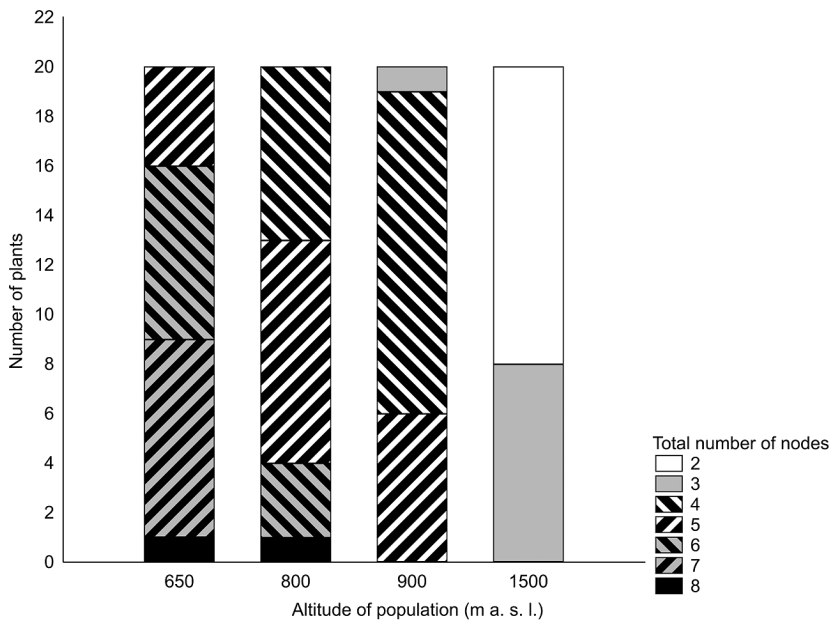


Fig. 2: Proportion of plants with different total number of internodes in populations along the altitudinal gradient. – Abb. 2: Anteil der Pflanzen mit verschiedener Internodiengesamtzahl in Einzelpopulationen entlang eines Höhengradienten.

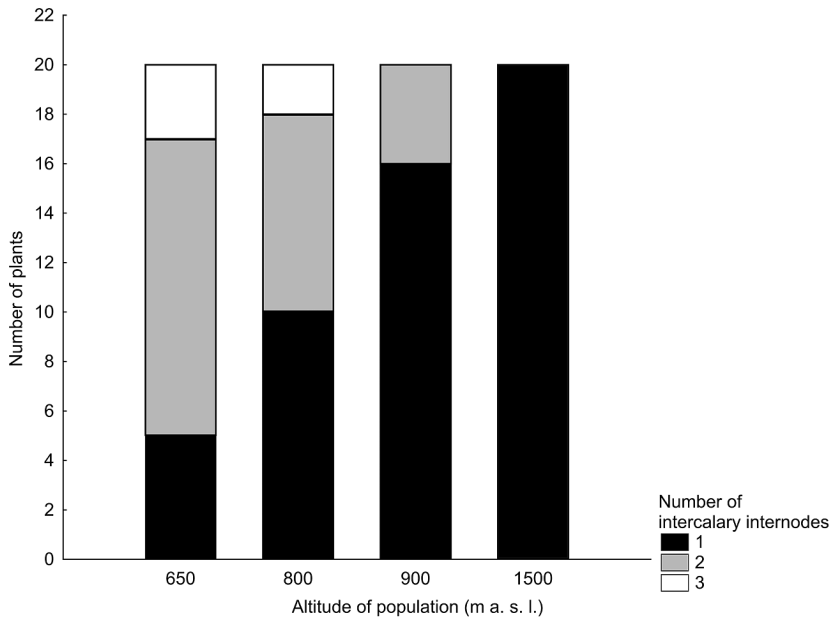


Fig. 3: Proportion of plants with different intercalary internodes in populations along the altitudinal gradient. – Abb. 3: Anteil der Pflanzen mit verschiedener Intercalarinternodienzahl in Einzelpopulationen entlang eines Höhengradienten.

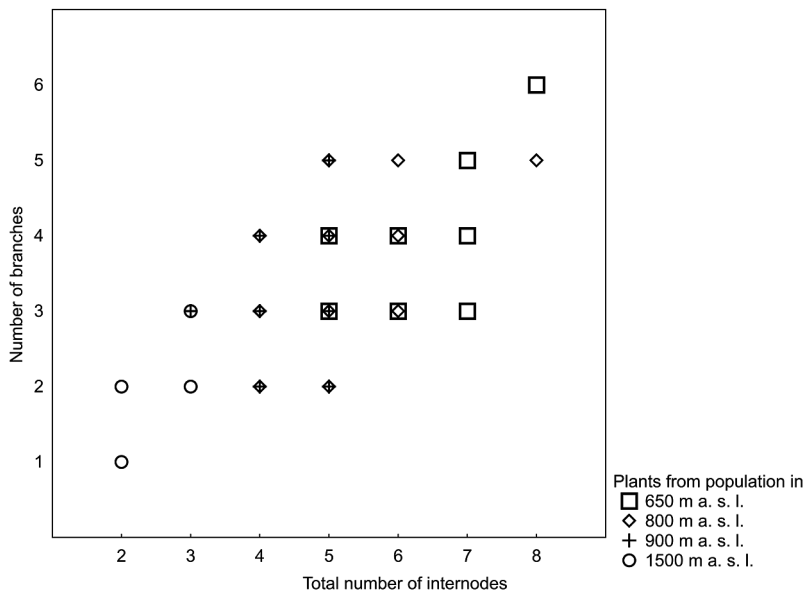


Fig. 4: Total number of internodes and number of branches in individual plants. Plants from populations from different altitudes are marked by different symbols. – Abb. 4: Internodiengesamtzahl und Zweiggesamtzahl für Einzelpflanzen. Pflanzen der verschiedenen Populationen entlang eines Höhengradienten sind mit verschiedenen Symbolen gekennzeichnet.

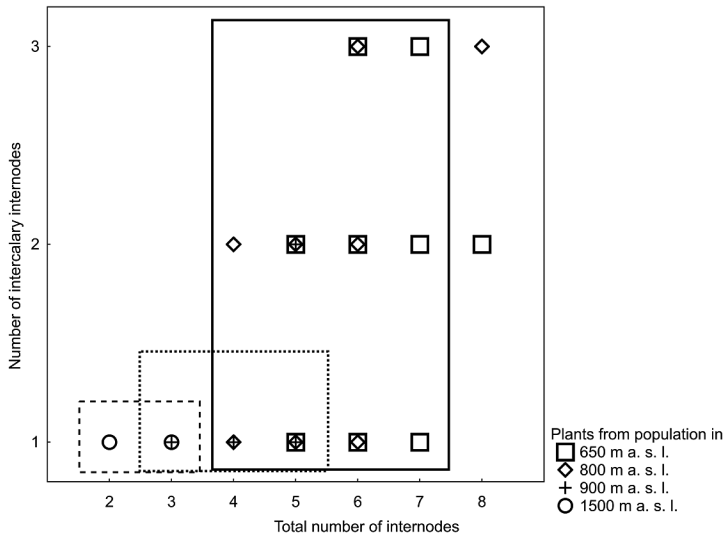


Fig. 5: Total number of internodes and number of intercalary internodes in individual plants. Plants from populations from different altitudes are marked by different symbols. A combination of characters (after Soó 1926–1927) indicated for autumnal *Melampyrum sylvaticum* subsp. *sylvaticum* is marked as a solid line, that for montane *Melampyrum sylvaticum* subsp. *intermedium* as a dotted line and that for aestival *Melampyrum sylvaticum* subsp. *aestivale* as a dashed line. – Abb. 5: Internodiengesamtzahl und Interkalarinternodienzahl für Einzelpflanzen. Pflanzen aus verschiedenen Populationen entlang eines Höhengradienten sind mit verschiedenen Symbolen gekennzeichnet. Jene Kombination von Merkmalen (nach Soó 1926–1927), die für das autumnale *Melampyrum sylvaticum* subsp. *sylvaticum* charakteristisch ist, wird mit einer durchgezogenen Linie, die für das montane *Melampyrum sylvaticum* subsp. *intermedium* mit einer gepunkteten Linie und die für das aestivale *Melampyrum sylvaticum* subsp. *aestivale* mit einer gestrichelten Linie gezeichnet.

Discussion

A heritability of seasonal characters is supported by cultivation experiments with *M. sylvaticum* (ŠTECH unpublished data) or with other species of the genus *Melampyrum* (ŠTECH 2000a) as like as with other genera with pseudoseasonal variation (e.g. ZOPFI 1993b, 1995, LENNARTSSON 1997). The total number of internodes seems to be the most important character for plant architecture. It is in a close correlation with altitude, which determines growing season length. The correlation between the number of internodes and the length of growing season found in the species *Euphrasia stricta* KARLSSON (1976). Also ZOPFI (1995) considered the total number of internodes as the most stabile seasonal character in the genus *Rhinanthus*. All other seasonal characters are constrained by the number of internodes. They may be a part of this character (the number of intercalary internodes) or the total number of internodes determines a maximum value of them (e.g. the number of branches).

Acquired dataset showed a completely continuous variation of the seasonal characters at the plant level. On the other hand a morphological differentiation of populations is obvious and an architectural distinction of plants from the opposite sites of this continuous pattern is unquestionable. A preadaptation for quick evolution is a source of the population differentiation along altitudinal gradient probably. Short life cycle, number of plants

in one population and number of seeds per plants are considered to be important for this evolution in many hemiparasitic plants (ZOPFI 1993b). Beginning of flowering time is determined by the total number of internodes therefore a quick adaptation of flowering time by environmental selection is the most probable base of a seasonal differentiation of population.

Many infraspecific taxa of *Melampyrum sylvaticum* were described and number of them is reported from Austria in the old literature (e.g. SOÓ 1926–1927, HARTL 1974). However, infraspecific taxonomy is justly considered to be unresolved satisfactorily (FISCHER, OSWALD & ADLER 2008). Three basic seasonal taxa – autumnal *M. sylvaticum* subsp. *sylvaticum*, aestival *M. sylvaticum* subsp. *aestivale* RONNIGER et SCHINZ and montane *M. sylvaticum* subsp. *intermedium* RONNIGER et SCHINZ are delimited mostly on the basis of the seasonal characters (especially the total number of internodes and the intercalary internodes). In spite of only four populations were studied, all three seasonal taxa could be distinguished in the detected range of the seasonal characters formally (Fig. 4). A similar variation patterns were observed in Krkonoše Mts, Czech Republic and in the Velká Fatra Mts, Slovakia (ŠTECH 1998). The continual pattern of individual variation and probable a reticulate variation pattern on the population level make delimitation of a taxon questionable and artificial. Although a pure seasonal variation seems to have low taxonomic importance, another infraspecific variation trends seem to be important in the group *Melampyrum sylvaticum*. A difference of Eastern Carpathian populations from the other Central European populations of *Melampyrum sylvaticum* group is supported by both “non-seasonal” morphologically characters and molecular markers (ŠTECH & DRÁBKOVÁ 2005, TĚŠITEL & ŠTECH 2007, TĚŠITEL et al. 2009).

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