Folia Geobot. Phytotax., Praha, 29: 3-14, 1994

ESTABLISHMENT SUCCESS OF PLANT IMMIGRANTS IN A NEW WATER RESERVOIR

František Krahulec[1] & Jan Lepš[2]

1) *Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic fax. + 42 2 6436529, E-mail KRAHULEC@EARN.CVUT.CZ*

2) *Faculty of Biological Sciences, University of South Bohemia and Institute of Entomology, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic fax. + 42 38 45985, E-mail SUSPA@ENTU.CAS.CZ*

Keywords: Dispersal, Establishment, Life form, Migration, Reproductive system, Seed size

Abstract: The set of 25 aquatic and shoreline species which immigrated to the new reservoir Rozkoš during the 21 years after its creation were analyzed with respect to their time of immigration, distance of nearest source localities, life form, seed size, and reproductive system. The reservoir consists of two parts, one with fluctuating and the other with stabilized water level. The immigrating species originated from various distances, from nearby to more than 100 km away. A distance of tens of kilometers can be overcome by many shoreline species, provided that suitable (low competition) habitats are available. The survival time was correlated with the reproductive system: species with autogamic or vegetative reproduction survived longer. Establishment was more successful under a fluctuating water level, which decreased the competitive exclusion of immigrated species by helophytes.

INTRODUCTION

The distribution of organisms results from various processes: evolution, dispersal, and extinction. Systematic collection of detailed data is needed to test the hypotheses of each particular process. Successful dispersal (BERG 1983) depends on the probability of dispersal (which includes the effects of distance from propagule source and commonness/rarity of suitable habitat), the probability of establishment, and the formation of viable populations. These processes depend on the habitat parameters, life history, and competition (e.g. KEDDY 1976). Knowledge of initial conditions is crucial for all case studies: this makes newly formed islands (including habitat islands) suitable objects for this type of research. Classical studies include: (a) islands destroyed by volcanic activity: (e.g. Krakatau - summarized by WHITTAKER et al. 1989); (b) newly emerged islands such as volcanic Surtsey near Iceland (FRIDRIKSSON 1975, 1987); (c) new islands which have appeared after water level manipulation, for example in a few Swedish lakes - Hjälmaren (RYDIN & BORGEGÅRD 1991) and Möckeln (NILSSON &

Vol. 28, No. 4 (pages 337-464) of the Folia Geobotanica et Phytotaxonomica was issued 31st December 1993

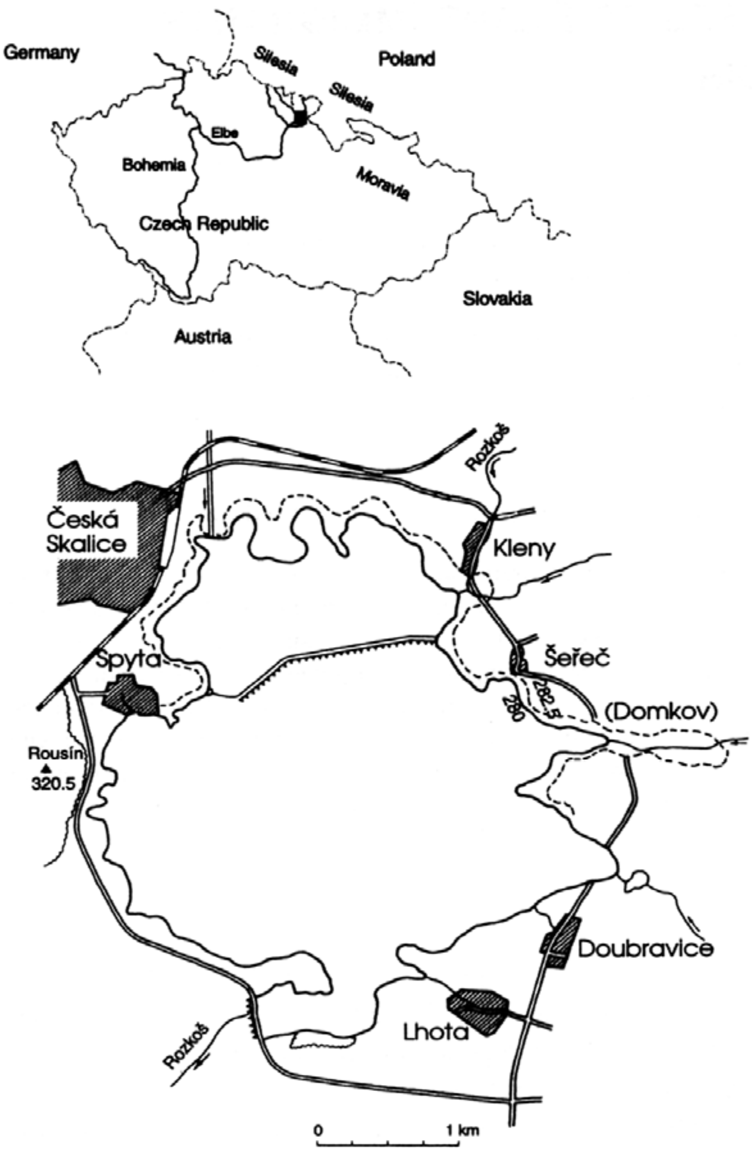

Fig. 1. Localization of the Rozkoš reservoir (indicated by box) and its map. The reservoir is divided into two parts by a dam with a spillway at an altitude of 280.9 m, which is situated between the villages of Spyta and Šeřeč. The upper part of the reservoir has a relatively stable water level, the water in the lower reservoir fluctuates irregularly.

NILSSON 1978), or as a result of land uplift such as in the Baltic area (ITÄMIES 1980). Another group of studies deals with the process of colonization of new polders in the Netherlands (BRUINENBERG et al. 1980, JOENJE 1978, JOENJE & DURING 1977, NIP-VAN DER VOORT et al. 1979) and new volcanoes (REJMÁNEK et al. 1982). A summary of different migration studies was published by SAUER (1988). However, most of these studies register only dispersal events which have proved successful. If the inter-census intervals are long, species can colonize and become extinct between surveys. Therefore, turnover rates may be significantly underestimated, leaving the real immigration and establishment rates unknown. One of the exceptions to this generalization is the detailed and careful study done on the island of Surtsey (FRIDRIKSSON 1975).

Since reservoirs are habitat islands (KEDDY 1976), they are suitable objects for a study of the colonization process provided that initial conditions are known. The object of our study, the aquatic and shoreline flora of the Rozkoš reservoir area, meets these conditions: flora and vegetation have been investigated by many local botanists since the last century and a detailed floral inventory was undertaken in the 5 years preceding flooding. The size of the reservoir (about 10 square kilometers and a 15 km shoreline) allows detailed and regular observations of flora and vegetation on the landscape scale and also enable us to record immigration and subsequent colonization events as well as estimate the proportion of species which have arrived but failed to establish viable populations. Detailed data on plant distribution in Central Europe, collected by generations of local botanists, has enabled us to estimate the propagule source distance for particular species and in this way evaluate migration and dispersal events on a geographical scale. The aim of this paper is to estimate immigration rate and to find the environmental and life history correlates of successful dispersal. The data could provide some insight into the importance of dispersal and habitat limitations for the present distribution of aquatic macrophytes.

Study site

The study was carried out on the Rozkoš reservoir (16^o4'N, 50^o22'E, altitude 280 m) situated in eastern Bohemia (Fig. 1). The bedrock of the area is a lime rich marl of Cretaceous (Turonian) age weathering into deep lime- and clay-rich soils. The locality is situated on the northeastern margin of the Elbe lowland, which is characterized by relatively warm conditions compared to the area more to the East and North. Acidic bedrock is found outside the Elbe basin to the East and North.

The Rozkoš reservoir was filled in 1973. It is situated on a small brook, but most of the water flows into the reservoir through an artificial canal from the Úpa river. In the flooded area there were previously only small water bodies, the largest with an area of 15 ha. Most of the present shores were once arable fields or meadows. The reservoir (Fig. 1) is divided into two parts by a dam with a spillway at an altitude of 280.9 m. When the water level is above this level, there is only one reservoir, otherwise there are two partially separated reservoirs. The upper part of the reservoir has a relatively stable water level - only occasionally does the level increase (max. 0.6 m) above the normal level, but it never decreases. The water level in the lower reservoir fluctuates irregularly: from rare increases to 0.6 m to common decreases of 2-3 (rarely 5) m (KRAHULEC & LEPŠ unpubl. data). The area is about 200 and 800 ha for the upper and lower reservoirs respectively. The timing of fluctuation is rather uniform: the water level usually starts dropping in July, the re-filling of the reservoir starts in spring with melt water. High spring-early summer high water levels are rare. The reservoir has a volume of 76 x 10^6 m^3, a maximum flooded area of 1001 ha, and an approximate average throughflow (Q_{355}) of 2 m^3s^{-1}. For this reason there is no regular flow through the reservoir; the transport of diaspores and other material is more influenced by wind. The results of floristic and succesion studies were summarized by KRAHULEC (1975, 1981) and the vegetation succession after flooding was described by KRAHULEC, LEPŠ & RAUCH (1980, 1984, 1986). More detailed data on substrata and water chemistry are given in KRAHULEC, LEPŠ & RAUCH (1980) and in MAIXNER & SLÁDEČEK (1983). The two parts of the reservoir differ in a number of other features:

The upper reservoir is more eutrophic and has a direct connection with the Úpa river. There is very little wave action due to its small area and mildly sloped shores. The lower reservoir is more mesotrophic and large wave action has strongly eroded some shores.

From 1980, differences in the composition in water plants in the two parts of reservoir has been observed, probably caused by differences of the water chemistry. In the upper reservoir *Zannichellia palustris, Potamogeton berchtoldii*, and *P. pectinatus* were common. The shores were covered quickly by stands of *Typha latifolia* immediately after flooding. In the lower reservoir, broad-leaved species of *Potamogeton* (*P. crispus, P. lucens*), and (in some years) *Callitriche hermaphroditica* were abundant. The shores had only small areas with emergent vegetation.

Data collection

Data were collected within the area delimited by the highest water level that had occurred in the past and which is now indicated by scattered occurrence of some helophytes such as *Phragmites australis* or *Phalaris arundinacea*. Arable fields, meadows and small forests form the adjacent habitats. The reservoir was visited every year at least twice, in midsummer and early autumn. This means at least 7 full days of excursions per year. The occurrence of new species was mapped and special attention was paid to their further fate (whether it disappeared, survived as a single specimen or formed a viable population).

RESULTS

Immigrant plants (Tab. 1) are defined as those species which were not known in the area before the filling or if known, the time gap between the last observation and filling is long enough (at least ten years) to justify the assumption that the present occurrence is not a continuation of the previous one. Because it is not possible to study seed rain or seed bank on the landscape scale, immigration was considered when at least one established plant was observed. The local details on individual immigration events are given in a separate paper (Krahulec & Lepš 1993). A total of 25 species of vascular plants were registered as new immigrants during a period of 21 years (Fig. 2). We believe that we observed the first specimens of the following 12 species: *Althaea officinalis, Acorus calamus, Bolboschoenus compactus, Carex pseudocyperus, Cuscuta campestris, Euphorbia* * *literata, Limosella aquatica, Rorippa amphibia, Rumex aquaticus, Schoenoplectus tabernaemontani, Spirodela polyrhiza, Trifolium fragiferum*. For some of them (*Acorus calamus, Carex pseudocyperus, Schoenoplectus tabernaemontani*). the first individuals were the only ones observed and later died. The other species, when observed for the first time, formed more or less numerous populations suggesting that the very first specimens have been overlooked. This gives some indication of possible species immigration and mortality events missed in the study. *Bolboschoenus compactus* invaded the area at least twice (very probably three times). The first recorded colonist failed due to long-term decrease of water level (about 0.5 m) after 1981. The same happened to *Petasites hybridus*. These repeated colonizations explain the higher number of species than 25 given in the Fig. 2.

There was no pronounced difference between the number of immigrants recorded in the upper and lower reservoirs (Fig. 2, Tab. 2) even though the area of the lower reservoir is four times as large and its shore line is three times as long. However, there was a pronounced

Tab. 1. List of species immigrating to the upper and lower parts of the Rozkoš reservoir; the following data[1] are given: the year of arrival, surviving period, form of survival (P - population, P! - extremely large population, I - one or two individuals, C - larger clone), life form (H - hemikryptophyte, T - therophyte, G - geophyte, Hy - hydrophyte), breeding system and pollination (A - autogamy, C - cleistogamy, I - insect poll., W - wind poll., Wa - water poll.), seed size, and distance to the nearest known localities as possible source of diaspores. Upper reservoir has stable water level, lower reservoir has fluctuating water level.

Species	upper arrival	upper surviving	lower arrival	lower surviving	survival form	life form	pollination	seed size [mm]	nearest locality [km]
Alisma gramineum LEJ.			79	79-93	P!	H	I	2-2.7	10-50
Althaea officinalis L.			83	83-93	P	H	A,I	3-3.5	0-50
Bidens radiata THUILL.		77-93	76	76-93	P!	T	A,I	4-5	>50
Acorus calamus L.	89				I	G	vegetative repr.		<10
Bolboschoenus compactus HOFFM.			81	81-82	I	G	W	3	10-50
	91	91-92	91	91-93	C				
Callitriche hermaphroditica L.			79	79-89	P!	Hy	Wa	1.5-2	>50
Carduus crispus L.	86,92	92-93			I	H	AI	3	<10
Carex pseudocyperus L.	86	86-88			I	H	W	2	10-50
Ceratophyllum demersum L.	74	74-90		75-90	P	Hy	Wa	4-5	<10
Cuscuta campestris YUNCKER			81	81-86,89	P	T	A,I	1	>50
Euphorbia platyphyllos L. subsp. *literata* (JACQ.) HOLUB			76		I	T	I	1.8-2.0	>50
Juncus sphaerocarpus NEES in FUNCK			93		P	T	A?	0.3-0.5	>50
Leersia oryzoides (L.) SWARTZ			93		P	H,Hy	A	5	<10
Limosella aquatica L.		80,93	79	79-93	P!	T	C,A,I	0.5-0.7	<10
Myriophyllum spicatum L.	74		74	74-80	P	Hy	Wa	2-3	<10
Petasites hybridus (L.) P. GAERTNER, B. MEYER et SCHERB.	90,92	92-93			C	H	I,dioec.	2-3	<10
Potamogeton acutifolius LINK in ROEMER et SCHULT.	77				I	Hy	I	2-3	10-50
Potamogeton friesii RUPR.			77	77-86	P?	Hy	I	2-3	>50
Potamogeton obtusifolius MERT. et KOCH	71	71-79			P!	Hy	I	2-3.5	10-50
Potamogeton x *zizii* KOCH ex ROTH	77		77	77-82	P	Hy	I	2	>50
Rorippa amphibia (L.) BESSER		76-93	74	74-93	P	H	A,I	0.6-1.2	<10
Rumex aquaticus L.	92	92-93			I	H	W	3.0-3.8	<10
Schoenoplectus tabernaemontani (C.C. GMELIN) PALLA			78	78-86	I	G	W	2-2.5	10-50
Spirodela polyrhiza (L.) SCHLEIDEN			87	87-93	P	Hy	I	2-3[2]	<10
Trifolium fragiferum L. subsp. *fragiferum*	89	89-93			C	H	I	1.6-2	<10

1) Sources: CASPER & KRAUSCH (1980, 1981), FRANK et al. (1988), for information on nearest localities and on the spread on the reservoir see KRAHULEC & LEPŠ (1993).

2) turions.

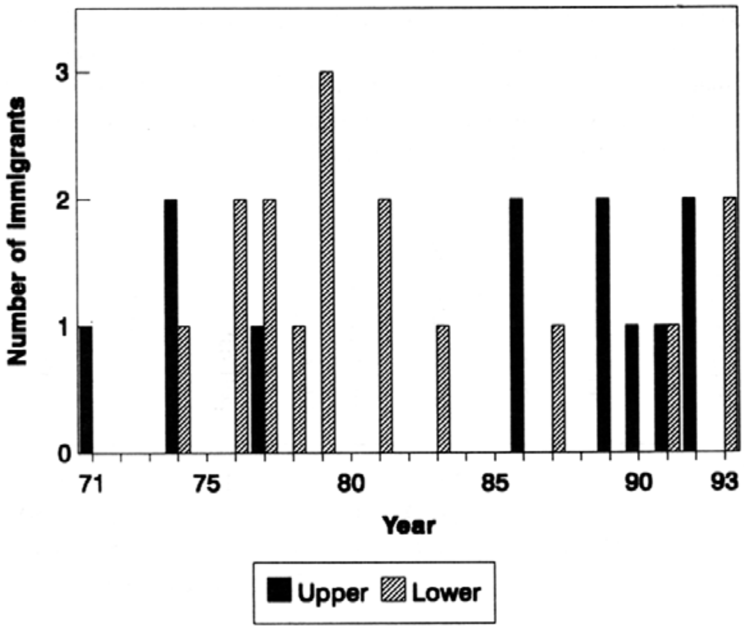

Fig. 2. Number of new immigrant plants registered in upper and lower parts of the reservoir during the period 1971-1993.

difference between survival time of individual species. Most of the immigrants which were observed at the upper reservoir disappeared within three years, whereas in the lower reservoir nine species survived for more than 7 years (the difference in average survival time is significant, $P<0.05$, Mann-Whitney test, species immigrating after 1989 and still present were excluded from the analysis).

Groups with immigration success (not only survival time) differed in their reproductive systems. The most successful group of species contained a greater proportion of autogamous species and also a high proportion of species with the potential for vegetative reproduction, mostly by buds (turions) (Tab. 3). The differences are not statistically significant (chi-square test), but the power of the test is low. Nevertheless, seed size varied considerably among immigrant species: only four species had smaller seeds than 1 mm, 5 species had a seed size between 1 and 2 mm, and 13 species had seeds larger than 2 mm. No correlation was found between successful establishment and seed size.

The life form of immigrants slightly changed over time (Tab. 4). The first period was characterized by a high proportion of hydrophytes and a slightly higher proportion of therophytes. Later stages saw a slightly higher proportion of hemicryptophytes. (Again, no statistically significant differences were found).

The nearest known localities of 11 new immigrants (Tab. 1) were within 10 km of the reservoir, for seven species the nearest localities were between 10 and 50 km distant, and another seven species localities lie more than 50 km away. The species occurring 50 km away or further are either rare (sometimes extremely rare), so that their localities are sparsely scattered within their area of distribution, or the Rozkoš reservoir was outside their continuous distribution area (e.g. *Euphorbia* *literata, Callitriche hermaphroditica, Juncus sphaerocarpus*). A detailed discussion of local geographic relationships is given in KRAHULEC & LEPŠ (1993). Fig. 3 gives examples of two species with contrasting ecological characteristics and distribution: *Bidens radiata* is a species of predominantly acidic substrates and colder regions, common in such areas as Southern Bohemia, and *Juncus sphaerocarpus* is more or

Tab. 2. Number of immigrant species in the two parts of the Rozkoš reservoir, the length of their survival, and the number of species with autogamous and vegetative reproduction among the immigrants surviving more than 7 years.

	No. of immigrant species	No. of species surviving				Out of species surviving >7 yrs	
		<4 yrs	4-5 yrs	6-7 yrs	7 yrs	autogamous	with vegetative reproduction
Stable water level	12	7	1	2	2	0	2
Fluctuating water level	16	5	0	2	9	6	6

Total number of new immigrants to both reservoirs (28) includes three independent colonizations by *Bolboschoenus compactus* and two colonizations by *Petasites hybridus*.

Tab. 3. The type of reproduction within immigrants and within the two highêst classes of surviving species.

	autogamous	allogamous*	allogamous with vegetative reproduction	only vegetative reproduction
No. of immigrants	8	16	10	1
No. of species surviving				
4-7 yrs	1	4	4	
7 yrs	6	5	5	

* occurrence of autogamy unknown.

Tab. 4. The number of immigrating species of each life form in different time periods.

	Hydrophytes	Hemicryptophytes	Therophytes	Geophytes	Total
1973-79	7	2	2	1	12
1980-85	0	1	2	1	4
1986-93	2	5	2	3	12
Total	9	8	6	5	28*
Surviving 7 yrs	4	3	3	1	11

*Three invasions of *Bolboschoenus compactus* and two invasions of *Petasites hybridus* are included.

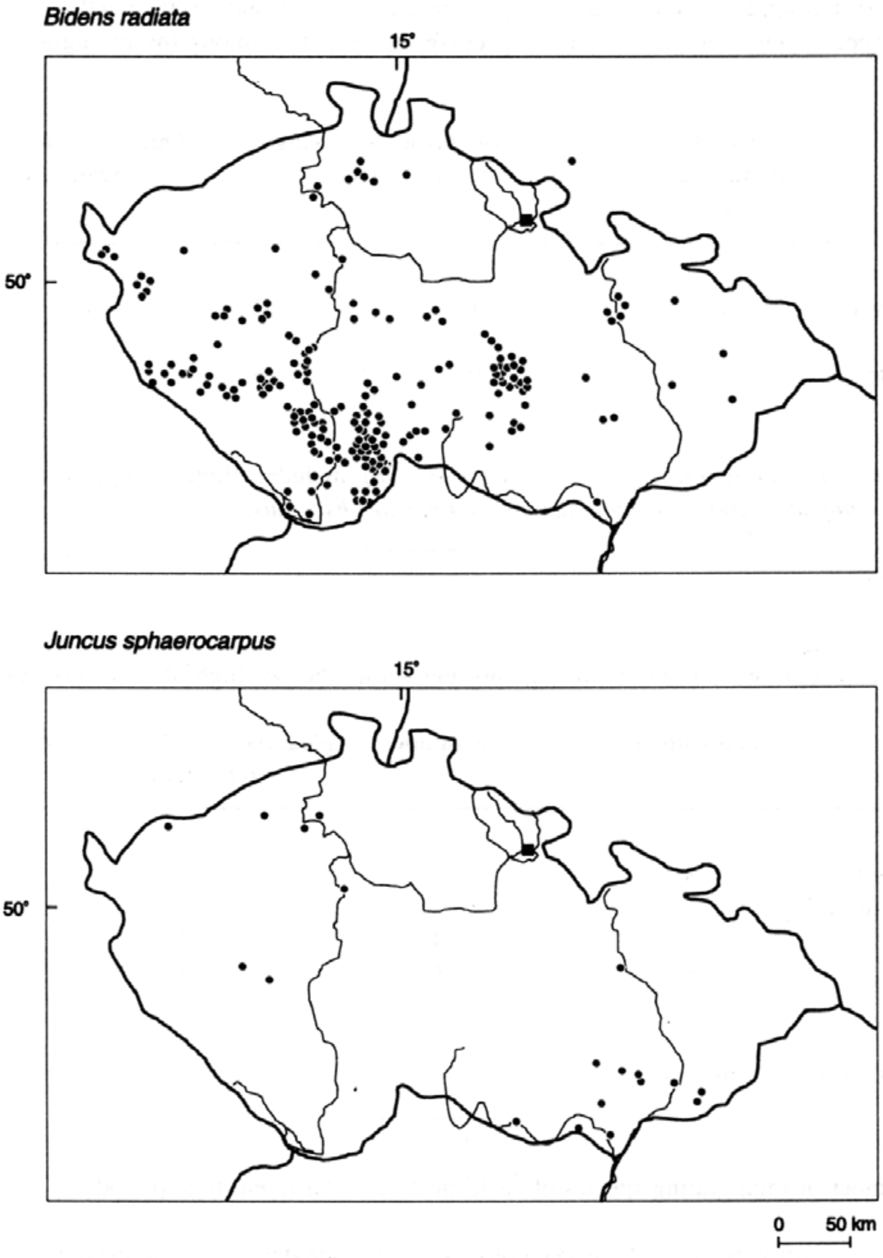

Fig. 3. The distribution of *Bidens radiata* and *Juncus sphaerocarpus*, two species with isolated occurrence at the Rozkoš reservoir (indicated by box). The distribution of *Bidens radiata* is acccording to LHOTSKÁ (1968), nearest occurrence in Poland was added; the distribution of *Juncus sphaerocarpus* is according to KUBÁT (1986, simplified), new localitites published by GRULICH (1989) and PLUHAŘ (1992) were added.

less a subhalophyte with regular occurrence only in warm regions of this country (it is absent from Poland).

Why some species failed to establish a viable population is not known except in a few cases. The extinction of *Bolboschoenus compactus* and *Schoenoplectus tabernaemontani* was probably caused by the 0.5 m decrease of water level which led to a decrease in their vitality and subsequent suppression by other species. Direct competitive exclusion probably caused the extinction of *Carex pseudocyperus* and *Acorus*, since in both cases they were overgrown by *Typha latifolia*. The causes of other species' extinctions remain unknown.

DISCUSSION

Limitations of statistical treatment

The statistical evaluation of data was difficult mainly for two reasons:

(1) The number of immigration events is low. Consequently, any statistical test performed on such data is extremely weak (the probability of Type II error is very high), especially when those immigrations are to be divided into several groups. Obviously, the number of immigrations is out of our control.

(2) We cannot define a set of potential immigrants; their basic pool is unknown. For example, should the flora of Eastern Bohemia be considered, a number of alpine species must be included. On the other hand, it is nearly impossible to construct a selection of species; there are some immigrants, that we would never include in such a set, as *Juncus sphaerocarpus* or *Euphorbia *literata*, and yet they were found in the reservoir. For this reason we can compare features only within a limited set of immigrants and not with some unknown pool.

Invasion and establishment

Young artificial reservoirs usually undergo rapid vegetational changes and their trophic conditions also change rapidly (GODSHALK & BARKO 1985). Extraordinarily species-poor plant communities (WESTHUS 1987) change constantly through a rapid sequence of colonizations (KRAHULEC, LEPŠ & RAUCH 1986, KUFLIKOWSKI 1986). Initially the plant communities are formed by remnants of previous vegetation, with large gaps open to new colonizations. The large total area of gaps, together with plots where competition is lessened by various types of disturbance provide a high number of safe sites (HARPER 1977, JOHNSTONE 1986) for species establishment. The large total competition free space increases the probability that randomly dispersed seeds will reach a safe place for their establishment. Successful dispersal depends (e.g. BERG 1983, RUNEMARK 1969, EHRENDORFER 1979): on the source of diaspores, diaspore dispersal, the establishment of individuals, and the ability to form a viable population, dependent mainly on the characteristics of the reproductive system and competitive ability.

The distance from the nearest localities should be considered as the minimum distance for putative migration events. It seems that the formation of a new, sufficiently large and competition free habitat promotes the expansion of species outside their local distributional limits and that a distance of tens of kilometers does not play an important barrier for migration even for such a short period, for some species. The Rozkoš reservoir is situated at the margin of a relatively warm area with lime-rich marl as bedrock. There are a number of fishponds (potential targets) throughout the region. It is not clear why some of the species are absent from those fishponds, but yet they were able to immigrate to the Rozkoš reservoir. Most of the new immigrants are species occurring at different distances within that warm area; species of colder areas and acidic substrata (e.g. *Callitriche hermaphroditica*) form a low proportion of the immigrants.

For at least one species (*Bidens radiata*), successful establishment and the formation of a large population at the Rozkoš reservoir probably promoted its dispersal in localities within tens of kilometers of the reservoir (Krahulec & Lepš 1993).

Species with relatively large diaspores without any specialized surface structures predominated among the immigrating species. Although usually not considered good colonizers among water plants, species with larger diaspores prevailed even in early successional stages (see also Rydin & Borgegård 1991). Only a few of the species studied possess specialized dispersal mechanisms: *Bidens* is specialized for exozoochorous dispersal, *Petasites* and *Carduus* are wind dispersed. Although feasible for all the species studied, dispersal by water to the Rozkoš reservoir is improbable (with the exception of species within the first distance category - distance < 10 km) because they occur mostly downstream. Water birds and human activities are probably the most important dispersal agents, but direct evidence is lacking. Berg (1983) found species without a specialized dispersal mechanism to be successful in long distance dispersal.

The proportion of species which survived more than 7 years is similar among all life forms. The survival of species at the newly colonized locality was more influenced by the type of reproductive system: within the group of species surviving seven or more years, uniparental species (autogamous species and those with vegetative reproduction) predominated. This is in agreement with theoretical predictions as well as with some direct observations (e.g. Price & Jain 1981, Ebenhard 1991).

Both parts of the reservoir had comparable conditions for the establishment of the first individuals of the new immigrants (the conditions in the upper reservoir were probably slightly better). However, species persisted longer, on the average, in the lower part of the reservoir. That immigration was less successful in the upper reservoir was probably due more eutrophic conditions (and lower transparency of water; see Maixner & Sládeček 1983) and a higher percentage of shore covered by dense stands of *Typha latifolia* and *Phalaris arundinacea* (Krahulec & Lepš in prep.), which decrease the available free space and competitively suppress other species. Linhart (1980), after analyzing the species composition of some tropical islands, speaks of a biotic filter caused by existing vegetation.

A high proportion of species disappeared after some time. However, it is not possible to consider them as extinct because they may be present as seeds. To be a seed is a prevailing life stage of many plants not only of annuals.

We do not believe that we have found all new immigrants; those which were present as individual specimens could easily be overlooked because of the length of the shore. The number of immigrants found by us should be considered as a lower estimate. Despite obvious limitations in our data, they indicate that species "jumps" over more than 100 km (as happened to *Euphorbia* **literata* and *Juncus sphaerocarpus*) are not an exceptionally rare phenomenon and they could be observed even during a short period of regular study. The frontiers of species' area of distribution are rather dynamic (particularly on the scale of tens of kilometers). This should be kept in mind particularly in local phytogeographical studies and in discussion of the native nature of recent localities.

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.

BRUINENBERG J., JOENJE W. & WIERENGA T. (1980): Hapaxanth species of coastal beach plains colonizing embanked sand flats. - Acta Bot. Neerl. 29: 497-508.

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

EBENHARD T. (1991): Colonizations in metapopulations: a review of theory and observations. - Biol. J. Linn. Soc. 42: 105-121.

EHRENDORFER F. (1979): Reproductive biology in island plants. - In: BRAMWELL D. [ed.]: Plants and islands, Academic Press, pp. 293-306.

FRANK D., KLOTZ S. & WESTHUS W. (1988): Biologisch-ökologische Daten zur Flora der DDR. - Wiss. Beitr. Martin-Luther-Univ. Halle/Wittenberg 1988/60: 1-103.

FRIDRIKSSON S. (1975): Surtsey. Evolution of life on a volcanic island. - Butterworths, London.

FRIDRIKSSON S. (1987): Plant colonization of a volcanic island, Surtsey, Iceland. - Arctic Alpine Res. 19: 425-431.

GODSHALK G.L. & BARKO J.W. (1985): Vegetative succession and decomposition in reservoirs. - In: GUNNISON D. [ed.]: Microbial processes in reservoirs, pp. 59-77, Dr. W. Junk Publishers, Dordrecht.

GRULICH V. (1989): Výsledky floristického kursu ČSBS v Uherském Hradišti 1987 (Floristic material collected during a course in floristics held in Uherské Hradiště, 1987). - Uherské Hradiště.

HARPER J.L. (1977): Population biology of plants. - Academic Press.

ITÄMIES J. (1980) The plant succession on the islands of Rauma, SW Finland. - Aquilo, Ser. Bot. 17: 18-38.

JOENJE W. (1978): Migration and colonization by vascular plants in a new polder. - Vegetatio 38: 95-102.

JOENJE W. & DURING H.J. (1977): Colonisation of a desalinizating wadden-polder by bryophytes. - Vegetatio 35: 177-185.

JOHNSTONE I.M. (1986): Plant invasion windows: a time-based classification of invasion potential. - Biol. Rev. 61: 369-394.

KEDDY P.A. (1976): Lakes as islands: the distribution of two aquatic plants, *Lemna minor* L. and *Lemna trisulca* L. - Ecology 57: 353-359.

KRAHULEC F. (1975): Vegetationsverhältnisse im Überschwemmungsgebiet Rozkoš bei Česká Skalice. - Acta Musei Reginaehradecensis, S.A. 13: 45-69.

KRAHULEC F. (1981): Vegetationsverhältnisse im Überschwemmungsgebiet Rozkoš bei Česká Skalice II. - Acta Musei Reginaehradecensis, S.A. 16: 155-161.

KRAHULEC F. & LEPŠ J. (1993): The migration of vascular plants to a new water reservoir: geographic relationships. - Preslia 65: 149-164.

KRAHULEC F., LEPŠ J. & 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. 15: 321-362.

KRAHULEC F., LEPŠ J. & RAUCH O. (1984): Vegetation of the Rozkoš reservoir near Česká Skalice II. The formation and differentiation of communities of flooded soils. (*Agropyro-Rumicion crispi*). - Folia Geobot. Phytotax. 19: 227-254.

KRAHULEC F., LEPŠ J. & RAUCH O. (1986): Vegetation succession on a new lowland reservoir. - Arch. Hydrobiol., Beih. Ergebnisse Limnol. 27: 83-93.

KUBÁT K. (1986): Červená kniha vyšších rostlin Severočeského kraje (Red book of vascular plants of Northern Bohemia).- Praha.

KUFLIKOWSKI T. (1986): Development and structure of the Goczałkowice reservoir ecosystem X. Macrophytes. - Ekol. Pol. 34: 429-445.

LINHART Y.B. (1980): Local biogeography of plants on a Caribbean atoll. - J. Biogeogr. 1: 159-171.

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

MAIXNER J. & SLÁDEČEK V. (1983): Elimination of nutrients in the Rozkoš-Reservoir. - Acta Hydrochim. et Hydrobiol. 11: 657-665.

NILSSON S.G. & NILSSON I.N. (1978): Species richness and dispersal of vascular plants to islands in lake Möckeln, Southern Sweden. - Ecology 59: 473-480.

NIP-VAN DER VOORT J., HENGEVELD R. & HAECK J. (1979): Immigration rates of plant species in three Dutch polders. - J. Biogeogr. 6: 301-308.

PLUHAŘ V. (1992): Contribution to the flora of Central Moravia (with special attention to the Chřiby Highlands). - Acta Univ. Palack. Olomucensis, Fac. Rer. Natur. Biologica, 107: 81-87.

PRICE S.C. & JAIN S. (1981): Are inbreeders better colonizers? - Oecologia 49: 283-286.

REJMÁNEK M., HAAGEROVÁ R. & HAAGER J. (1982): Progress of plant succession on the Parícutin volcano: 25 years after activity ceased. - Am. Midl. Nat. 108: 194-198.

RUNEMARK H. (1969): Reproductive drift, a neglected principle in reproductive biology. - Bot. Notiser 122: 90-129.

RYDIN H. & BORGEGÅRD S.-O. (1991): Plant characteristics over a century of primary succession on islands: lake Hjälmaren. - Ecology 72: 1089-1101.

SAUER J.D. (1988): Plant migration. The dynamics of geographic patterning in seed plant species. - Univ. of California Press, Berkeley.

WESTHUS W. (1987): Zur Vegetation landwirtschaftlicher Wasserspeicher im Thüringer Becken. - Limnologica 18: 381-403.

WHITTAKER R.J., BUSH M.B. & RICHARDS K. (1989): Plant recolonization and vegetation succession on the Krakatau islands, Indonesia. - Ecol. Monogr. 59: 59-153.

Received 16 November 1993, accepted 8 February 1994