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The migration of vascular plants to a new water reservoir: geographic relationships

Migrace rostlin na nově vytvořenou přehradní nádrž - analýza geografických vztahů

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K e y w o r d s : Dispersal, immigration, establishment, relation to distribution

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23 species that immigrated to a new reservoir (Rozkoš) during the 20 years after it was first filled are discussed, with respect to their distribution: 10 of these species occur at vicinity of the reservoir, 7 species are distributed in the distances between 10 and 50 kilometers of it, and 6 species are found not nearer than 50 km to it. The immigration rate was related more to life-form than to distance. The present distribution of at least some species seems to be rather habitat- than dispersal-limited. Possible dispersal mechanisms are discussed.

Introduction

The dynamic character of plant distribution has often been badly evaluated. As Berg (1983: 14) wrote: „... facts are rare and speculations plentiful; the literature is boundless; and a firm stand on anything means heated discussions for the rest of your life." In Central Europe, most studies on species distribution dynamics deal with introduced species; direct observation of native species is rather rare. Likewise, studies on species extinction are more common than those on their spread.

In 1968, the first of this paper's authors started detailed floristical research in an area of eastern Bohemia, that was later (in 1973) flooded, forming a new water reservoir there. This reservoir was regularly observed several times every year. Detailed knowledge of the original conditions (Krahulec 1975, 1981) allowed us to detect new immigrants and to study their success. We believe that, after 20 years of continuous study of species dynamics, we have an opportunity to summarize our observations. The aim of this paper is to evaluate the observed facts in a geographical context. The study is based on a rather deep knowledge of species distribution in E Bohemia, which is at present being summarized by V. Faltys and E. Hadač in their manuscript, Atlas of the distribution of E Bohemian flora. Other papers discuss the ecological aspects of immigration and the formation of established populations (Krahulec et Lepš 1993a), and the formation of helophyte stands under the influence of stabilized or fluctuating water level (Krahulec et Lepš 1993b).

Study site

The study was carried out at the Rozkoš reservoir (16° 4' E, 50° 22' N) situated in eastern Bohemia (Fig. 1), at the altitude of about 280 m. The bedrock of the area is lime-rich chalk of Cretaceous (Turonian) age, weathering into deep lime- and clay-rich soils. The site is situated on the northeastern margin of the Elbe lowland, which is characterized by relatively warm condition, compared to eastly and northerly adjacent areas. Similarly, the bedrock is acidic to the east and north. This position with respect to climate and bedrock coincides also with a phytogeographical division of Bohemia: it is a marginal part of the Thermophyticum region. The relatively warm climate and calcium carbonate-rich soil result in the subhalophytic character of the locality under study.

The Rozkoš reservoir was filled in 1973. It is situated by 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 hm^3, a maximum flooded area of 1001 ha and an approximate average throughflow (Q_{355}) of 2 m^3s^{-1}. Consequently, the flow through the reservoir is negligible and the transport of diaspores and other material is more influenced by wind and wave action. More detailed data on substrata and water chemistry are given in Krahulec, Lepš et Rauch (1980) and in Maixner et Sládeček (1983).

There were originally only small water bodies in the flooded area, the largest having an area of 15 ha. The reservoir is divided into two parts by a dam with a spillway at the altitude of 280.9 m. When the water level climbs above this altitude, both parts of the reservoir fuse into one; when the water level remains below this point there are two partially separated reservoirs. The upper part of the reservoir has a relatively stable water level, which only occasionally increases above the normal level (max. 0.6 m), and never falls below it. The water level in the lower reservoir fluctuated between a 0.6 m increase and a 2-3(-5) m decrease (see Krahulec et Lepš 1993: Fig. 1, and Žďárek 1987: Fig. 9; for early years, see also Krahulec et al. 1980). The area at damming stage is about 200 and 800 ha for the upper and lower reservoirs, respectively. The timing of fluctuation is rather uniform: the drop in the water level usually starts in July, and replenishment the re-filling of the reservoir comes with melting water in springtime.

The parts of the reservoir differ in several respects. The upper reservoir has a relatively constant water level, without decreases. The conditions are more eutrophic, because most of the water flowing into it also comes directly from the Úpa river. There is low wave action, due to its smaller area and the mild slope of its shores.

In the lower reservoir, the water level decreases strongly (up to 5m) during dry years. Conditions here are more mesotrophic, due to a high degree of nutrient elimination (Maixner et Sládeček 1983), and heavy wave action has formed some heavily eroded shores.

After 1980, the water plant species composition of the two reservoirs started to differ, probably because of a differentiation in the reservoir water chemistry. Abundant populations of *Zannichellia palustris, Potamogeton berchtoldii* and *P. pectinatus* developed in the upper reservoir, and its shores were rapidly overgrown by stands of *Typha latifolia*. The lower reservoir harboured abundant populations of broad-leaved species of *Potamogeton* (*P. crispus, P. lucens*) and, in some years, a large population of *Callitriche hermaphroditica*. Only a small portion of the shore harboured emergent vegetation.

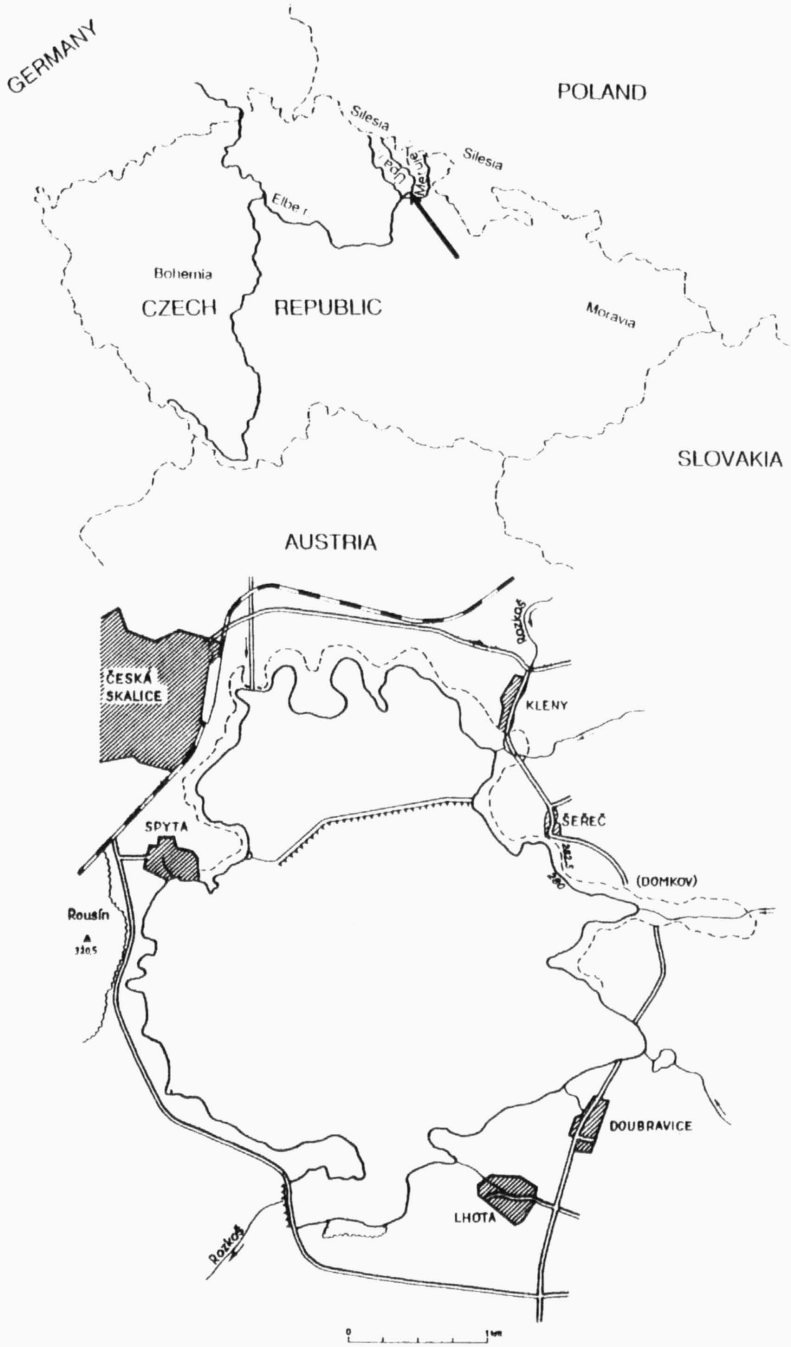

Fig. 1. - Map of the Rozkoš reservoir and its geographic location.

Results

In the years after it was flooded, a set of species immigrated to the reservoir. Lists of them were subsequently published in several reports: Krahulec et al. (1980, 1986 1987), Krahulec, Rauch et Žďárek (1980), Krahulec (1989). Localities of the first specimens of newly-found species are given in Fig. 2. In this paper these newly-recorded species will be discussed in detail, with respect to their distribution and history of establishment. The following species were identified as immigrants to the Rozkoš reservoir:

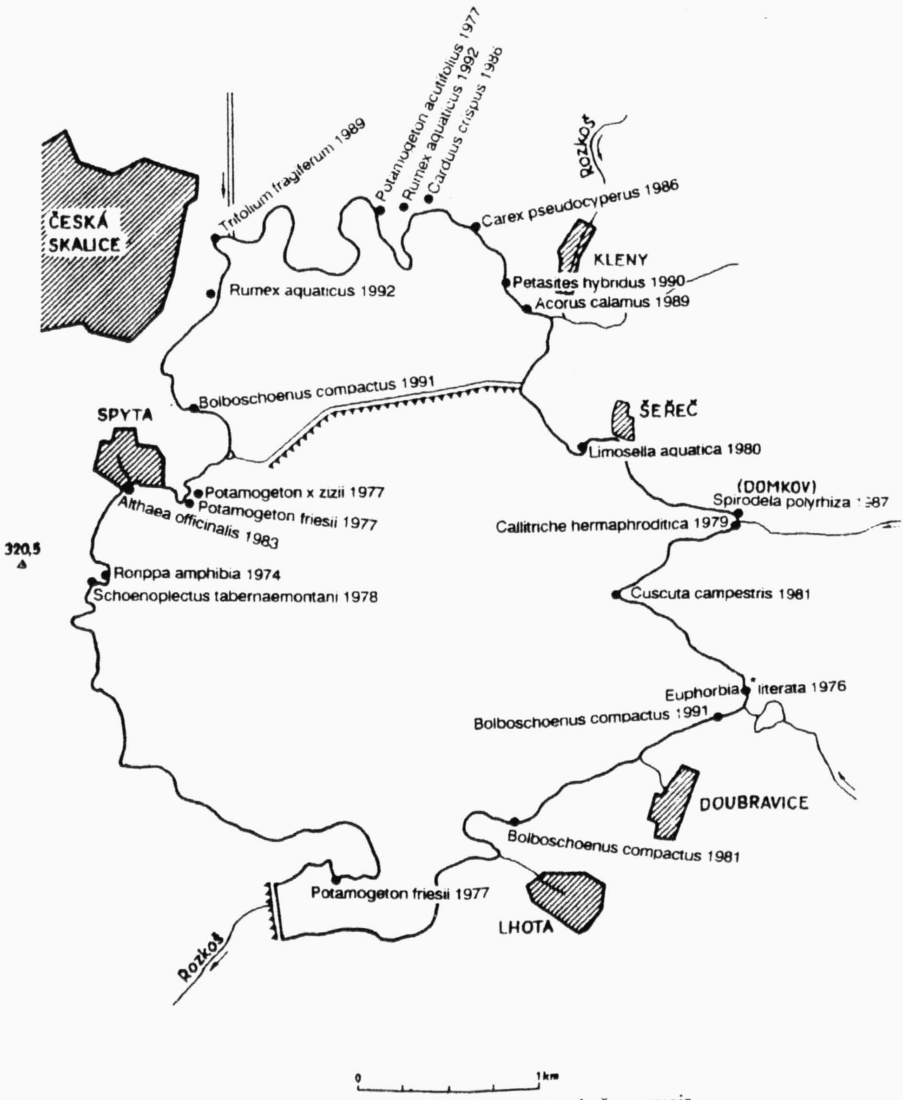

Fig. 2. - The first known localities of the new immigrants at the Rozkoš reservoir.

Acorus calamus L.

This species was reported in the area of the present reservoir (Krahulec 1975) and, at present, is found in its immediate vicinity (a small pond near Doubravice). It was, however, absent from the shores for a long time. In 1989, one small tussock was observed in shallows of the upper reservoir near Kleny, but it was overgrown there by a dense stand of *Typha latifolia*, and not found in the three subsequent seasons. Because this species reproduces in Central Europe only by means of rhizomes, this new occurrence can hardly have derived from those plants present in the area before flooding, and so we consider it to be a new immigrant.

Alisma gramineum Lej.

This species was found during the 1930s in the immediate vicinity of the reservoir, at a small fishpond near Doubravice (Krčan et Kopecký 1959, Krahulec 1975), but it was absent from the area both before flooding and in the first years after filling of the reservoir. Its explosive spread in 1979 suggests a genuine invasion. No map showing the distribution of this species in Bohemia has been published; its distribution is scattered throughout the NE part of Bohemia (Krčan et Kopecký 1960, Dostál 1989). It is absent from the neighboring part of Silesia (Schube 1903).

Althaea officinalis L.

Slavík (1990: distribution map 579, 1992: 296) considers this species to have been introduced to Bohemia, but some 19th century authors considered it to be native (Čelakovský 1877, Fiek 1881), but with some localities originating from cultivation. Fiek (1881) thought that this species had been introduced to Silesia. At the Rozkoš reservoir it occurs in a habitat similar to that of other Bohemian localities (heavy soils of subhalophytic character); this locality is found at the margin of its distribution area in Bohemia. The diaspores may have come from any other Bohemian locality. We are not aware of this species being planted in gardens in E Bohemia.

Bidens radiata Thuill.

This species was absent from the NE part of Bohemia; see the distribution map published by Lhotská (1968). It is also rare in adjacent Silesia (Fiek 1881, Schube 1903, Trzcinska in Pawlowski et Jasiewicz 1971). The nearest localities are known, in Dzierżoniów (= Reichenbach) in Silesia (Poland) at a distance greater than 50 km. The Rozkoš reservoir differs from the other localities in the Czech Republic by its Ca-rich soil and warm climate (see Lhotská 1968); the only similar locality is the Mlýnský rybník fishpond near Lednice in southern Moravia. It was discovered in 1976 at the Rozkoš and since then has been a regular and common component of its flora. In 1988, this species was found at the fishpond of Broumar near Opočno, at a distance of about 10 km from the reservoir (Faltys in litt.). Since the Broumar area has been investigated many times by generations of botanists and *Bidens radiata* had never been found there before 1988, this locality could be considered as that of a newly established population. The rich population at Rozkoš may thus serve as a diaspore source for the forming of new localities in NE Bohemia.

Bolboschoenus compactus (Hoffm.) Drobov

This species usually prefers halophytic or subhalophytic habitats. Its distribution is not fully known because of problems in determination. However, it can be supposed that some localities do exist in the Elbe lowland. It was recorded at Rozkoš three times. One fertile specimen was found on the SE shore of the lower reservoir in 1981, but this occurrence was not confirmed after the 1981 decrease of the water level. Two more records come from the 1990s: one specimen on the upper reservoir in 1991, and a small, loose tussock near Doubravice in 1991. Due to the gap in time between the discoveries of these individuals, we presume that at least two different and independent immigrations have occurred.

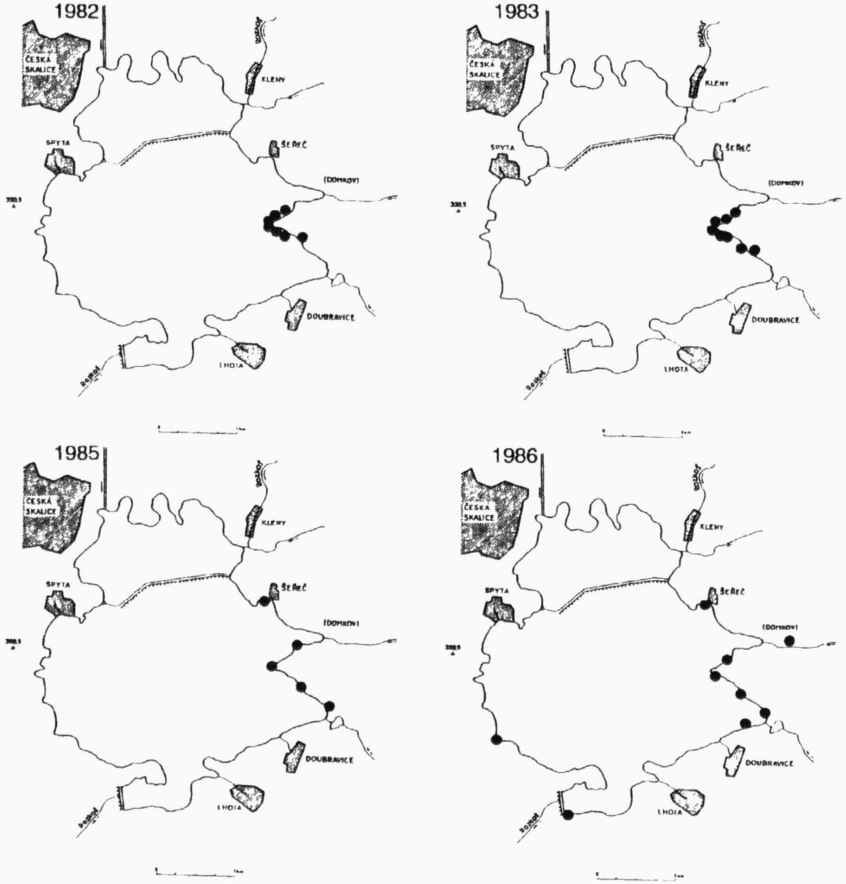

Fig. 3. - The distribution of *Cuscuta campestris* in selected years, showing its establishment on the shores of the Rozkoš reservoir. After 1986 it was found only once (1989) at the main dam.

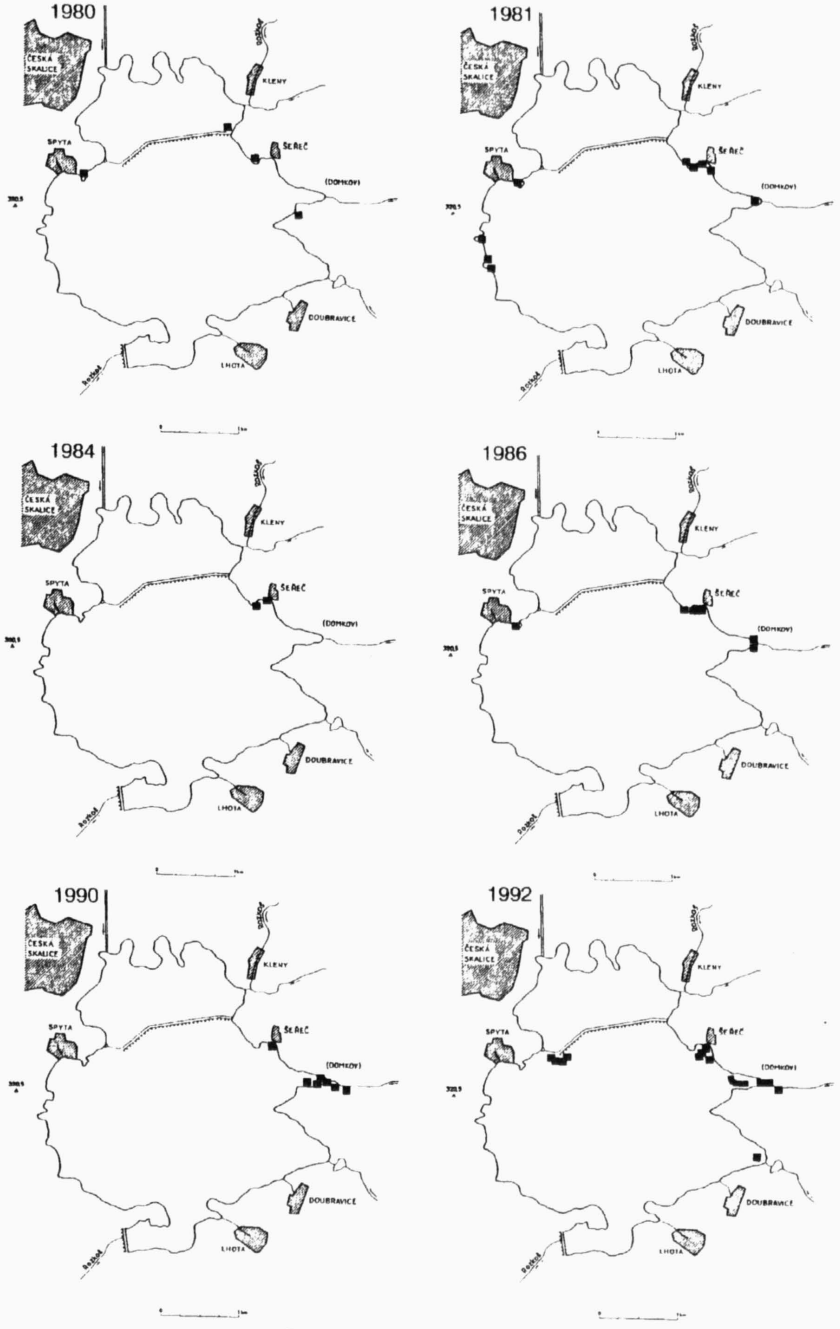

Fig. 4. - The distribution of *Limosella aquatica* in selected years, illustrating a species with successful establishment of its whole population.

Callitriche hermaphroditica L.

The first specimen of this species was found in 1979 at the lower reservoir. In 1980 and 1981, there was an explosive occurrence of it in the lower reservoir, which has less eutrophic conditions than the upper. In subsequent years this species declined; the last record comes from 1989. The first record from Rozkoš came at almost the same time as this species was discovered in another place in E Bohemia (1978 - Černohous 1980). In 1987, Kusák (1989) found two new localities of this species in E Bohemia. A mass occurrence was indicated in all new localities, which seems to us a typically explosive spread of a new immigrant. Since all these localities occur outside the main distribution area of this species (for map, see Meusel et al. 1978), we think that these new discoveries of *C.h.* reflect a recent migration to the South.

Carduus crispus L.

Two specimens were found in 1986 on the northern shore of the reservoir. In 1992 this species was found again at the same place. This species does not occur in the immediate vicinity of the reservoir, and has a rather discontinuous distribution in E Bohemia.

Carex pseudocyperus L.

One fertile tussock was found in 1986 on the NE shore, near the village of Kleny. The same tussock was observed in the following two seasons; later it was overgrown by *Typha latifolia* and *Phalaris arundinacea* and, from 1989 on, was no longer found. The nearest localities are found at a distance of more than 10 km, in the vicinity of the town of Jaroměř (Prokeš et Válek 1946, Faltys in litt.).

Ceratophyllum demersum L.

This species appeared immediately after the reservoir was filled, in 1974. The distribution map published by Slavík (1986: map 74) shows that the present occurrence is situated inside the common distribution area of this species.

Cuscuta campestris Yuncker

The first specimen of this species was found in 1981; in subsequent years it has spread along the shores (Fig. 3). The number of its host plants also increased: in 1981 it was found to be parasiting *Polygonum persicaria, P. aviculare* and *Chenopodium polyspermum*. In 1983 it was found on *Bidens tripartita, Chenopodium album, Cirsium arvense, Gnaphalium uliginosum, Inula britannica, Lactuca serriola, Lotus corniculatus, Matricaria maritima, Mentha arvensis, Potentilla anserina, Plantago major, Trifolium hybridum*, and *T. pratense*. In addition to these species, *Polygonum lapathifolium, Ranunculus repens, Rorippa palustris* and *Echinochloa crus-galli* were identified as host plants in 1984. The species appeared to be well established, until after 1986.

After 1986 the sudden population decline started and in 1989 only one specimen was found near the main dam, where it has been observed in previous years. The reason for the sudden extinction of this species, which had occurred on 4 kilometers of shore is

unknown. The map of its distribution in Czechoslovakia was published by Chrtek (1986). The species is rather rare in Bohemia and occurs in warmer regions, mainly in habitats with a strong anthropic influence: railway stations, margins of roads and the like. In southern Moravia and Slovakia, it was also observed in grasslands, including halophytic habitats. One group of localities in Bohemia consists of those having different character: the emerged bottoms and shores of fishponds in southern Bohemia, between Vodňany and České Budějovice. This habitat type corresponds to that of the Rozkoš reservoir. Although the nearest locality was the railway station in Náchod (found in 1975), we think the immigration is more likely related to the species' occurrence at fishponds in S Bohemia.

Euphorbia platyphyllos L. subsp. *literata* (Jacq.) Holub

One specimen was found on an emerged bottom near Doubravice in 1976. This occurrence lies outside the distribution area of this subspecies, possessing a halophilous character with the nearest known localities in southern Slovakia (Chrtek et Křísa 1993). The occurrence at Rozkoš had an only ephemeral character; it might have been favoured by the extremely hot and dry spring and summer of 1976.

Limosella aquatica L.

In 1979, the first colony of this species was found on an emerged bottom near Šeřeč, and subsequently spread throughout the reservoir (Fig. 4). Its population seems to be fully established. With respect to its distribution in E Bohemia (Faltys, in manuscript), the present locality forms the margin of its local area but is part of a continuous distribution. The success in colonization of this species is highly influenced by its being an annual, combining clonal growth by runners with seed reproduction. The species is insect-pollinated, but can, however, be autogamous and even cleistogamous, and can produce new seeds several weeks after germination. It produces a number of small seeds, and can be considered as a typical plant with fugitive strategy.

Myriophyllum spicatum L.

The species was found in both parts of the reservoir in the second year after filling (1974). Later, it was found only irregularly. The species has a number of localities in NE Bohemia (Černohous 1978), so that its occurrence at the Rozkoš reservoir can be considered part of its continuous distribution area.

Petasites hybridus (L.) P. Gaertner, B. Meyer et Scherb.

This species occurred in the reservoir area before its flooding. In 1990, a young (but not seedling) specimen was found in drifted material near the village of Kleny. It was not found in subsequent years, and probably became extinct. This occurrence was probably not related to the previous one in the area, which stemmed from new diaspores (the species is common upstream, along the Úpa river).

Potamogeton acutifolius Link in Roemer et Schult.

This species was found only once, in 1977. According to the survey of macrophytes of E Bohemia (Černohous 1978), the occurrence at Rozkoš falls outside the main distribution area, the nearest localities being near Hradec Králové.

Potamogeton friesii Rupr.

This species was found for the first time in 1977; it was also recorded at the main dam in some subsequent years (1978, 1980, 1986). It is an extremely rare species in Bohemia; there is no other recent report of its occurrence in the NE part of the country. The species was slightly more common (yet also rare) in Silesia (Fiek 1881, Schube 1903), but the present status of its localities there is unknown.

Potamogeton obtusifolius Mert. et Koch

An explosive increase of this species occurred in 1971, during the time of the filling of the upper reservoir; it was subsequently found several times during the 1970s. A map of its distribution in E Bohemia was published by Černohous (1978); the nearest localities are those along the Orlice river.

Potamogeton x *zizii* Koch ex Roth

P. x *zizii* was found several times (1977, 1979, 1982) in the western part of the lower reservoir, near the village of Spyta. It is a hybridogeneous species which occurs extremely rarely both in Silesia (Schube 1903) and in the Czech Republic (Nováková 1982). Nováková published a distribution map for this area; and while the Rozkoš occurrence is given on her map, it is not mentioned in the list of localities. She also characterized this species as having a slightly subhalophytic character. Černohous (1978) found only one locality existing in E Bohemia during the 1970s. This species was also rare in Silesia (Schube 1903). However, it is not known, whether this stabilized fertile hybrid immigrated to the reservoir or originated there; both parent species (*P. gramineus* and *P. lucens*) were present at the site (Krahulec 1981).

Rorippa amphibia (L.) Besser

First specimen was found in 1974, and from 1977 it has been a regular (although not common) component of the flora of this reservoir (Krahulec 1989). The distribution map for this species (Tomšovic 1969) shows that this locality lies on the margin of the local area. It occurs along the Metuje (localities given by Krčan et Kopecký 1959) and Úpa rivers, upstream from the Rozkoš reservoir (Faltys 1988).

Rumex aquaticus L.

In 1992, two fertile specimens of this species were found on the western and northern shores of the upper reservoir. This species occurs along the Metuje (Krčan et Kopecký 1959) and Úpa rivers, upstream from the reservoir (Krčan in Buřil et al. 1941). According to the distribution map (Slavík 1986), it is common throughout NE Bohemia.

Schoenoplectus tabernaemontani (C. C. Gmelin) Palla

The first specimen of this subhalophytic species was found on the western shores in 1978, and another flowering one not far from there in 1984. Their vitality declined after the decrease of the water level in 1982, and they were later overgrown by *Phalaris arundinacea*; they were observed for the last time in 1986. Distribution maps (Fiedler 1954, Slavík 1988: 82) show that the occurrence at Rozkoš is outside the main distribution area, the nearest localities being more than 15 kilometers from the reservoir. Some other localities on the periphery of the regular distribution were also in man-made habitats (see Fiedler 1954). The species tends to spread when a suitable habitat is available.

Spirodela polyrhiza (L.) Schleiden

Surprisingly, this species was absent in the area under study and, in fact, is rather rare in the chalk area of the foothills of the Orlické hory Mts. (manuscript of the distribution map by V. Faltys). However, it occurs in the area upstream. The species immigrated into the reservoir relatively late and, at present, occurs rarely in the bays of the former village of Domkov (where we found it for the first time), and in a bay polluted by a brook flowing from the village of Lhota.

Trifolium fragiferum L. subsp. *fragiferum*

A small colony of this species was found on the NW shore of the upper reservoir in 1989. This species was present in the center of the flooded area (cf. Krahulec 1975). The new occurrence presumably resulted from a new immigration: the original population occurred in a relatively distant place at the center of the later reservoir, and was flooded 18 years before the new population appeared. This species is not very rare over the broader area (e.g. Krčan et Kopecký 1959), although it was not found in the immediate surroundings of the reservoir.

Discussion

Rate of immigration: effects of distance and life form

At least three groups of species may be distinguished, with respect to the possible origin of immigrants:

(i) Species occurring in the vicinity of the reservoir (up to a distance of 10 kilometers) or upstream: *Acorus calamus, Alisma gramineum, Ceratophyllum demersum, Limosella aquatica, Myriophyllum spicatum, Petasites hybridus, Rorippa amphibia, Rumex aquaticus, Spirodela polyrhiza, Trifolium fragiferum*. The occurrence of these species at the Rozkoš reservoir lies within the area of their continuous distribution in Bohemia.

(ii) Species occurring at a medium distance, between 10 and 50 kilometers away from the reservoir: *Althaea officinalis, Carduus crispus, Carex pseudocyperus, Potamogeton acutifolius, P. obtusifolius, Schoenoplectus tabernaemontani*. The occurrence of these species at the Rozkoš reservoir is marginal, with respect to their distribution in Bohemia.

(iii) Species at a distance greater than 50 kilometers: *Bidens radiata, Callitriche hermaphroditica, Cuscuta campestris, Euphorbia* * *literata, Potamogeton friesii, P.* x *zizii*.

The present distribution of *Bolboschoenus compactus* is not known, but it probably

Table 1. - List of species immigrating to the upper and lower parts of the Rozkoš reservoir. The following data are given: the year of arrival (ARRIV), surviving period (SURV), life form (H - hemikryptophyte, T- therophyte, G - geophyte, Hy - hydrophyte), breeding system and pollination (A - autogamy, I - insect pollinated, W - wind pollinated, Wa - water pollinated, d - dioecious), seed size (in mm), relation to the local distribution area (within = the nearest locality up to 10 km distance, margin = the nearest locality between 10 and 50 km; distant = above 50 km).

Species	Reservoir							
	Upper		Lower					
	ARRIV	SURV	ARRIV	SURV	Life form	Pollination system	Seed size	Relation to the area
Alisma gramineum			79	79-92	H	I	2-2.7	margin
Althaea officinalis			83	83-90	H	A,I	3-3.5	margin
Bidens radiata		77-92	76	76-92	T	A,I	4-5	distant
Acorus calamus	89				G	vegetative reprod.		within
Bolboschoenus compactus	91	81 91-92	81-82 91	91-92	G	W	3	margin
Callitriche hermaphroditica			79	79-89	Hy	Wa	1.5-2	distant
Carduus crispus	86,92				H	A,I	3	within
Carex pseudocyperus	86	86-88			H	W	2	margin
Ceratophyllum demersum	74	74-90		75-90	Hy	Wa	4-5	within
Cuscuta campestris			81	81-86,89	T	A,I	1	distant
Euphorbia platyphyllos subsp. *literata*			76		T	I	1.8-2.0	distant
Limosella aquatica		80	79	79-92	T	C,A,I	0.5-0.7	within
Myriophyllum spicatum			74	74-80	Hy	Wa	2-3	within
Petasites hybridus	90				H	I,d	2-3	within
Potamigeton acutifolius	77				Hy	I	2-3	margin
Potamogeton friesii			77	77-86	Hy	I	2-3	distant
Potamogeton obtusifolius	71	71-79			Hy	I	2-3.5	margin
Potamogeton x *zizii*			77	77-82	Hy	I	2	distant
Rorippa amphibia		76-92	74	74-92	H	A,I	0.6-1.2	within
Rumex aquaticus	92				H	W	3.0-3.8	within
Schoenoplectus tabernaemontani			78	78-86	G	W	2-2.5	margin
Spirodela polyrhiza			87	87-92	Hy	I	turions 2-3	within
Trifolium fragiferum s.s.	89	89-92			H	I	1.6-2	within

Sources: Casper et Krausch (1980, 1981), Frank et al. (1988), for the details on distributional data see Krahulec et Lepš (1993a).

has some localities up to a distance of 50 kilometers. Unfortunately, the published records are not reliable, because previous descriptions were ambiguous (that is, not all plants with „compact" cyme do belong to *B. compactus*).

There is no clear correlation between distance and immigration time: most of the species from distant (i.e. more than 50 km) localities immigrated during the early years, whereas the immigrations of species from the other two groups are more or less evenly scattered

throughout the entire 20- year period (Table 1). This difference, however, is not statistically significant. (Owing to the small sample size, given strictly by the number of immigrating species, and the character of the data, which are often not suitable for parametrical tests, statistical analysis is often difficult and test power is low.) On the other hand, the first period (before 1979) was characterized by the immigration of most hydrophytes and therophytes (the difference between immigration times of species of different life forms is close to significant, P=0.05 and P=0.08 for parametrical and nonparametrical analyses, respectively). All of the species from distant localities are therophytes and hydrophytes. Species with different life forms and inhabiting different habitats possess different rates of dispersal and different probabilities of forming a new population.

Dispersal mechanisms

Only a few of the new immigrants possess specialized dispersal mechanisms: *Petasites hybridus* and *Carduus crispus* are adapted to wind dispersal, and *Bidens radiata* is dispersed by animals (exozoochory). All of the species could disperse by water; nevertheless, this mechanism can only be expected to work for species occurring upstream, so that only species from nearby localities come into account. Most of the new immigrants have rather large seeds: in 12 species the seeds are larger than 2 mm, and only one species has seeds smaller than 1 mm (Krahulec et Lepš 1993a). Human activity and water birds may be considered to be the main dispersal vectors. It is interesting that the first period, with a rapid immigration of hydrophytes, coincided with an extremely high number of various water birds visiting and wintering at this locality. Fortunately, continuous observations of bird fauna are available (Žďárek 1987). The period after the filling was characterized by high populations of the herbivorous birds *Fulica atra, Anas platyrhynchos*, attaining 12,000 and 5,300 individuals, respectively, in one winter (Fiala 1975-76, 1977). These high numbers probably resulted from a greater food supply, due to a high production of submersed vegetation (Krahulec et al. 1980). This coincidence between the high production of submersed vegetation, high number of herbivorous birds and high number of new immigrants, mainly hydrophytes, probably reflects causal relationships. Rapid establishment of hydrophytes might also have been facilitated by a high transparency of water, typical of the first years after filling.

Phytogeographic implications

The rapid immigration of various species to the new water reservoir suggests that the present distribution of at least some species is more habitat- than dispersal-limited. Some hydrophytes which are believed to be dispersed predominantly by birds invaded the new locality especially quickly. This is most obvious in those species that occur near the limit of their local distribution. On the other hand, a number of the new immigrants failed to establish a viable permanent population. Some occurred as a single individual for some time - from one to nine seasons (*Schoenoplectus tabernaemontani*) - and then became extinct for various, mainly unknown reasons. An unsuccessful immigration might be followed by another one (*Bolboschoenus compactus*). Such pulses at the margin of a distribution area are probably rather common. In phytogeographical analyses, short-term occurrences should be distinguished from permanent localities (for example, they should be indicated as such in distribution maps). The occurrence of *Euphorbia *literata*, which

is only present in this locality (quite distant from its main distribution area) as one specimen found during part of one vegetation season, could hardly be interpreted as a change in the species' distribution area. A new immigrant is to be considered fully established when it can serve as a source of diaspores for other localities (as probably happened in *Bidens radiata*). One should be aware that ordinary floristical records report a mixture of both permanent and ephemerous occurrences.

The Rozkoš reservoir, with its calcium carbonate rich soils, has served as a target for the expansion of species with an alcalitrophic or subhalophytic character, e.g. *Althaea officinalis, Bolboschoenus compactus, Cuscuta campestris, Euphorbia *literata, Potamogeton* x *zizii, Schoenoplectus tabernaemontani*, and *Trifolium fragiferum*. Similarly, this area was suitable for the newly-immigrating mollusk *Dreissenia polymorpha* (Krahulec, Rauch et Žďárek 1980) which also has similar ecological (i.e. hard water) demands. It will be interesting to see whether changes in sediments (mainly in the upper reservoir) make the immigration of some more acidophytic species possible.

The distribution of plants is the result of such highly dynamic processes as immigration, establishment and extinction. This dynamics is not only important in fugitive or man dispersed species, but also in species where good colonization abilities are not to be expected. Only systematic, long-term studies can provide reliable evidence of the extent of these processes and their relative importance to present species distribution.

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Souhrn

V této studii jsou shrnuty údaje o druzích, které migrovaly v posledních 20 letech na nově napuštěnou přehradu Rozkoš u České Skalice. Je uvedena doba migrace a úspěšnost uchycení. Výskyt na Rozkoši je zhodnocen z hlediska znalostí o rozšíření jednotlivých druhů, především ve východních Čechách a v přilehlé oblasti Slezska. Z celkového počtu 23 druhů, které se nově objevily, se 10 druhů vyskytovalo ve vzdálenosti do 10 km, 7 druhů mělo nejbližší známé lokality mezi 10 a 50 km, u 6 druhů byly nejbližší lokality více než 50 km vzdálené. Některé další aspekty jsou diskutovány v samostatném článku (Krahulec et Lepš 1993a) a mohou být stručně shrnuty takto: rychlost přicestování nebyla závislá na vzdálenosti nejbližších lokalit, ale byla daleko více ovlivněna životní formou; hydrofytní druhy se v nové přehradě objevily během prvních 7 let po napuštění, stejně jako terofyta. Rychlost migrace nebyla také ovlivněna velikostí semen: většina druhů (12) má poměrně velká semena, větší než 2 mm. Naopak pouze jeden druh má semena menší než 1 mm. U většiny druhů se také jedná o semena bez specializovaných mechanismů k rozšiřování.

Za nejvíce pravděpodobný mechanismus šíření považujeme vodní ptactvo, kterého se zejména v prvním období po napuštění zdržovala na přehradě velká hejna (zejména šlo o lysku a kachnu divokou). V diskusi je dále poukázáno na to, že rozšíření řady druhů je limitováno spíše nedostatkem stanovišť než neschopností překonat vzdálenost: po vytvoření vhodného stanoviště dochází k jeho poměrně rychlé kolonizaci. V případě přehrady Rozkoš docházelo k šíření řady alkalitrofních až subhalofytních druhů: *Althaea officinalis, Bolboschoenus compactus, Cuscuta campestris, Euphorbia *literata, Potamogeton* x *zizii, Schoenoplectus tabernaemontani* a *Trifolium fragiferum*. U řady druhů šlo o jednorázový průnik za hranice rozšíření, druh přežíval v jednom exempláři a nedošlo k založení životaschopné populace (např. *Schoenoplectus tabernaemontani, Carex pseudocyperus, Euphorbia platyphyllos* subsp. *literata*), u dalších druhů došlo k jejich rozšíření a k vytvoření větších populací, které mohou dále sloužit jako zdroj diaspor pro širší okolí. Tento případ se jeví doložen u druhu *Bidens radiata*, který zcela chyběl v SV Čechách. Úspěšně kolonizoval přehradu Rozkoš v roce 1976 a v roce 1988 byl objeven na lokalitě u Opočna. Konstatujeme, že pohyb rostlinných druhů v krajině je dosti velký a jeho rozsah není ještě plně doceněn.

References

Berg R. Y. (1983): Plant distribution as seen from plant dispersal: General principles and basic modes of plant dispersal. - Sonderb. Naturwiss. Ver. Hamburg 7:13-36.

Buřil V. et al. (1941): Nové zajímavé lokality květeny ze severovýchodních Čech. - Zemědělský ústav v Hradci Králové, Publikace 8:17-34.

Casper S. J. et Krausch H.-D. (1980, 1981): *Pteridophyta* und *Anthophyta*. 1. und 2. Teil - Süsswasserflora von Mitteleuropa, Vol. 23 u. 24. - Gustav Fischer-Verlag, Jena.

Chrtek J. (1986): Poznámky k československým druhům rodu *Cuscuta* s.l. II. - Zpr. Čs. Bot. Společ., Praha, 21:107-118.

Chrtek J. et Křísa B. (1993): 3. *Tithymalus* Gaertner - pryšec. - In: Slavík B. et Hejný S. [red.], Květena České republiky, Vol. 3, p. 321-346, Academia, Praha.

Čelakovský L. (1877): Prodromus květeny české. Vol. 3. - Praha.

Černohous F. (1978): Příspěvek k současnému rozšíření vodních makrofyt ve východních Čechách. - Zprav. Kraj. Muz. Východních Čech, Hradec Králové, 5/3:31-50.

Černohous F. (1980): *Callitriche hermaphroditica* v Československu. - Preslia, Praha, 52:203-208.

Dostál J. (1989): Nová květena ČSSR. - Academia, Praha.

Faltys V. (1988): Inventarizační průzkum vegetačního krytu SPR Babiččino údolí. - Ms. [Depon. in Český ústav ochrany přírody, Pardubice.]

Fiala V. (1975-76): Mezinárodní sčítání vodních ptáků 1974/75 na území ČSSR. - Vertebrat. Zprav., Brno, 1975-76:75-81.

Fiala V. (1977): Mezinárodní sčítání vodních ptáků 1975/76 na území ČSSR. - Ibid., 1977:65-71.

Fiedler J. (1954): Příspěvek ke květeně kraje Královéhradeckého. - Čas. Nár. Muz., odd. přírod., Praha, 123:115-119.

Fiek E. (1881): Flora von Schlesien.... - Breslau.

Frank. D., Klotz S. et Westhus W. (1988): Biologisch-ökologische Daten zur Flora der DDR. - Wiss. Beitr. Martin-Luther-Univ. Halle/Wittenberg 1986/60:1-103.

Krahulec F. (1975): Vegetační poměry zátopové oblasti Rozkoš u České Skalice. - Acta Mus. Reginaehradecensis, S.A., Hradec Králové, 13:45-69.

Krahulec F. (1981): Vegetační poměry zátopové oblasti Rozkoš u České Skalice II. - Acta Musei Reginaehradecensis, S.A., Hradec Králové, 16:155-161.

Krahulec F. (1989): Poznámky k flóře přehradní nádrže Rozkoš u České Skalice (SV Čechy). - Zpr. Čs. Bot. Společ., Praha, 24:129-136.

Krahulec F. et Lepš J. (1993a): Migration and colonization by vascular plants to a new water reservoir. - J. Biogeogr., Oxford [submitted]

Krahulec F. et Lepš J. (1993b): The succession on the shores of a new water reservoir: the effect of shore type and fluctuating water level. - J. Veget. Sci., Uppsala [submitted].

Krahulec F., Lepš J. et Rauch O. (1980): Vegetation of the Rozkoš reservoir near Česká Skalice (East Bohemia). 1. The vegetation development during the first five years after its filling. - Folia Geobot. Phytotax., Praha, 15:321-362.

Krahulec F., Lepš J. et Rauch O. (1986): Vegetation succession on a new lowland reservoir. - Arch. Hydrobiol., Beih. Ergebnisse Limnol., Stuttgart, 27:83-93.

Krahulec F., Lepš J. et Rauch O. (1987): Dálkové šíření jako faktor ovlivňující současné rozšíření rostlin. - Zpr. Čs. Bot. Společ., Praha, 22, Mater. 7:71-76.

Krahulec F., Rauch O. et Žďárek P. (1980): Slávička mnohotvárná znovu nalezena v Čechách. - Živa, Praha, 66/5:182.

Krčan K. et Kopecký K. (1959): Květena okolí Nového Města nad Metují. - Preslia, Praha, 31:52-77.

Krčan K. et Kopecký K. (1960): Příspěvek k flóře okolí Opočna a Týniště nad Orlicí. - Acta Mus. Reginaehradecensis, S.A., Hradec Králové, 2:149-190.

Kusák P. (1989): Další nálezy *Callitriche hermaphroditica* ve východních Čechách. - Zpr. Čs. Bot. Společ., Praha, 24: 98-100.

Lhotská M. (1968): Die Gattung *Bidens* L. in der Tschechoslowakei. - Folia Geobot. Phytotax., Praha, 3:65-98.

Maixner J. et Sládeček V. (1983): Elimination of nutrients in the Rozkoš-Reservoir. - Acta Hydrochim. Hydrobiol., Dresden, 11:657-665.

Meusel H. et al. (1978): Vergleichende Chorologie der zentraleuropäischen Flora, Band II. - Jena.

Nováková H. (1982): Rozšíření některých druhů rodu *Potamogeton* v ČSR. - Práce a Studie, Přír., Pardubice, 13-14:49-71.

Pawłowski B. et Jasiewicz A. (1971): Flora Polska. Vol. 12. - Warszawa et Kraków.

Prokeš K. et Válek B. (1946): Příspěvky ke květeně severovýchodních Čech. - Příroda, Brno, 38/9-10: 2-4.
Schube T. (1903): Die Verbreitung der Gefässpflanzen in Schlesien preussischen und österreichischen Anteils. - Breslau.
Slavík B. (1986): Fytokartografické syntézy ČR. 1. - Botanický ústav ČSAV, Průhonice.
Slavík B. (1988): Fytogeografická charakteristika. - In: Hejný S. et Slavík B. [red.], Květena České socialistické republiky, 1:65-102, Academia, Praha.
Slavík B. (1990): Fytokartografické syntézy ČR. 2. - Botanický ústav ČSAV, Průhonice.
Slavík B. (1992): 75. *Malvaceae* Juss.- Slézovité. - In: Slavík B. et Hejný S. [red.], Květena České republiky, 3:282-316, Academia, Praha.
Tomšovic P. (1969): Nejdůležitější výsledky revize československých rukví (*Rorippa* Scop. em. Reichenb.). - Preslia, Praha, 41:21-38.
Žďárek P. (1987): Ptactvo přehradní nádrže Rozkoš (SV Čechy). - Východočeská pobočka České společnosti ornitologické, ZK ROH Tesla Pardubice, Sborník 9:1-102.

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