Morphological variation of *Bolboschoenus maritimus* population over a ten year period

Morfologická variabilita populace *Bolboschoenus maritimus* v průběhu desetiletého sledování

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Dedicated to Professor Zdeněk Černohorský on his 85th birthday

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The morphological variation of clones of *Bolboschoenus maritimus* was studied during a ten year period on the Rozkoš reservoir, Czech Republic. The reservoir consists of two partly isolated sections, one with stable and the other with fluctuating water levels. Variations between individual localities (effect of clone and site) was more important than temporal variations within the same clone (plasticity). With respect to some morphological characters there was a tendency for the formation of subpopulations at particular sections of the reservoir.

Keywords: *Bolboschoenus maritimus*, morphology, population, spatial variation, temporal variation

Introduction

Bolboschoenus maritimus (L.) Palla (syn. *Scirpus maritimus* L.) belongs to a taxonomically rather complicated species of the European flora; some other types (taxonomically accepted at different levels) are known from North America, South Africa and Asia. In Europe, this species is divided into several intraspecific taxa by some authors (Casper et Krausch 1980, Dostál 1989, Hejný 1960, Jegorova 1976, Robertus-Koster 1969); other author consider these as unimportant variations or even as only individual variations or modifications caused by changing ecological conditions (Norlindh 1972, Schulze-Motel 1967–1980). Some other authors do not evaluate its variation at all (DeFillips 1980, Rothmaler 1976). In addition, the nomenclature is complicated by the fact that the type specimen bearing the Linnean name comes (probably) from N. America and there is uncertainty as to whether the European plant is the same taxon.

As stated above, some taxonomists consider variations within *B. maritimus* as being induced by changes in ecological factors, e.g. the often cited paper by Norlindh (1972). However, observations of the same plants under different ecological conditions have been confined to studies of production (e.g. Coops et Smit 1991, Dykyjová 1986, Liefers et Shay 1981, Podlejski 1982) or vegetative characters not usually used by taxonomists (Clevering 1995, Coops et Smit 1991). Observations with respect to morphological characters used in taxonomy, i.e. number of inflorescence branches and their length, number of sessile spikelets, size etc. are rare.

Fertile plants of all existing clones of *B. maritimus* were collected regularly at the Rozkoš reservoir during the 1980s allowing us to evaluate both the variations within the same clone in different years under different water level conditions and the variation between individual clones under the same water level conditions.

Study site

As a detailed description of the locality has been published by Krahulec et al. (1980) and by Krahulec et Lepš (1993) only basic data are given here. The study was carried out on the Rozkoš reservoir (16°4'N, 50°22'E) situated in eastern Bohemia (Fig. 2), at an altitude of c. 280 m. The bedrock of the area is a lime-rich chalk of Cretaceous (Turonian) age, weathering into deep lime- and clay-rich soils. Average yearly temperature is 7.3°C, average total yearly precipitation is 641 mm (see Krahulec et al. 1980). The relatively warm climate and calcium carbonate-rich soil are responsible for subhalophytic conditions in this locality.

The Rozkoš reservoir was filled in 1973. It is situated on a small brook, but most of the water flows into the reservoir through an artificial canal from the Úpa river. The reservoir has a volume of 76.10^6 m^3, a maximum flooded area of 1001 ha but an approximate average throughflow (Q_{355}) of only 2 m^3s^{-1}. For this reason, there is no constant flow through the reservoir; the transport of diaspores and other material is influenced more by wind and wave action.

In the flooded area, there were formerly only small water bodies, the largest being 15 ha. The reservoir is divided into two parts by a dam with a spillway at an altitude of 280.9 m. When the water level is above this, there is only one reservoir, but when the water level is lower there are two partially separated reservoirs. The areas of the upper and lower reservoirs are c. 200 and 800 ha, respectively. The upper part of the reservoir has a relatively stable water level – it only occasionally rises above normal (max. 0.6 m) and the water has a higher nutrient content. The water level in the lower reservoir fluctuated during the study period from +0.6 to –(2–3(–5)) m. The timing of the fluctuation is rather uniform: the drop in water level usually starts in July, the re-filling of the reservoir starts in spring with melt-water. Situations with high water level in spring-early summer were rare.

Species studied

Bolboschoenus maritimus is a perennial species, overwintering by means of tubers. It grows in the shallow littoral zone of ponds, lakes, small rivers, oxbows etc., on emergent bottoms of periodic water bodies and also as a weed in wet arable fields (Hejný 1960, Hilbig 1994). Its inflorescence consists of several fascicles of spikelets, some on branches, some sessile (Fig. 1). It seems that at least in some parts of Europe the type without inflorescence branches (usually named as *B.m.* subsp. *compactus*) has a subhalophytic character and differs in a number of other characteristics from the type with branched inflorescence (named as *B.m.* subsp. *maritimus*) – for details see Hejný 1960, Zákravský et Hroudová 1994. Reproduction of *B. maritimus* is by seed and by tubers produced on rhizomes. Because seeds are also produced by rather isolated tussocks, it is reasonable to consider that this species is at least partly self-compatible.

Before the flooding, *B. maritimus* occurred at several localities within the Rozkoš area but only the type with branched inflorescence was observed (Krahulec 1975). After the flooding, a number of young plants were observed along the shoreline, and, based on their size, they were considered by the first author to be seedlings. Only a few of them survived and developed into fertile clones; their location is given in Fig. 2.

Material and methods

At least 5 fertile shoots were collected at regular intervals from each of these clones during the 1980s. A number of morphological characters (quantity and length) were measured and variations (including their ratios) were then analyzed (Table 1). The ratios of length were calculated with respect to mean values within the same inflorescence. In the analysis two main sources of variation were considered: spatial variation reflecting the effect of the clone and local differences of substrate conditions and temporal variation which reflects the differences within a clone over a period of years. It may include effects of changing environmental conditions together with the effect of clone age. Their relative share in the total variation was evaluated using the ratio of the respective sum of squares to the total sum of squares in the one-way ANOVA table. The significance of the source of variation was tested by the two-way ANOVA without interactions in the case of normally distributed data sets or by the Kruskal-Wallis "distribution-free" test (Siegel 1956). The significance level of p=0.05 was used.

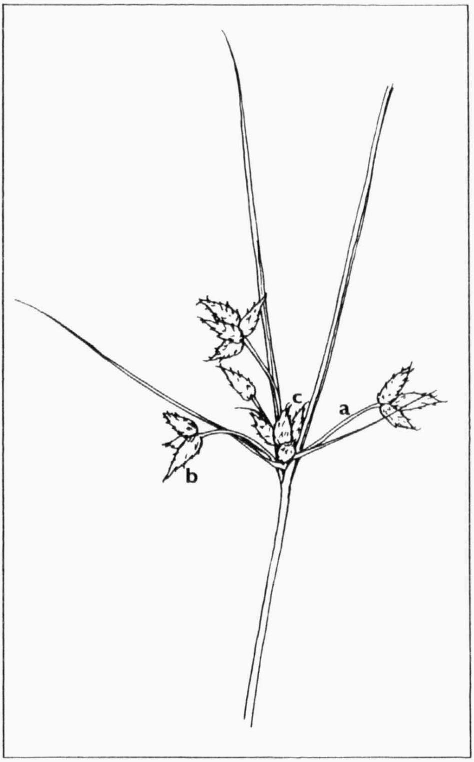

Fig. 1. – Inflorescence of *Bolboschoenus maritimus*. a – inflorescence branch; b – branch spikelets; c – sessile spikelets.

Results

The results of the analysis of individual morphological characters are given in Table 2. For most of the characters the spatial and temporal variations are significant. The comparison of spatial and temporal variation is given in Fig. 3. It is evident that spatial variation is more important than temporal variation (influenced mainly by changes of environmental conditions between individual years). In fact, only three characters lie near the diagonal; other characters have greater spatial than temporal variation.

The sum of spatial and temporal variation is plotted against the coefficient of variation (the measure of total variation) to determine characters with low and high variation and also to differentiate between characters with high error or (spatial + temporal) variation (Fig. 4). Some characters with similar coefficients of variation have four a times greater share of variation explained by the differences between the clones than between years within a clone. The unexplained proportion of total variation (error) may be influenced,

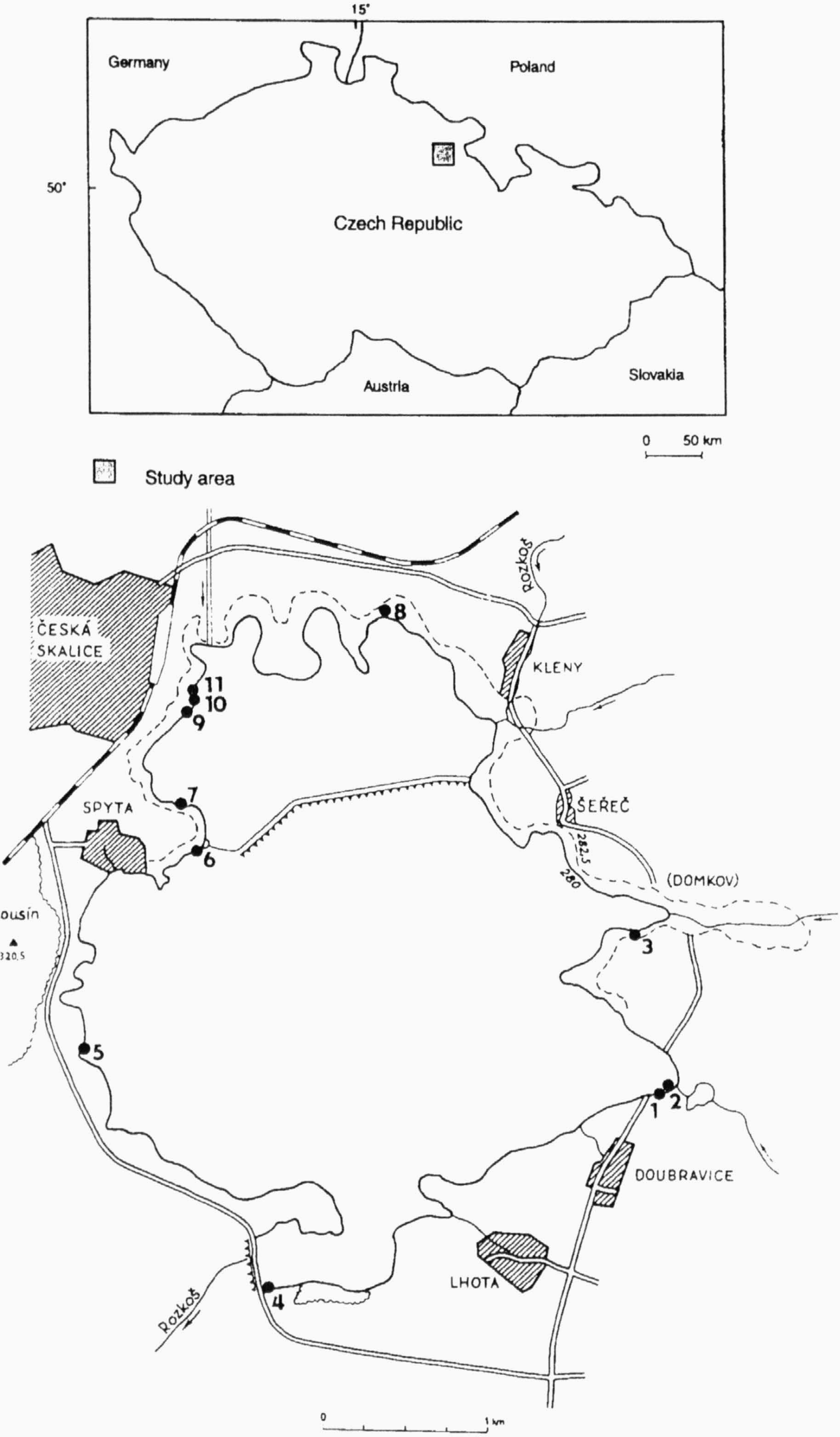

Fig. 2. – Location of *Bolboschoenus maritimus* clones on the shores of the Rozkoš reservoir.

Table 1. – List of morphological characters of *Bolboschoenus maritimus* which were measured and calculated

No	Code	Character
1	NB	Number of branches per inflorescence
2	LB	Length of the inflorescence branch
3	NBS	Sum of spikelets on branches per inflorescence
4	LBS	Length of the spikelet in a branched fascicle
5	NSS	Number of sessile spikelets per inflorescence
6	LSS	Length of sessile spikelet
7	NSF	Number of spikelets per branched fascicle
8	NBS/NSS	Ratio: number of spikelets on all branches within one inflorescence/number of sessile spikelets within that inflorescence
9	LBS/LB	Ratio: length of branch spikelet/mean length of a branch in the same inflorescence
10	LBS/LSS	Ratio: length of branch spikelet/mean length of sessile spikelet in the same inflorescence
11	LSS/LBS	Ratio: length of sessile spikelet/mean length of branch spikelet in the same inflorescence
12	LSS/LB	Ratio: length of sessile spikelet/mean length of branch in the same inflorescence
13	LSS/L(B+S)	Ratio: length of sessile spikelet/mean (length of branch + length of the longest spikelet on this branch) in the same inflorescence

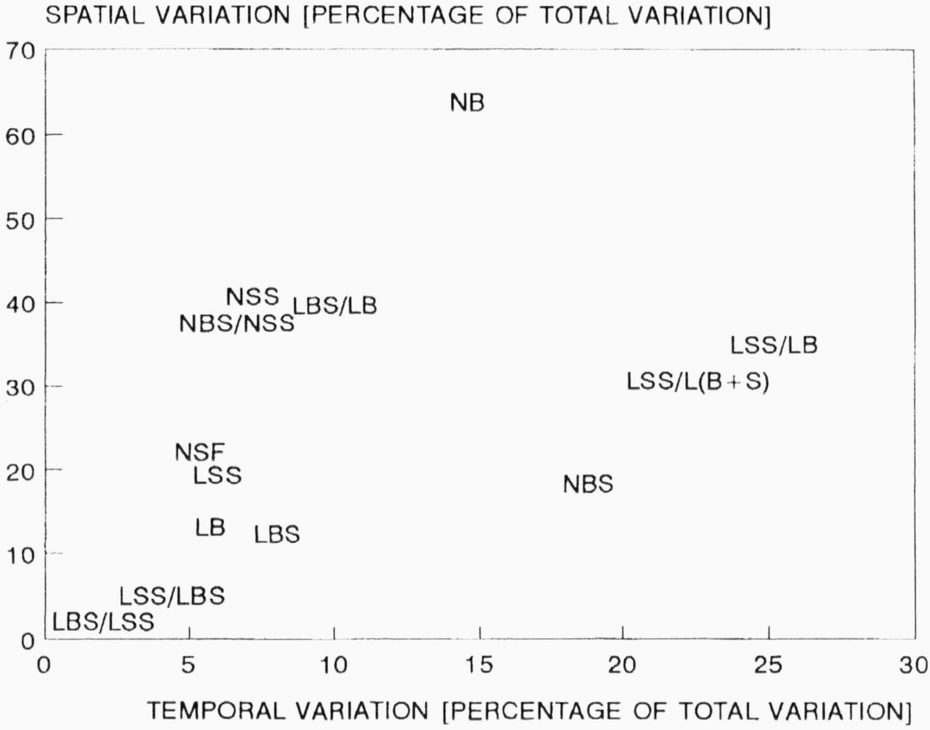

Fig. 3. – Comparison of spatial (mainly between clones) and temporal (between years) variation of individual morphological characters of *Bolboschoenus maritimus*. For character abbreviations see Table 1.

Table 2. – Variation of individual morphological characters of *Bolboschoenus maritimus* at the Rozkoš reservoir during the 1980s. The following characters are given for each value: normality of distribution, mean, coefficient of variation (C.V.), range involving 80 % values, significance of spatial and temporal variation ($p < 0.05$).

Character	Normality mean	Normality s.d.	Mean	C.V.	80%	Space	Time
1 No. of inflorescence branches		+	6	0.393	3-9	sign.	sign.
2 Branch length		-	37.17	0.423	17-57	sign.*	sign.*
3 No. of branch spikelets per inflorescence		-	13.05	0.575	4-22	sign.	sign.
4 Length of branch spikelet		-	12.22	0.248	9-16	sign.	sign.
5 No. of sessile spikelets per inflorescence		+	3.49	0.538	1-6	sign.	sign.
6 Length of sessile spikelet	+	-	13.52	0.204	10-17	sign.	sign.
7 No. branch spikelet/branch		-	2.18	0.437	1-3.5	sign.	n.s.
8 No. of branch spikelets/no. of sessile spikelets		-	4.55	0.786	1-9	sign.	sign.
9 Branch spikelet length/branch length mean		-	0.343	0.378	0.207-0.508	sign	sign.
10 Branch spikelet length/sessile spikelet length mean		-	0.922	0.226	0.678-1.185	sign.	sign.
11 Sessile spikelet length/branch spikelet length mean		-	1.11	0.178	0.89-1.33	sign.	sign.
12 Sessile spikelet length/branch length mean		-	0.413	0.411	0.246-0.610	sign.	sign.
13 Sessile spikelet length/length (branch+spikelet) mean		-	0.295	0.314	0.195-0.409	sign.	sign.

* indicates also significant differences of standard deviations (analyzed only for characters 2, 4, and 6).

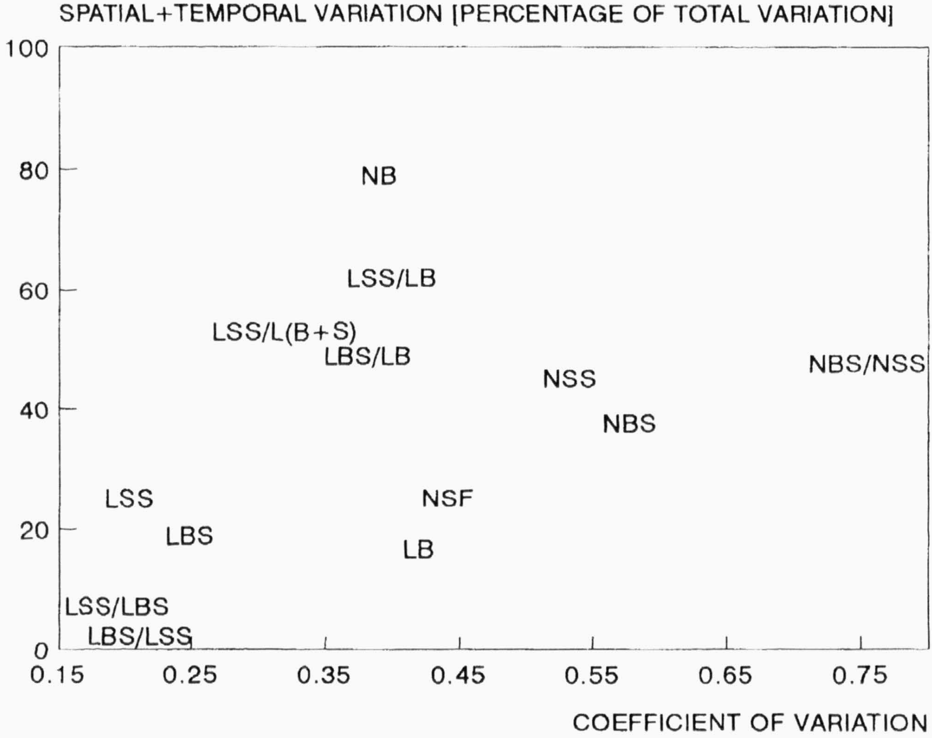

Fig. 4. – Proportion of temporal + spatial variation of the total variation compared with the coefficient of variation for individual morphological characters. For character abbreviations see Table 1.

for example, by phenological differences of individual shoots within a clone or between years or by more complicated interactions reflecting the history of individual tussocks.

Analyzing spatial variation we found that some characters differentiate clones occurring in the upper and lower part of the reservoir (two-way ANOVA with interactions applied to clone means): clones occurring in the lower reservoir have a higher number of inflorescence branches and a lower number of sessile spikelets (significant difference also occurs between their ratio).

Discussion

The comparison of variation of individual characters shows that the variation between clones of *B. maritimus* was higher than the variation (plasticity) within individual clones in different years during the 1980s. This observation contradicts the facts given in the literature (e.g. Norlindh 1972) which stress the importance of ecological conditions for morphological variation. However, Norlindh (1972) studied a different population which may have had higher variation and plasticity. Indeed, Hroudová (unpublished results) found that *B. maritimus* subsp. *compactus* is more variable than the freshwater *B. maritimus* subsp. *maritimus* with branched inflorescence. The soil conditions on the periphery of the Rozkoš reservoir are rather uniform but there are differences between different parts of the shores with respect to sedimentation/erosion processes (cf. Krahulec et al. 1980, Fig. 2), which produce differences with respect to the amount of decomposing organic material. However, the two reservoirs have different conditions with respect to water level (see Fig. 5). These large changes of water level induced a relatively low response in the morphological characters measured. There was no character having a higher temporal variation than a spatial one. Several characters have in general very low variation: number of sessile spikelets per inflorescence, number of spikelets per fascicle on inflorescence branches and their ratio. Some other characters had low variation between years but high spatial variation. Provided that there is a small influence of local soil differences these characters can serve as "good" morphological characters to differentiate individual clones.

With respect to spatial variation, there were no two clones in which all morphological characters displayed the same type of reaction. It seems that each tussock (clone) represents a different genet. It appears also that at least at the time of colonization of the shores of the new reservoir reproduction by seed had higher importance than reproduction by tubers. This view is supported by observation of *B. maritimus* seedlings during the period after the filling of the reservoir.

The detailed study of *B. maritimus* variation at the Rozkoš reservoir during the 1980s is also of interest from another point of view. *B. maritimus* having only sessile spikelets and no inflorescence branches (i.e. subsp. *compactus* (Hoffm.) Hejný) immigrated into the area for the first time in 1980 (Krahulec et Lepš 1994). This specimen did not survive, but two other immigration events occurred at the beginning of the 1990s. Within the Czech Republic two situations are known: the existence of both types at the same locality with or without the formation of transitive types. It is not clear if these transitive types are of hybrid origin or not. The future development of the Rozkoš population is of interest, because at present both morphological types occur at the same site (Fig. 2, locality of clones Nos. 1 and 2).

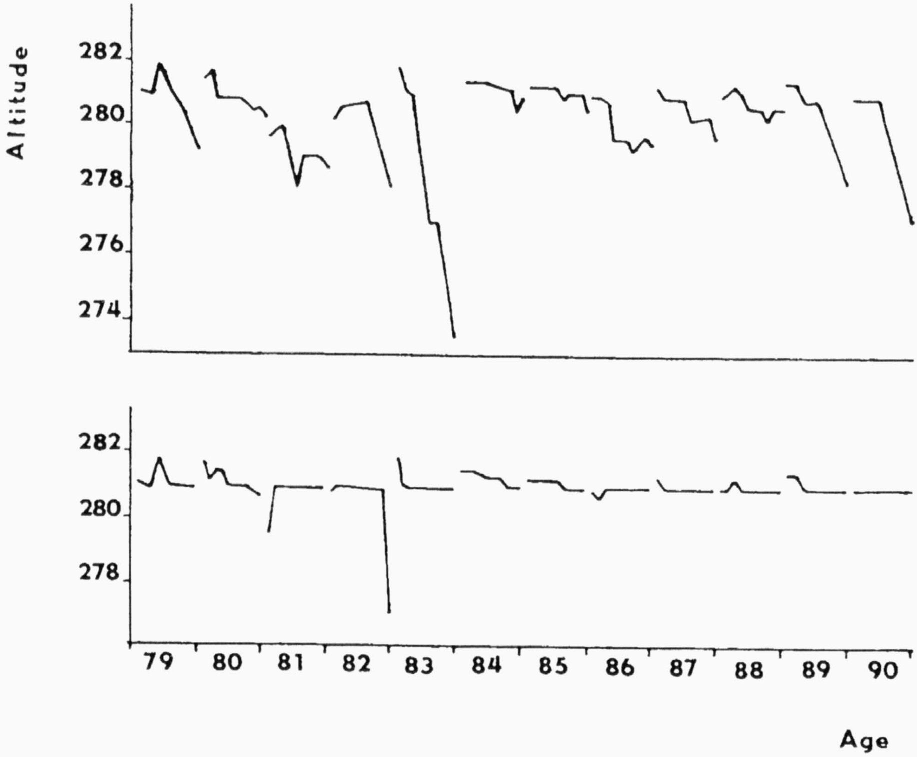

Fig. 5. – Changes of water level at the Rozkoš reservoir level during the 1980s: upper figure shows the reservoir with stable water level, lower figure the reservoir with fluctuating water level.

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Souhrn

Na přehradě Rozkoš u České Skalice byla studována v průběhu 80. let variabilita druhu *Bolboschoenus maritimus*, který se zde vyskytoval v typu s větveným květenstvím (což odpovídá dosavadnímu pojetí *B.m.* subsp. *maritimus*). Z každého klonu byly každý rok sbírány fertilní prýty, na nichž byly měřeny tyto znaky: počet a velikost přisedlých klásků, počet větví květenství, počet a velikost klásků na větvích, řada poměrů těchto veličin (tab. 1). Analýza variance (tab. 2, obr. 3) ukázala, že větším zdrojem variability byly rozdíly mezi jednotlivými klony (které zahrnují též vliv lokálních diferencí v půdních podmínkách) než rozdíly uvnitř jednotlivých trsů (klonů) v čase (odrážející plasticitu danou rozdíly v hladinách vody na nádrži). Srovnání variačního koeficientu s množstvím variance vysvětlené součtem její časové a prostorové složky ukázalo (obr. 4), že kromě několika znaků velmi málo proměnlivých existují dosti velké rozdíly mezi znaky: některé znaky se stejným variačním koeficientem mají až čtyřnásobně větší podíl variance nevysvětlený časovou a prostorovou proměnlivostí. Tyto znaky mohou být více ovlivněny fenologií, složitými interakcemi atd. Nebyly nalezeny žádné dva klony se stejnou kombinací morfologických znaků a jejich proměnlivostí: na základě této skutečnosti předpokládáme, že každý klon reprezentuje samostatné genetické individuum (genetu). Toto je podpořeno častým pozorováním semenáčů tohoto druhu na pobřežní čáře v letech těsně po napuštění nádrže. Klony na dolní nádrži s více kolísající hladinou vody měly statisticky významně vyšší počet větví ve květenství a nižší počet přisedlých klásků než klony v části se stálou hladinou; zdá se tedy, že se začínají vytvářet dílčí populace.

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