

Population biology and dynamics of a rare short-lived pond mud plant, *Carex bohemica* Schreber

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Synopsis

Population biology and population dynamics of a rare short-lived pond mud plant, *Carex bohemica*, was studied in South-West Germany. *Carex bohemica* was more widespread than previously believed as was shown by the "underground floristics-method". It had a long-term persistent diaspore bank (several decades). Dormancy was enforced by far red light and darkness, but constant temperatures induced dormancy only in a small percentage of diaspores.

Plant germination and establishment in the field site Gloggere Weiher occurred in 1993 only after draining the pond in winter 1992/1993 (until November 1993). No individual could be found at another point in time during the whole investigation period from autumn 1991 until autumn 1995. There was no germination during a short drainage period in December 1991 nor during the flood period (end of December 1991 until December 1992, November 1993 until autumn 1995). All individuals that germinated in the pond in 1993 survived and reproduced. Establishment rate and number of individuals were correlated with the distribution of the diaspore bank along the transect, which was investigated before the drainage period. On average, there were approximately 800 individuals per square meter. The time period from germination until reproduction and dispersal was relatively long: dispersal of diaspores began in August and increased until October. *Carex bohemica* formed an aerial diaspore bank until reflooding of the pond. Spatial dispersal was correlated with the distribution of the species along the transect, so dispersability of this species was very low. But dispersal by swimming has been shown and dispersal by birds is said to occur occasionally.

A summer drainage period every 10 to 20 years is recommended for the long term conservation management of *Carex bohemica*.

Carex bohemica, pond mud plant, diaspore bank, germination ecology, population dynamics, management, species conservation

Carex bohemica, Teichboden, Diasporenbank, Keimungsbiologie, Populationsdynamik, Management, Artenschutz

1 Introduction

Plants of mudflat sites were formerly a widespread species group on the shores of shallow lakes with high water table fluctuations, natural or artificial ponds and on the banks of rivers in flood plains. Due to the drainage of most shallow lakes and flood plains, the regulation of rivers and the loss of the traditional management of ponds, mudflat plants are strongly endangered and belong to one of the rare species groups in Middle Europe (HARMS & al. 1983, BLAB & al. 1984, FRANKE 1988, KORNECK & SUKOPP 1988).

Many of these rare species are restricted to specific habitats. This is the case for *Carex bohemica*, a typical pond mud plant (MOOR 1936, PIETSCH & MÜLLER-STOLL 1968; s.a. PHILIPPI in OBERDORFER 1977). It is regarded as endangered in South-West Germany (HARMS & al. 1983), the western part of Germany (KORNECK & SUKOPP 1988), and most other states within the whole of Germany (FINK & al. 1992). In traditional pond management, ponds were drained every second summer. Now, however, ponds are left with a water cover throughout the entire year or are drained only for a short time in autumn or winter. In these cases, the typical pond mud plants, mostly annuals, have no chance to establish themselves or to reproduce (FRANKE 1988). Plant growth is also inhibited by pond eutrophication, which can be caused by fertilization (quicklime, phosphate) and intensive feeding by fishes. In many cases a high fish stock or distinct species such as the grass carp (*Ctenopharyngodon idella* VALENCIENNES) prevents the growth of plants totally (KONOLD 1987, FRANKE 1988). However, plants can still be detected as germinable diaspores in the sediment even if they cannot be found as actual vegetation (POSCHLOD & al. 1993) or if no floristical records exist (POSCHLOD 1993a).

* Dedicated to Reinhard Bornkamm to his 65th birthday and his engagement in the population biology of plants. He also founded together with Jörg Pfadenhauer the very active working group on "population biology of plants" within the German Ecological Society, which had already its 8th meeting in 1995.

Many studies of the biology and population dynamics of plants, especially annuals, exist which allow us to understand their strategies for long term survival (summarized in HARPER 1977, BASKIN & BASKIN 1985, SILVERTOWN & LOVETT DOUST 1993). However, not many studies of pond mud plants exist (SALISBURY 1967a, b, 1970, OESAU 1976). The few studies of pond mud flora and vegetation contain some observations on the biological characteristics of these mostly annual mud plants (HEJNY 1960, PHILIPPI 1968, 1969). Most of the authors in Middle Europe, e.g. FRANKE (1986) or SCHÄFER-GUIGNIER (1994), report only on phytosociological aspects of the flora, only sometimes including habitat information (WISSKIRCHEN 1995). However, there are some

studies of vegetation dynamics and diaspore banks in similar habitats in North America, such as prairie marshes, lake shores or other tidal wetlands (VAN DER VALK & DAVIS 1976, 1978, KEDDY & REZNICEK 1982, 1986, SMITH & KADLEC 1983, PEDERSON & VAN DER VALK 1984, LECK & SIMPSON 1987, POIANI & JOHNSON 1989 a.o.).

Some studies of amphibious plants and diaspore germination in water exist (SCULTHORPE 1967, FRANKLAND & al. 1987), but little is known about mud plants (SALISBURY 1970, VOESENEK & BLOM 1992, BASKIN & al. 1993). Until now there was no study on *Carex bohemica* available. This species is a short-lived perennial, not an annual (HEGI 1980).

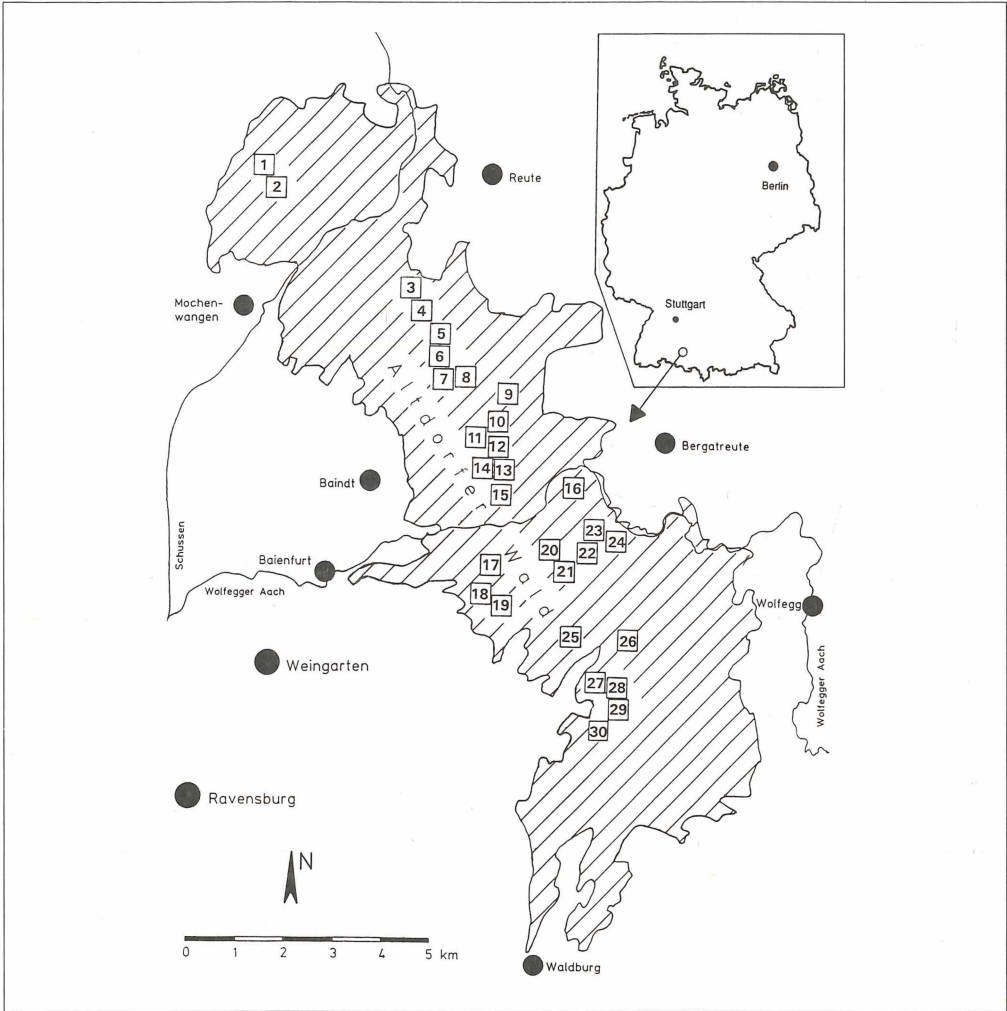


Fig. 1
Study region Altdorfer Wald and location of the investigated ponds (numbers see Table 2; Gloggere Weiher number 14) in South-West Germany.

It is obvious that there is a need for studies of the population biology and dynamics of pond mud species, in order to understand their survival in such an extreme habitat (see also SALISBURY 1970) and to develop management strategies for the long term conservation of these rare species in a human-made landscape. Therefore we focus this paper on the following questions: (1) how widespread is *Carex bohemica* in a selected landscape? Does it exist in a diaspore bank in the sediment (underground floristics, see POSCHLOD 1993a) and, if so, how persistent is this diaspore bank? (2) what germination requirements does this species have and (3) can a persistent diaspore bank be activated by draining a pond and, if so, how rapidly can a population develop to reproduction (flowering, fruiting, diaspore spreading)? (4) how and how far are the diaspores dispersed? (5) which recommendations for future management can be made?

2 Study area and methods

2.1 Study area

The study area was the Altdorfer Wald (region Oberschwaben, South-West Germany; Fig. 1). In total the diaspore banks of 30 ponds were investigated, all still managed by fisheries. One of them, the Gloggere Weiher, was selected for an artificial lowering of the water level in 1993, to study population dynamics (Fig. 1).

2.2 Distribution, persistence of diaspore bank

Species distributions were investigated by the study of the diaspore bank in the sediment (POSCHLOD 1993a). Sediment samples, in total five replicates per pond, were taken near the shore of each pond, under water by an excavator. Each replicate contained one liter of sediment. The sediment was cultivated in pots in a glass-house for three months. After that period, all seedlings were removed and classified to species, and the sediment was dried for two weeks. The sediment was then crumbled and cultivated for three more months under relatively dry conditions. Contamination of the sediment samples by the investigated species was controlled by using sterile substrate samples among the pots: Contamination was absent throughout the entire investigation period.

Management histories of the ponds were investigated through discussion with the pond owners and managers, and examination of records in the management books, which existed for most ponds. Persistence of the diaspore bank was also deduced from the knowledge of management history.

2.3 Germination tests

Germination tests and experiments were performed in a climate chamber in autumn and winter 1993. Diaspores of *Carex bohemica* were collected in the Gloggere Weiher in the Altdorfer Wald in september 1993. If the germination test was not carried out im-

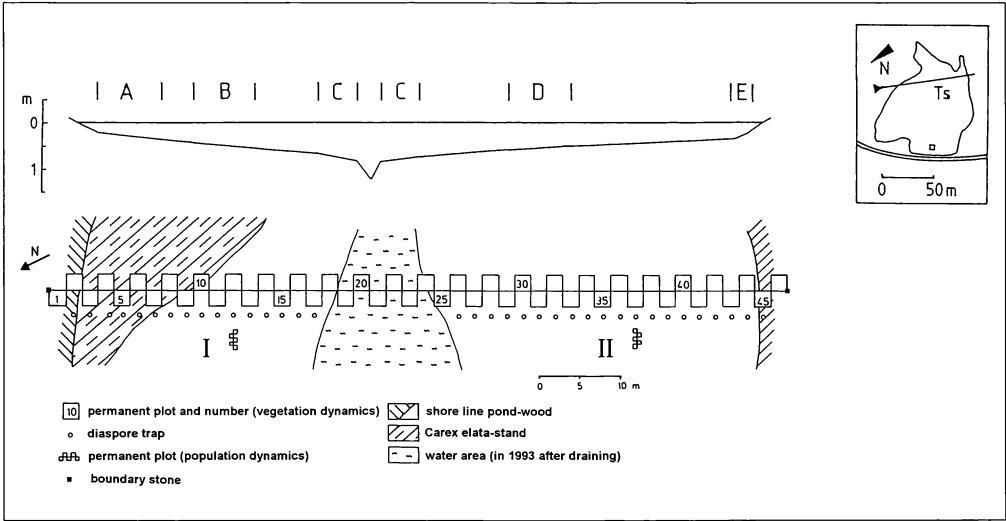


Fig. 2
Transect through the Gloggere Weiher (water level during first record in 1992) and sampling design. A–E – diaspore bank sampling zones; 1–46 – permanent plots (2 x 2 m²) for vegetation relevés; circles – diaspore traps; I, II – permanent plots for relevés of population dynamics.

Tab. 1
Germination experiments and their treatments (storage, pre-treatment, quality of light and temperature fluctuations)

Exp.	Storage	Pre-treatment	Light	Temperature
1	max. 10 days	—	warm-white	fluctuating
2	3 months	—	warm-white	fluctuating
3	3 months	chilling	warm-white	fluctuating
4	3 months	freezing	warm-white	fluctuating
5	3 months	-	warm-white	constant
6	3 months	-	warm-white	12 weeks constant, followed by fluctuating
7	3 months	—	warm-white	12 weeks constant, followed by fluctuating after 6 weeks chilling
8	3 months	chilling	far red	fluctuating
9	3 months	chilling	12 weeks far red, following warm-white	fluctuating
10	3 months	chilling	12 weeks far red, following warm-white after 6 weeks chilling	12 weeks fluctuating, following again fluctuating after 6 weeks chilling
11	3 months	chilling	dark	fluctuating
12	3 months	chilling	12 weeks dark, following warm-white	fluctuating
13	3 months	chilling	12 weeks dark, following warm-white after 6 weeks chilling	12 weeks fluctuating, following again fluctuating after 6 weeks chilling

mediately after sampling, diaspores were stored relatively dry (humidity 40%) and dark at room temperature for 3 months until the tests were performed (see Table 1). Before testing, diaspores were soaked for 10–15 minutes in a 2% sodiumhypochlorite solution (sterilization of the diaspore surface). Then the diaspores were filtered and washed with deionized water (ISTA 1993).

For all tests plastic petri dishes with a double layer of filter paper (Schleicher & Schüll, No. 595) were used. The paper was watered once or twice per week as long as germination was recorded. Diaspores were considered germinated when the radicle or cotyledon had protruded. Seedlings were removed from the petri dishes in a room with daylight, except for those seedlings used in the far red-light and darkness experiments, which were removed in a darkroom with safe green light. For each species and treatment, five replicates, each containing 50 diaspores, were used.

The treatments in the experiments in 1993 are listed in Table 1. The pre-treatments were carried out in a refrigeration chamber (chilling +3°C, freezing 1 week +3°C and 5 weeks –4°C), the tests in a growth chamber. Fluorescent tubes of the type warm-white-daylight (spectral composition approxi-

mately natural daylight) served as light sources for the light treatment. Light intensity over the petri dishes was about 3000 Lux. Far red-treatment was obtained by using fluorescent tubes of the type white light and an additional glass filter of suitable transmission (Göttinger Farbfilter GmbH, No. IR 1013, for wavelength 730nm). Fluctuating temperatures were 22°C during a 14h day and 14°C during a 10h night period.

After the treatments, germination was again tested under standard conditions (light warm-white, fluctuating temperature) to determine whether the treatment enforced or induced dormancy in the non-germinated diaspores. After experiments 5, 8 and 11 the type of dormancy was determined either by testing the germination immediately at standard conditions (6, 9, 12; enforced dormancy) or by chilling for six weeks after the treatment and then testing germination under standard conditions (7, 10, 13; induced dormancy).

Statistical treatment of the data consisted of data transformation according to the Arcussinus method (THÖNI 1967) and an analysis of variance. The Scheffé-test was chosen to determine if there are any significant differences ($p < 0,05$ and $p < 0,01$) between the treatments (WEBER 1980).

Tab. 2
Distribution of *Carex bohemica* in thirty ponds of the Altdorfer Wald (Oberschwaben, Southwest-Germany) studied by the »underground floristics-method« (presence in the sediment and number of germinable diaspores per liter sediment [d/l]).
* – number of germinable diaspores at the Gloggere Weiher not in detail because samples were taken systematically along a transect with a root auger during a period when the pond was drained (see chapter 2 and in detail Table 3).

Name of the pond	Site number	Last draining date	Total species number/pond	Number of mud species/pond	<i>Carex bohemica</i> (d/l)
Neuweiher Nord	1	1966	12	0	
Höllweiher	10	1974	20	1	
Unterer abgebrochener Weiher	11	?	19	2	
Gräfinnenweiher	18	?	20	2	
Mittlerer Kählsbühlweiher	28	—	23	2	
Kleiner Gräfinnenweiher	19	?	13	3	
Stockweiher	8	1967	14	3	
Hengstmoosweiher	15	1970	25	3	1
Kleiner Kiebesweiher	3	before 1989	25	3	
Tafelweiher	17	1983	27	3	
Schanzwiesweiher	6	before 1989	24	4	
Schwarzgrabenweiher	9	1984	27	4	
Köningerweiher	20	?	18	5	
Oberer abgebrochener Weiher	12	?	23	5	1
Neuweiher Süd	2	1966 ?	24	5	
Oberer Kählsbühlweiher	29	1960	24	5	
Unterer Kählsbühlweiher	27	1972	25	5	
Birkweiher	16	—	37	5	
Tiefweiher	13	ca. 1970	15	6	
Egelsee	7	ca. 1968	16	6	2
Truchsessenweiher	25	?	18	6	4
Kiebesweiher	4	?	22	6	
Kiliansweiher	24	1983	22	6	2
Bunkhoferweiher	5	before 1989	24	7	
Klosterweiher	23	—	24	7	
Bannbühlweiher	30	1960	24	8	
Langteichbühlweiher	26	1960	40	8	4
Hagenbacher Weiher	22	1982	23	9	5
Langmoosweiher	21	1980	29	9	5
Gloggereweiher*	14	1985	43	14	>10*

2.4 Population dynamics

The establishment of populations in the drained pond was studied along a transect through the pond.
Before draining the pond in summer 1993 the vertical distribution of the diaspore bank was investigated during a short drainage period in December 1991, along the transect, using a root-auger (method described in POSCHLOD & JACKEL 1993). Samples were taken from five sites along the transect (see fig. 1). Each site was sampled with 25 replicates by a root auger of 4cm diameter. At each site four depths (0–2cm, 2–6,5cm, 6,5–13cm, 13,5–20cm) were sampled. Sediment samples were cultivated as already mentioned above.

Phenology was studied at two sites with different water levels: a dry area near the shore of the pond and a wetter area in the middle of the pond. Population dynamics were studied in ten permanent quadrats, one square meter each, in the middle, wetter part of the pond.
Diaspore rain was investigated along the transect using funnels of 10cm diameter (method see JACKEL & POSCHLOD 1993). Experiments testing swimming ability were performed in the laboratory with chemical moistened to simulate water movement and non-moistened diaspores (method see POSCHLOD 1990).

3 Results

3.1 Distribution of *Carex bohemica* in the studied region

The investigation of the diaspore banks of thirty ponds in the Altdorfer Wald showed that *Carex bohemica* is relatively widespread in the studied region, although until now only one floristical record in the Altdorfer Wald (Kiliansweiher; KONOLD, pers. comm.) was known. *Carex bohemica* occurred in nine of the thirty studied ponds (Table 2). The density of diaspores in the sediment was low (1 to more than 10 germinable diaspores per m²). Only in the Gloggere Weiher the density was relatively high. However, the study of the diaspore bank with a root auger along the transect was much more detailed (see also number of species – 14) than the study by underwater excavation.

Carex bohemica was not found in the diaspore bank if only a few typical mud species occurred there (Table 2). This points to the fact that these species only established in ponds which offer the opportunity to settle down over a long time period.

3.2 Persistence of the diaspore bank

The persistence of the diaspores can be reconstructed using the last known pond drainage date. The management histories of all ponds in which *Carex bohemica* was found are not known. However, most data from the last drainage date available show that germinable diaspores could be found in the sediment even if the last drainage was more than 30 years ago (Langteichbühlweiher 1960; Table 2).

Furthermore the vertical distribution of the diaspores and the relationship of the number of diaspores in upper to lower soil layers (Table 3) also gives an impression of how persistent diaspores can be (BAKKER 1989). The diaspores of *Carex bohemica* were found in high numbers along the whole transect, including the deepest soil layer.

3.3 Germination requirements

The results of the germination experiments showed that *Carex bohemica* had no innate dormancy at all (Table 4); the highest germination rates were observed directly after diaspore sampling. Storage in dry conditions seems to have a dormancy-inducing effect which can be broken by chilling.

Diaspores also germinated at constant temperatures (Table 5). Darkness and far red light enforced a dormancy in all diaspores. Diaspores germinated immediately after exposure to light at fluctuating temperatures (Table 6, 7).

Germination occurred relatively quickly. More than 50% of the diaspores of *Carex bohemica* had germinated in experiment 2 after seven days, and more than 90% had germinated after 12 days. In experiment 3 (with stratification) germination even occurred after three (t50) and six days (t90). Constant temperatures delayed germination in *Carex bohemica* insignificantly (t50 and t90 12 days in each case).

3.4 Population dynamics after draining

Population dynamics were observed since autumn 1991, when the transect was established and the first record made. No individual or seedling of *Carex bohemica* could be found during a short drainage period in December 1991 nor when the pond was flooded until December 1992. The pond was drained in winter 1992/1993; however, drainage was not complete. There was still a cover of water in the middle of the pond, along the transect from plot number 19 to 24 (Fig. 2). In 1993 after draining *Carex bohemica* germinated and could establish itself (Fig. 3). The distribution of *Carex bohemica* along the transect showed that the species established itself better in the middle of the pond, although high numbers of diaspores were found along the whole transect (Table 3). There were almost no individuals in the *Carex elata*-zone (plot numbers 3–8) nor on the southern shore of the pond (plot numbers 41–44).

Germination began at the end of April and ended at the beginning of June (Fig. 4–6). *Carex bohemica* seemed to be characterized by spring germination, since in autumn no individual germinated despite the high reproduction rate and diaspore rain in the drained area. The first date of flowering was at the beginning of June but in populations near the shore of the pond it occurred two weeks earlier. The duration of flowering differed among populations. The population of the drier site, near the shore, flowered for a period of about six weeks, while the population near the middle of the pond flowered for about 10 weeks.

The time period of dispersal began at the end of July, had its peak in October or even later (Fig. 6) and continued until the pond was reflooded in winter. *Carex bohemica* formed an aerial or "above ground diaspore bank", which was mainly dispersed by flooding.

Mortality rate in seedlings could not be observed. All investigated seedlings of *Carex bohemica* survived. All established individuals flowered and formed diaspores. In the studied plots the average number of individuals of *Carex bohemica* was more than 800 per square meter.

Diaspore rain was partially heterogeneous along the transect (Fig. 7). The size of diaspore rain of

Tab. 3
Vertical and horizontal distribution of the diaspore bank of *Carex bohemica* along a transect in the Gloggere Weiher (see Fig. 2).
d/m² – diaspores per square meter; d/l – diaspores per liter sediment.

Zone of the transect	A d/m ² (d/l)	B d/m ² (d/l)	C d/m ² (d/l)	D d/m ² (d/l)	E d/m ² (d/l)
Depth (cm)					
0–2	1344 (67)	3136 (157)	960 (48)	2720 (136)	1728 (86)
3–6,5	1120 (25)	4768 (106)	6336 (141)	1570 (35)	1344 (30)
6,5–13	32 (1)	736 (11)	512 (8)	192 (3)	0 (0)
13,5–20	32 (1)	256 (4)	1824 (28)	96 (1)	64 (1)

Tab. 4
Germination rates (%) of *Carex bohemica* of the experiments 1, 2, 3 and 4 (see Table 1).
A, B, C, D – significant differences (* – $p \leq 0,05$, ** – $p \leq 0,01$) between the experiments 1 and 2 (A), 2 and 3 (B), 2 and 4 (C) and 3 and 4 (D).

Experiment	1	2	3	4	A	B	C	D
Species <i>Carex bohemica</i>	93.6	60.8	80.0	81.2	**	**	**	

Tab. 5
Germination rates (%) of *Carex bohemica* of the experiments 2, 5, 6 and 7 (see Table 1).
A, B, C, D – significant differences (* – $p \leq 0,05$, ** – $p \leq 0,01$) between the experiments 2 and 5 (A), 5 and 6 (B), 5 and 7 (C) and 6 and 7 (D).

Experiment	2	5	6	7	A	B	C	D
Species <i>Carex bohemica</i>	60.8	73.6	88.8	88.8		*	*	

Tab. 6
Germination rates (%) of *Carex bohemica* of the experiments 3, 8, 9 and 10 (see Table 1).
A, B, C, D – significant differences (* – $p \leq 0,05$, ** – $p \leq 0,01$) between the experiments 3 and 8 (A), 8 and 9 (B), 8 and 10 (C) and 9 and 10 (D).

Experiment	3	8	9	10	A	B	C	D
Species <i>Carex bohemica</i>	80.0	0.0	91.2	88.4	**	**	**	

Tab. 7
Germination rates (%) of *Carex bohemica* of the experiments 3, 11, 12 and 13 (see Table 1).
A, B, C, D – significant differences (* – $p \leq 0,05$, ** – $p \leq 0,01$) between the experiments 3 and 11 (A), 11 and 12 (B), 11 and 13 (C) and 12 and 13 (D).

Experiment	3	11	12	13	A	B	C	D
Species <i>Carex bohemica</i>	80.0	0.0	90.4	90.4	**	**	**	

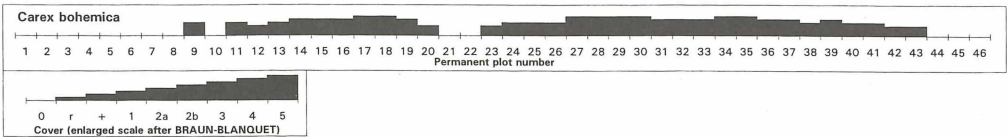


Fig. 3
Cover of *Carex bohemica* along the transect in the Gloggere Weiher in 1993. Explanation of the enlarged cover scale after BRAUN-BLANQUET: r – 1 to 3 individuals/4m², + – few individuals or <1%; 1 – several individuals or 1 to 5%; 2a – many individuals or 5 to 15%, 2b – 15 to 25%, 3 – 25 to 50%, 4 – 50 to 75%, 5 – 75 to 100%.

Tab. 8
Phenological key for grasses and herbs (changed after GRUNICKE & POSCHLOD 1991 and DIERSCHKE 1994).

Vegetative	Generative
1/2 Cotyledon/s or first leaf unfolded	1 without any visible inflorescence
3 2–3 leaves unfolded	2 inflorescence/flower buds visible
4/5 beginning blade development/several leaves unfolded	3 flowering
6 plant fully developed	4 fading
7 blade/shoot and/or first leaves becoming yellow	5 fruiting
8 until 50% becoming yellow	6 dispersing of diaspores
9 over 50% becoming yellow	7 end of dispersal
10 dead	

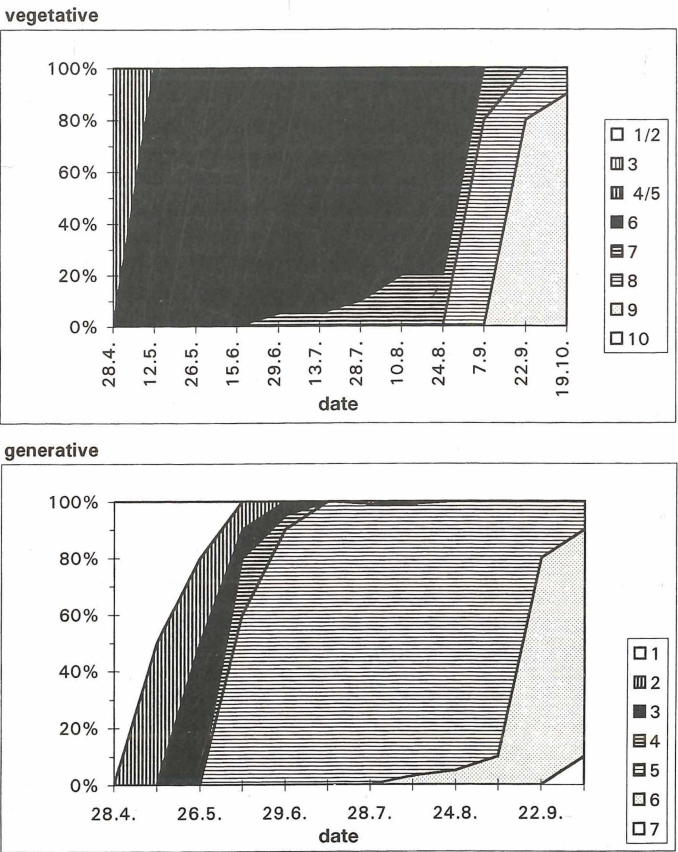


Fig. 4
Phenology of *Carex bohemica* near the shore of the pond (Gloggere Weiher) in 1993 (percentage of the different phenological stages of the whole studied population; legend see Tab. 8).

Carex bohemica was usually more than 10 000 per square meter with its peak in plot number 12 with more than 100 000 diaspores per square meter.

After flooding the pond again in November 1993 no individual was detected in 1994 and 1995. However, *Carex bohemica* was still present in the diaspore bank (POSCHLOD, unpublished data).

3.5 Dispersal of diaspores

Dispersal of diaspores did not occur over long distances in the pond, as the comparison of diaspore rain and distribution of species along the transect showed (Fig. 3, Fig. 7). However, diaspores of *Carex bohemica* could swim over a long period (Fig. 8). The ability to swim was reduced by the application of a tenside (Twen), which artificially imitates water movement, but the time period was not crucially reduced. Therefore diaspores could drift to the shore of the pond after reflooding.

4 Discussion

4.1 Distribution of the species and persistence of the diaspore bank

Taking into consideration that *Carex bohemica* could be found in the diaspore banks of at least 9 (of 30) ponds (Table 2) and was last drained in 1993, let us assume that the diaspores can persist over long time periods in the sediment. This is also shown by the vertical distribution of the diaspores along the transect (Table 3), where high percentages of germinable diaspores could be detected even in the deepest layers (especially zone C). The reason for the high percentages of germinable diaspores in the upper layers near the shore could be that most of the diaspores are dispersed very late in the year. That means that the diaspores, which are able to swim, could have been concentrated near the shoreline when the pond was re-dammed (PEDERSON 1981, JERLING 1983, SMITH & KADLEC 1985). Taking all these facts into consideration it is probable that diaspores of *Carex bohemica* persist several decades (according to the classification of POSCHLOD 1993b).

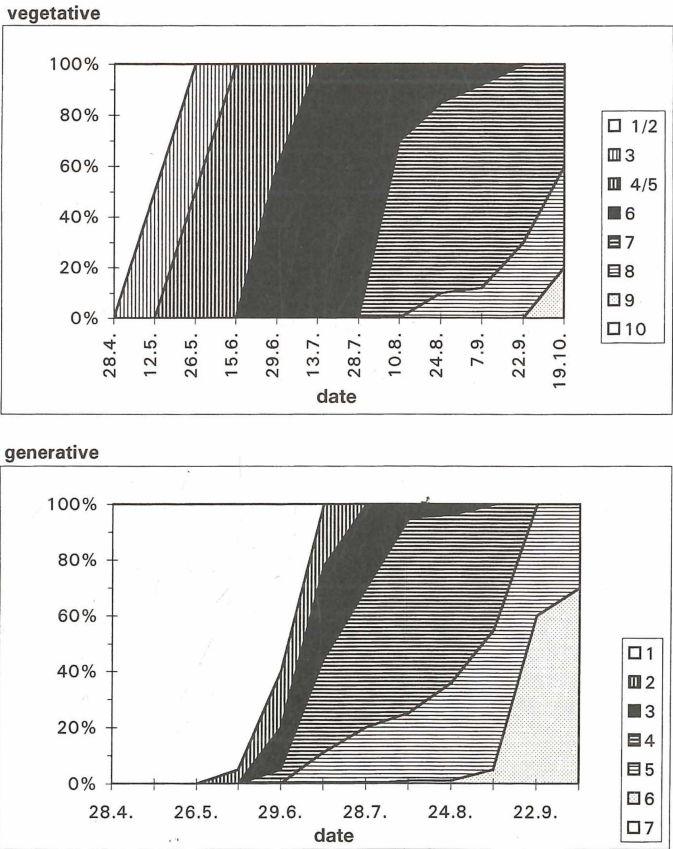


Fig. 5
Phenology of *Carex bohemica*
in the middle of the pond
(Gloggere Weiher) in 1993
(percentage of the different
phenological stages of the
whole studied population;
legend see Tab. 8).

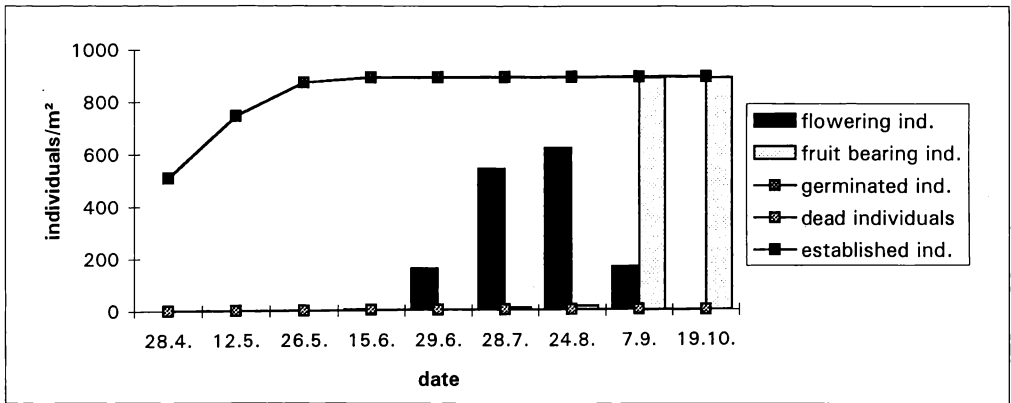


Fig. 6

Cumulative number of germinated*, established* and dead individuals and number of flowering and fruit-bearing individuals of *Carex bohemica* in the Gloggere Weiher in 1993.

* – curves of germinated and established individuals are identical, because no mortality occurred.

A long-term persistence of diaspores of *Carex bohemica* also seems to be supported by the numerous observations of the sporadic occurrence of this species (MOOR 1936, PIETSCH & MÜLLER-STOLL 1968 a.m.o.). POSCHLOD (1993a) investigated the diaspore bank of ponds for which historical floristical data existed. Germinable diaspores were found from *Carex bohemica* even if the last floristical records were nine years earlier (Neuweiher – last floristical record 1983, actual evidence in the diaspore bank 1992). In one pond, the Uhlenrückenweiher near Augsburg, *Carex bohemica* was first detected for the whole region, although the pond is visited every year and the flora of the region has been well known for years (HIEMEYER 1978, 1984).

But that would also mean that *Carex bohemica* is not as rare as the actual records indicate. Therefore it is recommended that the “underground floristics-method” should be used to get accurate impression of species distribution for future floristical mappings of landscapes with a high number of ponds (POSCHLOD 1993a). Already DARWIN (1859) wrote: “I do not believe that botanists are aware how charged the mud of ponds is with seeds...”, and “I took in February three tablespoonfuls of mud from three different points, beneath water, on the edge of a little pond; this mud when dried weighed only six and three-fourth ounces; I kept it covered up in my study for six months, pulling up and counting each plant as it grew; the plants were of many kinds, and were altogether 537 in number; and yet the viscid mud was all contained in a breakfast cup”.

Long persistence of diaspores is also known in other *Carex* species (*Carex acutiformis*, *C. davallia-*

na, *C. elata*, *C. flava*, *C. fusca*, *C. gracilis*, *C. hostiana*, *C. panicea*, *C. rostrata*, PFADENHAUER & MAAS 1987; *Carex caryophyllea*, *C. flacca*, *C. montana*, POSCHLOD 1993b; see also GRIME & al. 1988, BAKKER 1989). It is evident that among most plants of mudflats or generally amphibious sites, long term diaspore persistence is probably the most important regenerative strategy and strategy to persist high water inundations (BERNHARDT 1993, BERNHARDT & POSCHLOD 1993, POSCHLOD & al. 1993). VOESENK & BLOM (1992) showed this in more detail in an experiment in which diaspores of *Rumex palustris* were artificially buried. These diaspores had nearly the same germinability after three years as at the beginning of the experiment.

Finally, it is evident that long term persistence of diaspores is favoured if they are stored under wet and anaerobic field conditions (VILLIERS 1973, KEDDY & REZNICEK 1982; see also MURDOCH & ELLIS 1992). Therefore, it is not astonishing that often high numbers of germinable diaspores can be found in the soil of wetlands (LECK 1989, KOHN 1993, POSCHLOD & al. 1993). The highest numbers were found by SKOGLUND & HYTTBORN (1990) in the sediment of a shallow water lake (about 400 000 germinable diaspores/m², most of them *Carex*-species), down to a depth of 40cm.

4.2 Germination

BASKIN & al. (1993) already showed for four annual mudflat species of *Cyperaceae* that both innate dormancy and no innate dormancy can occur. Diaspores of one species, *Cyperus flavicomus*, were dormant at

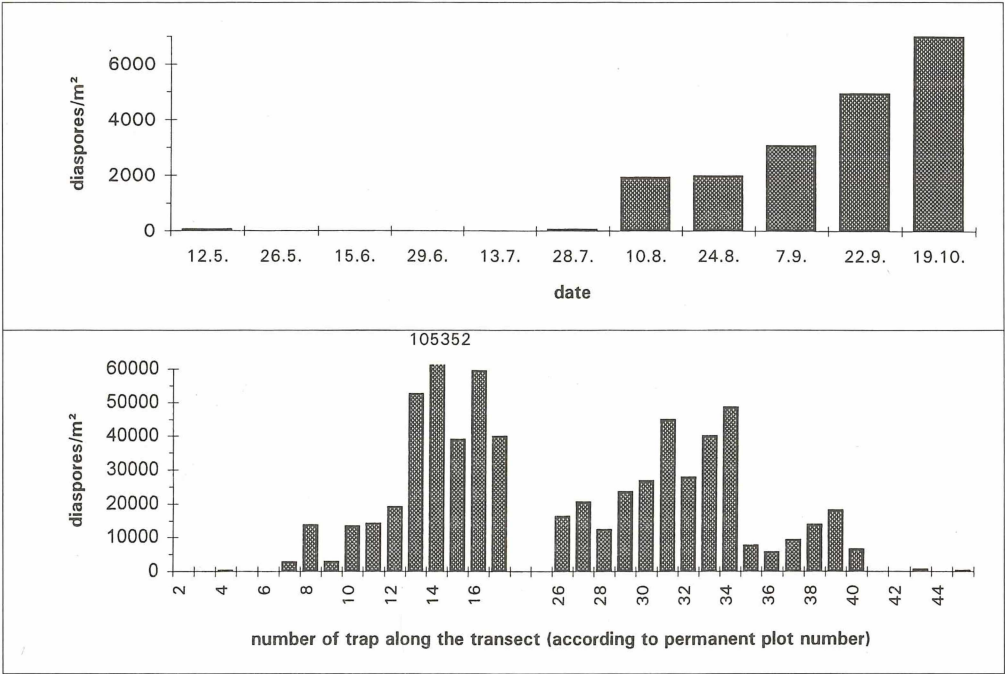


Fig. 7 Temporal (above) and spatial (below) distribution of the diaspore rain of *Carex bohemica* in the Gloggere Weiher in 1993.

maturity in autumn. Those of three other species, *Cyperus erythrorhizos*, *Fimbristylis autumnalis* and *F. vahlii*, could germinate in high numbers immediately after ripening, like *Carex bohemica* did it in this experiment.

Storage-induced dormancy is known in some species (ISTA 1993). But there is no reduction of viability of the diaspores by air-drying, which is known in some amphibious or water plants such as *Zizania aquatica* (SIMPSON 1966).

Large daily temperature fluctuations do not occur under water. Therefore germination at diurnal temperature fluctuations is characteristic of plants of shallow marginal waters, mudflats and marshes. These conditions promote the germination of *Carex bohemica* to a small but significant extent. A similar promotion of germination is reported for *Zizania aquatica* (SIMPSON 1966), *Bidens tripartita*, *Lycopus europaeus*, *Lythrum salicaria* (FRANKLAND & al. 1987; s.a. THOMPSON & al. 1977) and *Typha latifolia* (GRIME & al. 1988).

Light requirements for germination are, in most cases, typical in plants of the above mentioned sites (SALISBURY 1970; GRIME & al. 1981; e.g. *Elatine alsinastrum*, *Lobelia inflata*, MAYER & POLJAKOFF-MAYER 1982). This is interpreted by MAYER & MAYBER POLJAKOFF (1982) to be of adaptive signi-

ficance in these sites – it ensures that germination does not occur during high inundations or only in relatively shallow water which can be penetrated by light. Light in combination with diurnally fluctuating temperatures can have an additive stimulating effect on germination, which is the case in *Carex bohemica* (Table 5). This phenomenon is known to occur in other plants (TOOLE & KOCH 1977, ROBERTS & BENJAMIN 1979, PROBERT & al. 1985, SIMPSON 1989).

The establishment of pond mud species is mostly observed at sites without shading. Therefore it is plausible that *Carex bohemica* does not germinate under far red light conditions as in darkness, although longer wavelengths are absorbed by water (SPENCE & al. 1987).

A further factor influencing germination under water are anaerobic conditions, which were not investigated in this case study. The germination of some species such as *Nasturtium officinale* and *Typha latifolia* is favoured by reduced oxygen tension (MORINAGA 1926a, b, SIFTON 1959). In some species the germination rate is reduced under anaerobic conditions (KENNEDY & al. 1987). This could be also the case in *Carex bohemica*; otherwise, it should germinate under water if the water is clear and light reaches the surface of the soil.

4.3 Population dynamics

Distribution of the diaspore bank along the transect correlates with seed rain and population development after draining. This is also characteristic of wetlands with high water level fluctuations (tidal wetlands; PARKER & al. 1989, LECK & SIMPSON 1994). VAN DER VALK & PEDERSON (1989) and THOMPSON (1992) noted that the composition of the vegetation following draining can be predicted with reasonable accuracy from a knowledge of the contents of the diaspore bank, as was shown here (Table 2). But not in all cases germination from diaspores of the diaspore bank occurred. The number of germinable diaspores in the soil is much higher than the number that germinate in the field (Table 3, Fig. 6). Germination rate is affected not only by burial (GALINATO & VAN DER VALK 1986), but also by moisture regime (VAN DER VALK & DAVIS 1978, VAN DER VALK 1981, KEDDY & ELLIS 1985), substrate (MOOR 1936, KEDDY & CONSTABEL 1986, WHITE 1993) and amount of litter (VAN DER VALK 1986). Substrate and litter are in most cases linked to the hydrological cycle (WHITE 1993). All these factors were relatively constant in this study, with the exception of moisture regime, which probably prevented germination in the flooded zone in the middle of the pond. This is probably the most important factor controlling

germination rate. However, a low germination rate can be an advantage if reflooding disturbs an established population which has not yet reproduced. The part of the diaspore population which did not germinate represents a buffer for these unpredictable, catastrophic events (VOESENK & BLOM 1992). When the site conditions are optimal a new population can again be established.

BASKIN & al. (1993) showed in their aforementioned experiment, in which the diaspores of four summer annual mudflat species were buried that no species enter dormancy in spring or summer. They can germinate at any time during the growing season if mud becomes exposed. This makes it plausible that *Carex bohemica* germinates during a relatively long period (from April to June, Fig. 4–6). That means, that for germination and following establishment the exposure of mud is the most important factor. Conversely some mudflat plants can germinate under water, such as *Limosella aquatica* (LUTHER 1951, HEJNY 1960), although other authors did not make similar observations (SALISBURY 1967a, OESAU 1972).

It is remarkable that all seedlings survived. Rates of mortality among juvenile annual and short-lived plants are normally very high (COOK 1979). The time period from germination to reproduction is not as short in *Carex bohemica* as typically is in most annual mudflat plants. Some mudflat annuals, such as

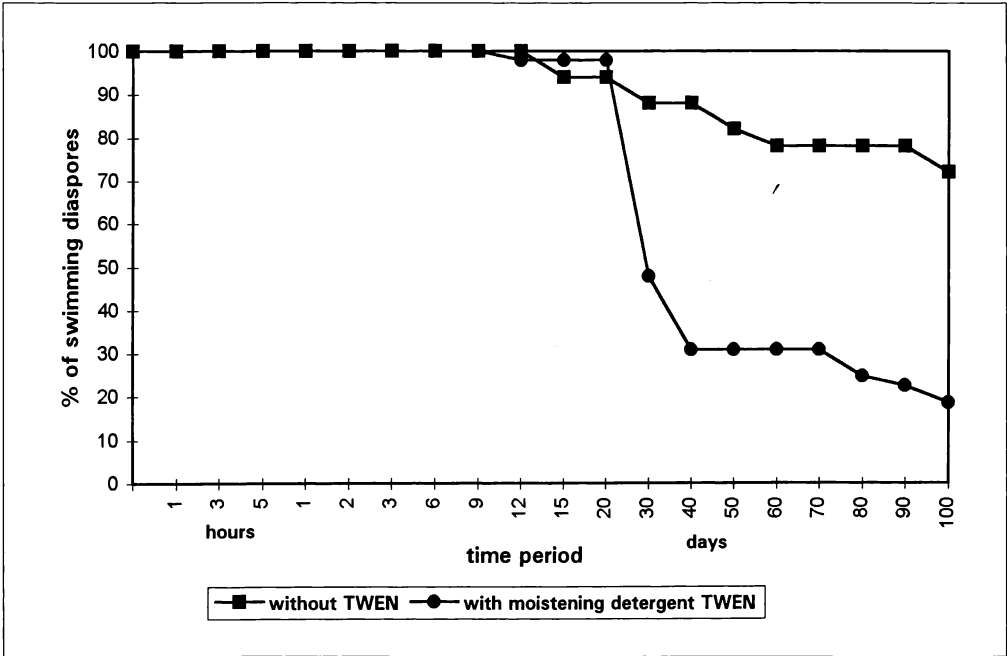


Fig. 8 Duration of swimming of diaspores of *Carex bohemica* (percentage of swimming diaspores after distinct time periods).

Limosella aquatica, need only weeks to go from germination to reproduction (PHILIPPI 1968, OESAU 1972). However, it is important to note that mud exposure late in the year can accelerate maturation of pond mud species. CUMMING (1959) showed that flowering and fruiting of *Chenopodium rubrum* occurs even after two to three weeks in a short-day photoperiod (November). But this phenomenon is probably not present in all mudflat species. Seedlings of *Carex bohemica* could not be observed in autumn or during a short drainage period in December 1991. Dry site conditions probably accelerate the onset of flowering and shorten the time until reproduction, as the comparison of populations near the shore and the middle of the pond shows (Fig. 4, 5).

High reproduction rates are also known in mudflat species, although seed rain along a tidal freshwater wetland zonation in New Jersey was not as high as here (in total for 13 species not more than 10 000 diaspores/m², LECK & SIMPSON 1994). SALISBURY (1970) showed that a single individual of a mudflat species could produce several hundred, thousands, ten thousands or even hundred thousands (*Chenopodium rubrum* ca. 586 000) of diaspores.

Reflooding destroyed the populations of *Carex bohemica*, but the first reproductive phase of this species was already finished when damming occurred again in late autumn. In this case, this species got an annual character. We have no idea whether or not this species is really perennial, as written in the literature (HEGL 1980). But usually pond mud vegetation or at least most of the typical species are destroyed by flooding, although they can still exist for certain time periods before dying (HEJNY 1960). Until now there existed only a few more detailed studies of the influence of flooding on the growth of seedlings or young plants. There is no effect in some species, but is in other species, depending on time and duration of flooding (KLIMESOVÁ 1994).

4.4 Dispersal

Dispersal of both the studied species and most mud plants of a mud flora occurs only around the mother plant, although ELLENBERG (1982) writes that the small diaspores can be very easily dispersed by wind. This is the case in the genus *Juncus*, as BERNHARDT (1993) showed. Diaspores can be theoretically dispersed over long distances when the mud containing them sticks to an animal (KERNER & HANSEN 1921, GILLHAM 1970, BERNHARDT 1989, STILES 1992), and possibly by "internal" transport (OLNEY 1963, 1967).

But dispersal is also a matter of time (LEVINS 1969, COOK 1980). Already GODWIN (1923) showed that older ponds have a higher species num-

ber than younger ones. This concept of dispersal over time begins with the fact that distinct dispersal events (e.g. dispersal of mud with diaspores by bird feet; dispersal by a wild pig taking up diaspores by wallowing in the pond mud, pers. comm. R. BÖCKER, Hohenheim) are very rare. Therefore, the chance that a species with a long living, persistent diaspore bank is dispersed during a period of, for example, several years is much higher than that of a species with a transient diaspore bank. Since *Carex bohemica* has a long living, persistent diaspore bank, dispersal over time is of great importance for this species, as the establishment and reproduction of a population in the investigated region is probably extremely rare. In this context, it is understandable that *Carex bohemica* is relatively widespread in the studied region (Table 2).

4.5 Implication for species conservation and management of ponds

Since changing the traditional management of ponds (FRANKE 1988) it has been recognized that reintroduction of the traditional or artificial management of water levels is an essential tool in conserving pond mud vegetation (BAUER & POSCHLOD 1994a, b) and other mud soil habitats (PEDERSON 1981, PEDERSON & VAN DER VALK 1984, VAN DER VALK & PEDERSON 1989). The ability to predict vegetation development after draining, by testing the diaspore bank, makes it possible to choose those ponds which still have potential (POSCHLOD 1993a, POSCHLOD & al. 1993). In another study it was shown that the draining of a pond without potential can also be successful if, at the same time, a neighbouring pond with potential is drained too. In the Tiefweiher, which neighbours the Gloggere Weiher and had almost no potential before an artificial draining, *Carex bohemica* settled during the drainage period (BAUER & POSCHLOD 1994b) and was found for the first time also in the diaspore bank (POSCHLOD, unpublished data) in the following year.

If the diaspore bank and the potential of a pond can be restored again by draining then it seems obvious from the knowledge of the persistence of the diaspores (POSCHLOD 1993a) that draining is not necessary every year. The data presented in this study of a rare and endangered pond mud species support the recommendation of POSCHLOD & al. (1993), that ponds with potential be drained every 10 to 20 years, in summer or late summer (PHILIPPI 1968, 1969) to freshen up the diaspore bank. This management strategy is already used in North America for the long term conservation of the mud flora in artificially-dammed lakes (KEDDY & REZNICEK 1982, 1986, NICHOLSON & KEDDY 1983).

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