Germination response to temperature and flooding of four Central European species of *Bolboschoenus*

Vliv teploty a zaplavování na klíčení čtyř středoevropských zástupců rodu *Bolboschoenus*

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Dedicated to the memory of Slavomil Hejný

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Germination of four Central European *Bolboschoenus* species (*B. yagara*, *B. koshewnikowii*, *B. maritimus* and *B. laticarpus*) was studied. The need for stratification and the influence of temperature and water regime on seed germination were tested in the laboratory. Cold wet stratification in the laboratory as well as water stratification in the field enhanced the germination of all species. Germination was facilitated by increasing stratification length, but differed between species. Field stratification in water improved the germination of all species compared to stratification in soil. Germination requirements of the four *Bolboschoenus* species, despite the broader ecological amplitude of *B. laticarpus*, were similar. The best germination occurred after four months of field stratification in cold water. All species germinated best in aerobic conditions when the day/night temperature fluctuations were high (30/10 °C). These conditions correspond to those occurring where the seedlings tend to establish themselves in the field: exposed pond bottoms or wet soil in field depressions.

Keywords: Closely related species, seed germination, temperature, water regime, *Bolboschoenus yagara*, *B. koshewnikowii*, *B. maritimus*, *B. laticarpus*

Introduction

Bolboschoenus maritimus group (*Cyperaceae*) is an interesting complex of closely related Central European species of perennial emergent macrophytes, with rhizomes bearing tubers. European plants of the genus *Bolboschoenus* were mostly included in one species *Bolboschoenus maritimus* (L.) Palla (= *Scirpus maritimus* L., e.g. de Filipps 1980), or divided into two taxa at different taxonomic levels. In Central Europe mostly two subspecies are recognized (Casper & Krausch 1980, Dostál 1958, 1982, 1989, Hejný 1960, Dykyjová 1986). Recently, a detailed examination of their morphology, ecology and taxonomy (e.g. Hroudová et al. 1997, 1998a, b, 1999a, b, 2001) resulted in new interpretation. Five taxa are present in Central Europe: *B. yagara* (Ohwi) Y. K. Yang et M. Zahn, *B. koshewnikowii* (Litv. ex Kots) A. E. Koshevnikov, *B. maritimus* (L.) Palla, *B. laticarpus* nom. prov. and *B. glaucus* (Lam.) S. G. Smith (Hroudová et al. 2001). The nature and range of habitats, and area of distribution of these species differ (Hroudová et al. 1999b, 2001). *B. yagara* and *B. laticarpus* occur in freshwater non-saline habitats. The former inhabits the litoral of standing water (fishponds) with a fluctuating water level. It grows mostly in acid nutrient-poor soils. The latter inhabits a wider range of habitats: standing water (fishponds, oxbows), temporarily flooded depressions in meadows and fields, river banks. The species typically occurs in river floodplains. *B. maritimus* and *B. koshewnikowii* occur in saline and/or more eutrophic habitats, where *B. maritimus* grows in littoral saline habitats and temporarily drying ditches with highly saline mineral soils as well as in temporarily flooded field depressions (the places of former saline wetlands), whereas *B. koshewnikowii* occurs mainly in semi-terrestrial temporarily flooded habitats (typical weed of arable lands) with slightly saline or nutrient-rich soils. *B. glaucus* was found in a single locality in Prague and was probably an alien there (Hroudová et al. 1999a). In this study, the germination ecology of four of the species (except of *B. glaucus*) was studied.

Beside vegetative reproduction by rhizomes bearing tubers, which is the usual mode of reproduction in aquatic plants (e.g., Sculthorpe 1967), all *Bolboschoenus* species produce seed under favourable conditions (Hroudová et al. 1996). The facultative generative reproduction is ecologically important for two reasons. First, the species is dispersed over long distances by hydrochory (seed buoynancy – Hroudová et al. 1997, 1999b) and endozoochory (transport by water birds – Charalambidou & Santamaria 2002). This was illustrated by finding of *B. koshewnikowii* (formerly determined as *B. maritimus* subsp. *compactus*) at the new water reservoir Rozkoš in NE Bohemia (Krahulec & Lepš 1993, 1994). Second, generative reproduction enables the species to survive unfavourable conditions; seeds survive periods unfavourable for vegetative growth in the soil seed bank (Smith & Kadlec 1983, Poiani & Johnson 1989). Therefore, a good knowledge of seed germination in *Bolboschoenus* species is important for understanding their ecology and distribution.

It is difficult to decide to which of the newly recognized taxa the germination data published on *Bolboschoenus maritimus* s.l. (Hejný 1960, Clevering 1995) relates. Since the habitats of the individual species differ in water regime (flooded littoral habitats vs. semiterrestrial field depressions) and consequently in the heating and cooling of surface soil, the flooding and temperature are likely to be the main factors affecting germination in these taxa. The aim of the present paper is to determine (1) the limits and optimum conditions of temperature and flooding for seed germination in the four taxa and (2) differences in germination between the species?

Material and methods

Seed[1] *collection*

Seeds were collected in the field (see Appendix 1 for the list of localities). From individual populations, seeds were taken from as many randomly chosen plants as possible, and mixed together. As the development of *Bolboschoenus* populations depends on habitat water regime seed production is variable. Therefore it was not possible to collect seed from the same number of localities for each species. In 1995, seeds of only three species were available.

Seed storage

Freshly harvested seeds were dried at laboratory temperature for three days. Some of the seeds were used immediately in stratification experiments in the laboratory and the rest were kept dry in dark at 6 °C prior to use in stratification experiments in the field.

[1] To simplify terminology, we used the term “seed” instead of achene in the sense of reproductive diaspore.

Stratification in the laboratory

The seeds were stored in beakers with distilled water (wet) and in paper bags (dry). Two different stratification temperatures: 20 °C (warm) and 6 °C (cold) were used. That is, four stratification treatments were used: warm wet, warm dry, cold wet and cold dry.

Stratification under field conditions

The seeds were stratified in an experimental garden either in soil or under water to simulate field conditions (seeds fall either into water or to mud) for four months (from December to March). For stratification in soil they were placed in fine nylon bags and buried 2 cm below the soil surface. For stratification in water seeds were placed into small plastic bottles with distilled water and then immersed in a garden reservoir at a depth of 1m.

Germination experiments

Germination was tested in growth chambers (Thermo forma). Seeds were placed on wet filter paper in standard Petri-dishes (aerobic condition), with one exception (see Experiment 4). All treatments (1, 2, 3a, 3b) consisted of five replicates of 50 seeds each, with the exception of Experiment 4, where eight replicates of 25 seeds were used. The filter paper was moistened with tap water and the number of germinated seeds (radicle already emerged from pericarp) recorded every two days. The germinated seeds were removed. All experiments lasted 1 month. The following day/night regime was used in the tests with fluctuating temperatures: 12 h of high temperature in the light, 12 h low temperature in the dark. When constant temperatures were used, the day/night regime was also 12h light/12 h dark. The following germination experiments were performed:

Experiment 1: Germination of fresh seeds

Recently harvested seeds were tested for germination under fluctuating temperature conditions of 25/10 °C.

Experiment 2: Response to stratification in the laboratory

The effect of duration of stratification was tested. The seeds were germinated after 3, 7 and 11 months of stratification in the laboratory at 25/10 °C using the stratification treatments described above. The seeds of three *Bolboschoenus* species (*B. koshewnikowii, B. yagara* and *B. laticarpus*) collected in 1994 were germinated in 1995. The seed of all species came from one locality.

Experiment 3: Response to temperature after stratification in the field

Seed stratified for 3 months in either terrestrial or submerged conditions were germinated at constant temperatures of 10, 15, 20, 25 or 30 °C (Experiment 3a) and fluctuating temperatures of 30/10, 25/10, 25/15 or 25/20 °C (Experiment 3b). The seeds of *B.*

koshewnikowii, B. yagara and *B. laticarpus* were collected in 1994 and germinated in 1995. The seed of all species came from one locality.

Experiment 4: Response to water regime and fluctuating temperatures

Seeds stratified for four months in submerged conditions were germinated either (a) in aerobic conditions on a wet filter paper or (b) in water (a beaker filled with tap water) at fluctuating temperatures of 25/15 and 30/10 °C. The seeds of four *Bolboschoenus* species (from 10 localities: *B. yagara* 3, *B. koshewnikowii* 3, *B. laticarpus* 2. *B. maritimus* 2 localities) were collected in 1998 and germinated in 1999.

Statistical analysis

Differences between means were tested using three-way ANOVA. In Experiment 4, the locality was treated as a nested random factor within species and the species were treated as fixed effects. The post hoc Duncan's test was used for every level of a non-tested factor separately. Prior to analyses (ANOVA) the data in the form of percentages was arcsin-sqrt transformed (because of non-normal distribution of the data). The programmes Statistica (StatSoft 1996) and Solo (BMDP Statistical Software 1991) were used for the statistical analysis.

Results

Experiment 1: Germination of fresh seeds

Fresh seeds of all three species did not germinate.

Experiment 2: Response to stratification in the laboratory

Significant effects of species, stratification length, stratification treatment and their interactions on germination were observed. Interactions between species and stratification length were least significant (Table 1). Under the stratification treatment leading to highest germination, differences between species were significant only after the longest period of stratification (Table 4). All species germinated best under the cold wet stratification treatment and worst under the cold dry one. Of all the species *B. koshewnikowii* germinated best. *B. laticarpus* and *B. yagara* germinated moderately well after the long warm wet treatment (Table 3).

Experiment 3a: Response to constant temperatures after stratification in the field

Significant effects of species, temperature regime and stratification treatment as well as their interactions were found (Table 1). Poor germination was recorded for all species in this experiment. *B. yagara and B. laticarpus* germinated only at 15 °C (up to 8.8%). Small percentages of *B. koshewnikowii* germinated at the low constant temperatures of 15 °C (up to 7.6%) and 10 °C (9.2%), and the higher constant temperatures of 25, 30 and 35 °C (up to 6%). All species germinated better following the field stratification under water (Table 5).

Table 1. – Germination experiments 2 and 3: The effect of laboratory or field stratification and temperature, and their interactions, on seed germination of *Bolboschoenus* species. 3-way ANOVA was performed on arcsin(sqrt) transformed data. * p < 0.05; ** p < 0.01; *** p < 0.001; **** p < 0.0001.

Germination experiment	Effect	d.f.	F – value	
2. Laboratory stratification	1 species	2	30.59	****
	2 stratification length	2	127.47	****
	3 stratification treatment	3	422.73	****
	1× 2	4	2.18	*
	1× 3	6	11.60	****
	2× 3	6	8.70	****
	1× 2× 3	12	4.25	****
3a. Constant temperature and field stratification	1 species	2	60.44	****
	2 stratification treatment	1	64.08	****
	3 temperatures	5	37.96	****
	1× 2	2	16.13	****
	1× 3	10	9.28	****
	2× 3	5	26.29	****
	1× 2× 3	10	12.82	****
3b. Fluctuating temperature and field stratification	1 species	2	6.46	**
	2 stratification treatment	1	193.19	****
	3 temperatures	3	196.83	****
	1× 2	2	20.75	****
	1× 3	6	24.65	****
	2× 3	3	8.14	***
	1× 2× 3	6	4.57	***

Table 2. – Germination experiment 4: The effect of temperature and germination water regime (aerobic/water environment), and their interactions on seed germination of four *Bolboschoenus* species from different localities. 3-way nested ANOVA was performed on arcsin(sqrt) transformed data. Locality was treated as a nested factor within a species. Species as well as other factors were treated as fixed factors. ns = not significant; * p < 0.05; ** p < 0.01; *** p < 0.001; **** p < 0.0001.

Germination experiment	Effect	d.f.	F-value	
4. Temperature and germination water regime	1 species	3	0.17	ns
	2 localities (species)	6	76.75	****
	3 water regime	1	76.95	****
	4 temperature	3	537.18	****
	1× 3	1	4.87	**
	1× 4	3	26.02	****
	3× 4	1	2.75	ns
	1× 3× 4	3	3.00	*

Experiment 3b: Response to fluctuating temperatures after stratification in the field

A strong effect of temperature and stratification treatment on seed germination was revealed; the weaker effect of species was also significant (Table 1). Field stratification under water resulted in better germination than stratification in soil in all the species at nearly all the temperatures used. A temperature fluctuation of 25/15 °C resulted in the best germination of *B. koshewnikowii* stratified under water. On the other hand, *B. yagara* and *B. laticarpus* germinated best when subjected to the highest day/night temperature fluctuations (30/10 °C). All three *Bolboschoenus* species germinated worst in the 25/20 °C temperature treatment (Table 6).

Table 3. – Germination experiment 2: The effect of the duration of the stratification in the laboratory and stratification treatment on germination. Mean germination rate (%; n=5) of *Bolboschoenus koshewnikowii, B. yagara* and *B. laticarpus* under a fluctuating temperature regime of 25/10 °C after three different stratification durations and after four different stratification treatments. Significant differences in stratification length are indicated by different capital letters in columns for every species and every stratification treatment separately. Significant differences due to stratification temperature regimes are indicated by different lower case letters for every species and every stratification duration separately. ANOVA and post hoc Duncan's test ($p < 0.001$) were used. Percentages were arcsin(sqrt) transformed prior to analysis. The untransformed data are shown.

Species	Stratification duration (month)	Stratification treament							
		warm wet		warm dry		cold wet		cold dry	
B. koshewnikowii	3	4.4	Bb	4.8	Ab	28.8	Ca	1.6	Ab
	7	17.6	Ab	12.4	Ac	59.2	Ba	8.4	Ac
	11	20.0	Ab	5.2	Ac	89.2	Aa	8.8	Ac
B. yagara	3	0.4	Bb	0.2	Bb	29.6	Ba	0.0	Bb
	7	4.8	Ab	9.2	Ab	40.8	ABa	1.6	ABc
	11	4.8	Abc	8.8	Ab	50.8	Aa	2.8	Ac
B. laticarpus	3	4.4	Cb	1.6	Ac	22.4	Ca	0.8	Bc
	7	14.8	Bb	4.8	Ac	49.6	Ba	2.0	Bc
	11	46.8	Ab	2.8	Ac	68.0	Aa	5.2	Ac

Table 4. – Germination experiment 2: The influence of stratification duration on seed germination in *Bolboschoenus koshewnikowii, B. yagara* and *B. laticarpus* under the most favourable stratification treatment (cold wet). Mean percentage germination (%; n=5) after three stratification durations under a fluctuating temperature regime of 25/10 °C were compared. Significant differences among the species are indicated by different letters for every stratification duration separately. ANOVA and post hoc Duncan's test ($p < 0.001$) were used. Percentages were arcsin(sqrt) transformed prior to analysis. The untransformed data are shown.

Stratification duration (month)	Species		
	B. koshewnikowii	*B. yagara*	*B. laticarpus*
3	28.8 a	29.6 a	22.4 a
7	59.2 a	40.8 b	49.6 ab
11	89.2 a	50.8 c	68 b

Table 5. – Germination experiment 3a: The effect of different constant temperatures and different stratification treatments on germination. Mean germination rate (%; n=5) of *Bolboschoenus koshewnikowii, B. yagara* and *B. laticarpus* under six constant temperatures and after two stratification treatments. Significant differences due to stratification treatment are indicated by different capital letters row-wise for individual species and temperature regimes separately. Significant differences due to temperature are indicated by different lower case letters column-wise for each species and stratification treatment separately. ANOVA and post hoc Duncan's test ($p < 0.001$) were used. Percentages were arcsin(sqrt) transformed prior to analysis. The untransformed data are shown.

Species	*B. koshewnikowii*				*B. yagara*				*B. laticarpus*			
Constant temperature (°C)	stratified in soil		stratified in water		stratified in soil		stratified in water		stratified in soil		stratified in water	
10	0.0	aB	9.2	aA	0.0	aA	0.0	aA	0.0	aA	0.0	aA
15	1.2	aB	7.6	aA	1.2	aB	2.0	bA	1.2	bB	8.8	bA
20	0.0	aA	0.0	bA	0.0	aA	0.0	aA	0.0	aA	0.0	aA
25	0.4	aA	0.8	bA	0.0	aA	0.0	aA	0.0	aA	0.0	aA
30	0.0	aA	6.0	aA	0.0	aA	0.0	aA	0.0	aA	0.0	aA
35	4.0	aA	0.0	bB	0.0	aA	0.0	aA	0.0	aA	0.0	aA

Table 6. – Germination experiment 3b: The effect of different fluctuating temperatures and different stratification treatments on germination. Mean germination rate (%; n=5) of *Bolboschoenus koshewnikowii, B. yagara* and *B. laticarpus* under four fluctuating temperature regimes after two stratification treatments. Significant differences due to stratification treatments are indicated by different capital letters in rows for individual species and temperature regimes separately. Significant differences due to fluctuating temperature regimes are indicated by different lower case letters in columns for every species and every stratification treatment separately. ANOVA and post hoc Duncan's test ($p < 0.001$) were used. Percentages were arcsin(sqrt) transformed prior to analysis. The untransformed data are shown.

Species	*B. koshewnikowii*				*B. yagara*				*B. laticarpus*			
Fluctuating temperature (°C)	stratified in soil		stratified in water		stratified in soil		stratified in water		stratified in soil		stratified in water	
25/10	13.4	aA	13.4	bA	5.4	cB	14.4	cA	12.8	bA	16.6	cA
25/15	18.2	aB	47.0	aA	8.8	bB	22.4	bA	5.6	cB	20.0	bA
25/20	3.4	bB	7.6	cA	0.4	dB	3.2	dA	1.6	dB	8.8	dA
30/10	15.8	aA	12.6	bA	17.8	aB	38.0	aA	21.8	aB	37.8	aA

Table 7. – Germination experiment 4: The effect of two fluctuating temperatures and two water regimes (wet or water) on germination. Mean germination rate (%; n=8) of *Bolboschoenus maritimus, B. koshewnikowii, B. yagara* and *B. laticarpus* after four months of cold field stratification are given. Significant differences due to water regime are indicated by different capital letters in rows for every species and every temperature separately. Significant differences in temperatures are indicated by different lower case letters in columns for every species and every water regime separately. ANOVA and post hoc Duncan's test ($p < 0.001$) were used. Locality was treated as a nested factor within species. Species were treated as a fixed factor. Percentages were arcsin(sqrt) transformed prior to analysis. The untransformed data are shown.

Species	*B. maritimus*		*B. koshewnikowii*		*B. yagara*		*B. laticarpus*	
germination water regime temperature	wet	water	wet	water	wet	water	wet	water
25/15	25.8 Ab	7.3 Bb	18.8 Ab	8.5 Bb	29.7 Ab	16.0 Bb	42.8 Aa	34.0 Aa
30/10	73.3 Aa	55.5Ba	61.3 Aa	37.2 Ba	47.2 Aa	47.2 Aa	59.0Aa	52.8 Aa

Experiment 4: Response to water regime and fluctuating temperatures

A strong effect of the temperature and water regime on germination was found. The effect of species was not significant, but that of localities nested within species was significant (Table 2). The best germination in all species occurred at high temperature fluctuations (30/10 °C) in wet conditions but not significantly so in *B. laticarpus* (Table 7). Some seeds of *B. maritimus* and *B. koshewnikowii* floated on water (cf. Hroudová et al. 1997).

Discussion

Immediately after harvest the seed of three of the studied species, *B. yagara*, *B. koshewnikowii* and *B. laticarpus*, did not germinate under fluctuating temperature conditions. The dormancy was broken after cold and water stratification for a minimum of three months. The seeds of *B. maritimus* exhibit the same behaviour (L. Moravcová, unpubl.). The *Bolboschoenus* species studied here exhibit physiological dormancy, which is common in plants of the temperate region (Nikolaeva et al. 1985, Baskin & Baskin 1989, 1998). The need for cold wet stratification confirm the findings of Hejný (1960) for *B. maritimus* s.l. and is common in many aquatic plants (Grime et al. 1981, Baskin & Baskin 1998). However, Clevering (1995) pointed out that stratification is not obligatory for breaking dormancy in *B. maritimus* s.l. (she used 14 month old seed in her experiments). Non-stratified seeds kept at high temperature germinated slowly and irregularly, whereas those treated by bleaching in 1–4% sodium hypochlorite germinated similarly to those stratified for 36 weeks. Thus germination in *B. maritimus* s.l. seems to depend on the permeability of the seed coat and not on an internal clock; in addition seed age could also play a role (Clevering 1995). Our results show that 7 months of stratification in warm water also initiated some germination in *B. laticarpus* and *B. koshewnikowii* (Table 3), but cold wet stratification is crucial for germination. Additional investigations indicate that although the seed of all four *Bolboschoenus* species did not germinate immediately after harvest, they are permeable to water, which was manifested by seed swelling (L. Moravcová, unpubl. data).

It appears that the germination requirements of *Bolboschoenus* species are similar. The differences between species (Table 6) disappear when large numbers of populations are included in comparisons (cf. Tables 6 and 7). The only exception is *B. laticarpus*, a species that germinated under a wide range of water regimes and fluctuating day/night temperature conditions. In all species, the best germination occurred after cold wet treatment in the laboratory or water stratification in the field, at widely fluctuating day/night temperature (about 20 °C) conditions. This indicates germination occurs late in spring when day temperature is already increasing (Clevering 1995). Temperature fluctuation is important in germination of some other ruderal and wetland plants. In wetland plants, the requirement for fluctuating day/night temperatures may be an adaptation to germination in exposed mud where the differences between day and night temperatures are likely to be considerable (Thompson & Grime 1983, Probert 1992, Ghersa et al. 1992, Schütz 1999). The results of our experiments on the duration of cold stratification and fluctuating temperatures in wet conditions suggest that seeds stratified for a short period of time germinate better when day and night temperatures differed markedly. On the other hand, seeds stratified for a long time do not need such high temperature fluctuations for germination (cf. Tables 4 and 7). This supports the hypothesis of Probert (1992) that an understanding of the interdependence between the requirement for fluctuating temperatures and stratification in the regulation of dormancy regulating can be derived from dose response temperature experiments and quantal analysis (Probert 1992).

In *Bolboschoenus* species, the effect of fluctuating temperatures and the positive influence of aerobic conditions on germination indicate that these plants are likely to germinate after a decrease in water level. This is supported by the field observations of seedling establishment of *Bolboschoenus* species on emergent bottoms (Hroudová et al. 1996, Krahulec et al. 1996). Our results indicate that the termination of dormancy in *Bolboschoenus* seeds is better achieved by stratification (overwinter) in water than in soil. The fact that flooding terminates seed dormancy is known for various plant species, especially aquatic plants (Simpson 1966, Baskin et al. 1993, 2000, Moravcová et al. 2001). Seeds of *Bolboschoenus* species are well adapted to germination in temperate regions, where water level fluctuates seasonally in wetland habitats. The sequence winter flooding

→ spring water subsides → emerged mud seems to be most suitable for seed germination in the field.

It is highly probable that seed dormancy and soil seed bank enable the species studied to survive unpredictable unfavourable conditions in wetlands (Smith & Kadlec 1983, Poiani & Johnson 1989, Grillas et al. 1993). We did not specifically study seed longevity but the stored samples of seeds were still viable after three or more years. Clevering (1995) records seed germination in *B. maritimus* s.l. after 66 months (5.5 years).

Seed germination is influenced by environmental factors operating during the development and maturation of the seed on mother plant, such as day length, light quality, temperature and altitude (Gutterman 1992). Consequently, germination may differ from year to year (cf. Tables 6 and 7). Z. Hroudová (unpubl.) observed such variation in germination. Nevertheless, this does not change the basic seed germination strategy of *Bolboschoenus* species.

Our results suggest that the germination requirements of the *Bolboschoenus* species tested, despite the wider range of conditions suitable for *B. laticarpus*, are similar. The best germination was obtained after 4 months of cold water stratification in the field in fluctuating temperature (30/10 °C) and aerobic conditions. This indicates an adaptation to the germination in exposed muddy bottom in late spring.

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Souhrn

Práce se zabývá studiem klíčení plodů čtyř středoevropských druhů rodu *Bolboschoenus*: *B. yagara*, *B. koshewnikowii*, *B. maritimus* a *B. laticarpus*, které byly dříve zařazovány do široce pojatého druhu *Bolboschoenus maritimus*. V laboratorních podmínkách byla sledována reakce klíčení jejich plodů na způsob stratifikace, teplotu a zaplavení.

Výsledky prokázaly, že chladná a vlhká stratifikace je nutným předpokladem pro přerušení dormance plodů. Se stoupající délkou chladné a vlhké stratifikace se výrazně zvyšuje počet vyklíčených plodů všech druhů. Chladná stratifikace pod vodou zvyšovala počet vyklíčených plodů ve větší míře než chladná stratifikace v půdě. Všechny studované druhy preferovaly při klíčení střídavé teploty s vyšším rozdílem denních a nočních teplot (20 °C) a aerobní podmínky (klíčení v Petriho miskách, vlhko). Požadavky jednotlivých druhů na klíčení jsou velmi podobné. Pouze *B. laticarpus* vykazoval při klíčení širší ekologickou amplitudu k vodnímu režimu a střídavým teplotám než ostatní druhy. Plody všech studovaných druhů nejlépe klíčily po čtyřměsíčním chladném skladování ve vodě (chladná vodní stratifikace) ve střídavé teplotě 30/10 °C při aerobních podmínkách. Toto zjištění dobře odpovídá podmínkám, za kterých dochází k úspěšnému vyklíčení druhů v přírodě, tj. na vlhké půdě obnažených rybničních den či polních depresí.

References

Baskin C. C., Baskin J. M. & Chester E. W. (1993): Germination ecology of *Leptochloa panicoides*, a summer annual grass of seasonally dewatered mudflats. – Acta Oecol. 14: 693–704.

Baskin C. C., Baskin J. M. & Chester E. W. (2000): Effect of flooding on the annual dormancy cycle and on germination of seeds of the summer annual *Schoenoplectus purshianus* (*Cyperaceae*). – Aquat. Bot. 67: 109–116.

Baskin C. C. & Baskin J. M. (1998): Seeds. Ecology, biogeography, and evolution of dormancy and germination. – Academic Press, San Diego.

BMDP Statistical Software (1991): SOLO Statistical system. – Los Angeles.

Casper S. J. & Krausch H.-D. (1980): Süswasserflora von Mitteleuropa. 1. Teil: *Lycopodiaceae* bis *Orchidaceae*. – Fischer Verlag, Jena.

Charalambidou I. & Santamaria L. (2002): Waterbirds as endozoochorous dispersers of aquatic plants: a review of experimental evidence. – Acta Oecol. 23: 165–176.

Clevering O. (1995): Life-history characteristics of *Scirpus lacustris* and *Scirpus maritimus* with special reference to the restoration of these species in former tidal areas. – PhD. Thesis, University of Nijmegen, Ponsen & Looyen, Wageningen.

Dostál J. (1958): Klíč k úplné květeně ČSR. – Nakladatelství ČSAV, Praha.

Dostál J. (1982): Seznam cévnatých rostlin květeny československé. – Pražská botanická zahrada, Praha-Troja.

Dostál J. (1989): Nová květena ČSSR. Vol. 2. – Academia, Praha.

Dykyjová D. (1986): Production ecology of *Bolboschoenus maritimus* (L.) Palla (*Scirpus maritimus* L. s.l.). – Folia Geobot. Phytotax. 21: 27–64.

Filipps P. de (1980): *Scirpus*. – In: Tutin T.G. et al. (eds.), Flora Europaea, 5: 277–279, Cambridge Univ. Press.

Ghersa C. M., Benech Arnold R. L. & Martinez-Ghersa M. A. (1992): The role of fluctuating temperatures in germination and establishment of *Sorghum halepense*. Regulation of germination at increasing depths. – Funct. Ecol. 6: 460–468.

Grillas P., Garcia-Murillo P., Geertz-Hansen, Marba N., Montes C., Tan Ham C. M. L. & Grossman A. (1993): Submerged macrophyte seed bank in a Mediterranean temporary marsh: abundance and relationship with established vegetation. – Oecologia 94: 1–6.

Grime J. P., Mason G., Curtis A.V., Rodman J., Band S. R., Mowforth M. A. G., Neal A. M. & Shaw S. (1981): A comparative study of germination characteristics in a local flora. – J. Ecol. 53: 621–642.

Gutterman Y. (1992): Maternal effect on seeds during development. – In: Fenner M. (ed.), Seeds. The ecology of regeneration in plant communities, p. 27–59, C.A.B. International, Wallingford.

Hejný S. (1960): Ökologische Characteristik der Wasser- und Sumpfplanzen in der Slowakischen Tiefebenen. – Vydavatel'stvo SAV, Bratislava.

Hroudová Z., Zákravský P. & Moravcová L. (1996): Poznámky k semennému rozmnožování *Bolboschoenus maritimus* – Zpr. Čes. Bot. Společ. 31: 71–74.

Hroudová Z., Moravcová L. & Zákravský P. (1997): Effect of anatomical structure on buoyancy of achenes of two subspecies of *Bolboschoenus maritimus*. – Folia Geobot. Phytotax. 32: 377–390.

Hroudová Z., Moravcová L. & Zákravský P. (1998a): Differentiation of the Central European *Bolboschoenus* taxa based on fruit shape and anatomy. – Thaiszia J. Bot. 8: 91–109.

Hroudová Z., Frantík T. & Zákravský P. (1998b): The differentiation of subspecies in *Bolboschoenus maritimus* based on the inflorescence structure. – Preslia 70: 135–154.

Hroudová Z., Zákravský P. & Jarolímová V. (1999a): *Bolboschoenus glaucus* – nový druh pro Českou republiku. – Preslia 71: 27–32.

Hroudová Z., Zákravský P. & Frantík T. (1999b): Ecological differentiation of Central Europaean *Bolboschoenus* taxa and their relationships to plant communities. – Folia Geobot. 34: 77–96.

Hroudová Z., Marhold K., Zákravský P. & Ducháček M. (2001): Rod *Bolboschoenus* – kamyšník v České republice. – Zpr. Čes. Bot. Společ. 36: 1–28.

Krahulec F. & Lepš J. (1993): The migration of vascular plants to a new water reservoir: geographic relationships. – Preslia 65: 147–162.

Krahulec F. & Lepš J. (1994): Establishment success of plant immigrants in a new water reservoir. – Folia Geobot. Phytotax. 29: 3–14.

Krahulec F., Frantík T. & Hroudová Z. (1996): Morphological variation of *Bolboschoenus maritimus* population over a ten year period. – Preslia 68: 13–22.

Moravcová L., Zákravský P. & Hroudová Z. (2001): Germination and seedling establishment in *Alisma gramineum*, *A. plantago-aquatica* and *A. lanceolatum* under different environmental conditions. – Folia Geobot. 36:131–146.

Nikolaeva M. G., Rasumova M. V. & Gladkova V. N. (1985): Reference book of dormant seed germination. – Nauka, Leningrad.

Poiani K. A. & Johnson W.C. (1989): Evaluation of the emergence method in estimating seed bank composition in semipermanent prairie wetlands. – Aquat. Bot. 32: 91–97.

Probert R. J. (1992): The role of temperature in germination ecophysiology. – In: Fenner M. (ed.), Seeds. The ecology of regeneration in plant communities, p. 285–325, C.A.B. International, Wallingford.

Schütz W. (1999): Germination responses of temperate *Carex*-species to diurnally fluctuating temperatures – a comparative study. – Flora 194: 21–32.
Sculthorpe C. D. (1967): The biology of aquatic vascular plants. – Edward Arnold, London.
Simpson G. M. (1966): A study of germination in the seed of wild rice (*Zizania aquatica*). – Can. J. Bot. 44: 1–9.
Smith L. M. & Kadlec J. A. (1983): Seed banks and their role during drawdown of a North American marsh. – J. Appl. Ecol. 20: 673–684.
StatSoft Inc. (1996): Statistica for Windows (Computer program manual. Version. 5). – Tulsa.
Thompson K. & Grime J. P. (1983): A comparative study of germination responses to diurnally-fluctuating temperatures. – J. Appl. Ecol. 20: 141–156.

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Appendix 1. – List of localities where seeds of Bolboschoenus species were collected.

B. maritimus. 1. Bečovský potok: a field depression near Bečovský brook about 1 km S of the village of Bečov near the road to the village of Volevčice, 9 km NW of Louny, NW Bohemia alt. 225 m (50°26' N, 13°42' E), Czech Republic, coll. in 1998. – 2. Skane, Kivik, Sweden coll. in 1998.

B. koshewnikowii. 1. Lenešice: field depression in a meadow below the dam of Lenešický fishpond on the W border of the village of Lenešice, 3 km NW of Louny, NW Bohemia, alt. 185 m (50°22' N, 13°45' E); Czech Republic, coll. in 1994. – 2. Dobroměřický: Dobroměřický fishpond, 3 km N of the town of Louny, NW Bohemia, alt. 195 m (50°23' N, 13°48' E); Czech Republic, coll. in 1998. – 3. Český Brod: field depression, 1.5 km W of the town of Český Brod, Central Bohemia, alt. 235 m (50°04' N, 14°50' E); Czech Republic, coll. in 1998.

B. yagara. 1. Tobolky fishpond, 1 km SW of the village of Branná, 4 km S of Třeboň, S Bohemia, alt. 442 m (48°57' N, 14°46' E); Czech Republic, coll 1994 and 1998. – 2. Černičný fishpond: 1.5 km N of the village of Lužnice, cca 2 km SE of the village of Lomnice nad Lužnicí, S Bohemia, alt. 420 m, (49°04' N, 14°45' E); Czech Republic, coll. in 1998. – 3. Stružky fishpond: 2.5 km NW of the town of Třeboň , S Bohemia, alt. 445 m, (49°00' N, 14°43' E); Czech Republic, coll. in 1998.

B. laticarpus. 1. Opatovický fishpond: on S border of town of Třeboň, S Bohemia, alt. 435 m (48°59' N, 14°46' E); Czech Republic, coll. in 1994 and 1998. – 2. Český Brod: field depression, 3 km W of the town of Český Brod, Central Bohemia, alt. 235 m (50°04' N, 14°50' E); Czech Republic, coll. in 1998.