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Distribution, Habitat Ecology, Soil Seed Bank and Seed Dispersal of Threatened *Lindernia procumbens* and Alien *Lindernia dubia* (*Antirrhinaceae*) in the Czech Republic

By

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With 5 Figures

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Summary

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Using recent data on wetland flora, vegetation, soil seed bank and seed dispersal, gathered in various parts of the Czech Republic, we compared the distribution and ecology of two wetland annuals, the native and threatened *Lindernia procumbens* (KOCKER) PHILCOX and the alien *L. dubia* (L.) PENNELL. While *L. procumbens* was documented in 16 localities in the Czech Republic, *L. dubia* only occurred in 9. The size of well-established populations of *L. dubia*, amounting to thousands of individuals, is, however, much larger than that of *L. procumbens* populations. Large differences in the population size of both species are also reflected in the density of the soil seed bank and the seed dispersal potential. We found that the alien *L. dubia* is able to colonize habitats with a broader range of moisture conditions and a longer duration of substrate exposure, i.e. with a higher cover of perennial plants. For *L. procumbens*, large inter-annual fluctuations in the size of populations are typical, as well as the preference for habitats with a short summer drainage. Both species survive unsuitable climatic or habitat conditions in the soil seed bank. Three populations of *L. procumbens* were only found due to the seed bank analysis because this species did not occur in the vegetation of the studied ponds. We found that small seeds of both *Lindernia* species can be spread by water and on rubber boots. For *L. dubia*, we also confirmed seed dispersal via vehicles used in fish farming. Source populations in fish storage ponds can help the survival of threatened *L. procumbens* in fishpond areas, but they also drive the invasion of neophyte *L. dubia*.

Zusammenfassung

ŠUMBEROVÁ K., LOSOSOVÁ Z., DUCHÁČEK M., HORÁKOVÁ V. & FABŠIČOVÁ M. 2012. Distribution, habitat ecology, soil seed bank and seed dispersal of threatened *Lindernia procumbens* and alien *Lindernia dubia* (*Antirrhinaceae*) in the Czech Republic. [Verbreitung, Standortsökologie, Samenbank and Samenausbreitung der gefährdeten *Lindernia procumbens* und der exotischen *Lindernia dubia* (*Antirrhinaceae*) in der Tschechischen Republik]. – Phyton (Horn, Austria) 52 (1): 39–72, mit 5 Abbildungen.

Wir benutzten aktuelle Angaben zu Flora, Vegetation, Samenbank und Samenausbreitung in verschiedenen Teilen der Tschechischen Republik für einen Vergleich der Verbreitung und Ökologie von zwei feuchtigkeitsliebenden einjährigen Pflanzen, der einheimischen und bedrohten *Lindernia procumbens* (KOCKER) PHILCOX und der verschleppten *L. dubia* (L.) PENNELL. Während *L. procumbens* aktuell von 16 Fundorten belegt wurde, kam *L. dubia* nur an 9 Fundorten in Tschechien vor. Die gut etablierten Populationen von *L. dubia* mit tausenden von Exemplaren sind jedoch viel grösser als die von *L. procumbens*. Die Unterschiede in der Populationsgröße der beiden Arten spiegeln sich auch in der Diasporenzahl in der Samenbank und Samenausbreitungspotential wider. Wir haben festgestellt, dass *L. dubia* Standorte mit einer breiteren Amplitude in Bezug auf die Feuchtigkeitsbedingungen und über eine längere Periode trockenen Bodens von Fischhältern (d.h. mit höherer Deckung ausdauernder Pflanzen) zu besiedeln vermag. Für *L. procumbens* sind große Schwankungen in der Populationsgröße zwischen einzelnen Jahren und die Präferenz von Standorten mit einer kurzen sommerlichen Trockenphase des Teichbodens typisch. Beide Arten überleben ungünstige Bedingungen in der Diasporenbank. Drei Populationen von *L. procumbens* wurden nur Dank der Samenbankanalyse entdeckt, weil die Art in der Vegetation der untersuchten Fischhälter nicht auftrat. Wir haben festgestellt, dass die kleinen Samen der beiden *Lindernia*-Arten durch Wasser und mit Gummistiefeln ausgebreitet werden können. Bei *L. dubia* haben wir auch die Ausbreitung mittels Fahrzeugen bestätigt. Quellpopulationen in den Fischhältern können der bedrohten *L. procumbens* helfen, in den Teichgebieten zu überleben. Sie fördern jedoch auch die Invasion des Neophyten *L. dubia*.

1. Introduction

Between 1994 and 2010 we intensively studied the wetland flora and vegetation in various parts of the Czech Republic. In selected localities this research was supplemented by investigations of the soil seed bank and seed dispersal vectors. Special attention was paid to the habitat of the exposed pond bottom, which is usually colonized by short-living wetland plant species with specific ecology. Among them, two species of the genus *Lindernia* (*Antirrhinaceae*), the neophytic *Lindernia dubia* and the threatened *Lindernia procumbens*, were documented in a number of localities. In this paper we attempt to (1) review the already published data about the distribution and the ecology of both *Lindernia* species; (2) summarize new data about the distribution of the alien *Lindernia dubia* and the native *L. procumbens* in the Czech Republic; (3) compare the habitat requirements and species composition of vegetation for both species; (4) estimate the potential for further spread of the neophytic *Lindernia dubia* and conservation of the threatened *L. procumbens*.

2. Methods

2.1. Study Sites

A map of the recent occurrences of *L. dubia* and *L. procumbens* in the Czech Republic (Fig. 1) shows that most of the localities are concentrated in southern Bohemia, with some isolated localities of *L. procumbens* also in eastern Bohemia, in the Czech-Moravian Highlands and in northern and southern Moravia. The landscape of these regions is mostly flat with numerous fishponds or an active river alluvium. This is reflected in the geology of the investigated regions, which is mostly formed by unstabilized sediments of the Mesozoic or Tertiary eras. They are of limnic or marine origin, and mostly non-calcareous. The youngest sediments are recent and include massive layers of flood sediments. The localities are mainly situated between 150 and 450 m a. s. l., exceptionally at higher altitudes (Table 1). The climate is warm temperate or warm. The mean annual temperature ranges between 7 and 10 °C, and the mean temperature of the warmest month (July) varies from about 17 to 20 °C. The mean annual precipitation ranges between 500 and 700 mm, and of this ca. 300–500 mm falls during the vegetation period (April-September) (Tolasz 2007).

2.1.1. Types of Ponds

During our research we investigated several types of ponds used for fish farming. Two of the most important types of these ponds are fishponds and fish storage ponds. A fishpond is an artificial water body primarily designed for fish breeding. Most of the Central-European fishponds are carp ponds, i.e. they serve for common carp (C y p r i n u s c a r p i o) breeding. According to fish age, several types of fishponds are historically distinguishable. Recently, the system of fish breeding was simplified because intensification practices enable fish to be stocked in one pond for a longer period of time. Therefore, from large number of various types of fishponds only fry (fingerling) ponds remain for the rearing of fish fry up to the age of 1 or 2 years, and main ponds for older fish up to a consumable size (Šumberová 2003). The fry ponds are characterized by relatively low pressures of the fish stock, which is an important premise of vegetation development. In addition, in some regions they are drained in summer and then slowly flooded.

The summer drainage of ponds is an old management practice, which by means of mineralization of the nutrients in deep bottom mud improves fishpond fertility. Common aquatic weeds and fish parasites can also be eliminated. Originally, summer drainage was applied in all types of fishponds. More recently, an increase in fish productivity has usually been achieved with the use of other practices, e.g. fish feeding and fishpond fertilization with organic fertilizers. Summer drainage has been restricted for economic reasons and also because of the lack of water in some pond systems. Nowadays, summer drainage is only widely used in fry ponds because the rearing of youngest fish, even today, is largely dependent on natural food sources, i.e. small invertebrates that develop in shallow flooded bottom vegetation (Čítek & al. 1998).

Fish storage ponds largely differ from the fishponds by their use and management. They are small ponds for the short-term storage of marketable fish in the time between fishing from the fishponds and the sale of the fish. Thus, although these ponds do not directly serve for fish production, they are essential in fish farming. In a single place, there is usually a number of fish storage ponds that are interconnected by ditches to the fish storage pond system. Each fish farm possesses one or more systems of fish storage ponds.

Fish storage ponds are continually supplied with water during fish storage. The water source can be a large fishpond or a smaller watercourse; either way, the water is often brought directly into the fish storage pond system by long artificial channels. The main fish storage period lasts from September or October until December, i.e. at the time of autumn fish harvesting and shortly thereafter. In larger fish farms, where some of the fishponds are fished out in early spring, a large proportion of the fish storage ponds is also used from March until April or May.

During the growing season the fish storage ponds are usually not utilized and are therefore drained. Summer drainage enables the development of various types of wetland vegetation. Thanks to the varying periods of bottom flood and exposure, fish storage ponds often represent habitats of high species and community diversity. The vegetation structure and species composition is further modified by additional management practices. Mowing, grazing or herbicides are used to retard the vigorous growth of the stands. These management practices lead to the restriction of strong competitors and support the growth of annual herbs, including both *Lindernia* species (for details about fish storage pond management see Šumberová & al. 2006).

2.2 Data Sampling

2.2.1 Floristic, Vegetation and Environmental Data Sampling

During the long research period, we concentrated our attention first on the wetland vegetation in the floodplains of southern Moravia (1994–1998), and then on the vegetation of exposed bottoms of fishponds and fish storage ponds throughout the whole territory of the Czech Republic (1999–2007). In the last three years (2008–2010), we particularly studied the flora and vegetation of fish storage ponds and other special types of ponds (e.g. ponds for ornamental and rare fish breeding) throughout the country. In some of the fish storage pond complexes we also performed seed bank analyses. Sediments from the surrounding fishponds, and also from potential propagule dispersal vectors (e.g. fish farming equipment, vehicles), were collected for a comparison of the species pool represented in both types of ponds and the species pool, which continually "travels" throughout the landscape. With the help of such data we wanted to explain the possible ways of plant species dispersal between the fishponds and fish storage ponds and their surroundings.

Thus, our study covered various aspects of wetland ecology research over a relatively long period. The data sampling did not primarily target *Lindernia* species, i.e. we did not make, for example, special field excursions to their historical localities. However, when found, as in the case of other threatened species or rare neophytes, a greater amount of attention was paid to both *Lindernia* species. The size of their populations was counted or estimated (in the case of larger populations). During repeated visits to the localities with a previous recorded occurrence of any *Lindernia* species, the status of the populations was controlled according to older data. This was especially important for *L. procumbens*, which can easily be overlooked due to its normally small plant size and small population density.

Floristic data were recorded in detail, especially in the fish storage pond systems. Scratch sheets were used to obtain as near as possible a complete list of vascular plants for each pond of a particular fish storage pond system. In other habitats, e.g. in fishponds, sand pits and river banks, phytosociological relevés were preferentially gathered and these were completed by floristic records on rarer species.

Phytosociological relevés were randomly collected for each distinct vegetation type, according to the Braun-Blanquet approach (BRAUN-BLANQUET 1964). The 9-grade scale (Braun-Blanquet's new scale; see VAN DER MAAREL 1979) was used to record the abundance and dominance of each species. In some cases, plots were selected in the stands with *Lindernia dubia* or *L. procumbens* to document the habitat preferences of these species. However, more frequently, the small *Lindernia* populations (especially those of *L. procumbens*) were only discovered during recording of the vegetation relevés. The size of all relevés was 1 m^2.

Regarding the environmental factors, we generally noted data on the type of subtrate (sand, clay or organic mud) and estimated its moisture status (dry, moist, waterlogged or shallow flooded). However, because these data were absent in some of the relevés (our own older relevés and the relevés of other authors), we did not use them directly in the analyses, but only for interpretation of the results.

Additionally, data about the time span of substrate exposure and flooding were noted for each relevé, as well as data about the management for each locality. In the fish storage ponds, from which most of the relevés originate, all these data were obtained from fish farmers (see Table 1 for a summary of management practices). In other habitats, this information was obtained during repeated observations in the field.

2.2.2. Seed Bank and Seed Dispersal Vectors

We analysed various types of soil sediments and drifts in order to obtain information about soil seed bank density and composition, and seed dispersal in selected localities. The samples were collected either before the growing season in March and April (63 samples) or after in September-November (24 samples). In total, 87 samples from 24 localities were taken. Samples from fishponds (22 samples, 10 localities), fish storage ponds (18 samples, 8 localities; 15 samples of bottom sediments and 3 samples of drifts), supply and drainage ditches (7 samples from 4 ditches in one fish storage pond system; 4 samples of bottom sediments and 3 drift samples), puddles on roads and parking places of fish farming vehicles (3 samples from one fish storage pond system), fish farming vehicles (lorries, terrain motorcars, tractors and trailers for the transport of live fish, fish farming equipment, and fish farmers; in total 18 samples from vehicles in 9 localities), fish farming equipment (fishing nets, dipping nets, water tanks, boats, etc., in total 11 samples from 8 localities), and rubber boots (8 samples from 6 localities) were represented in this number. Most of the samples originated from southern and south-western Bohemia; only three samples originated from the fish storage pond systems in eastern Bohemia (one locality – see loc. 19 in Fig. 1 and Table 1) and the Bohemian-Moravian Uplands (one locality). In the set of sediments from fishponds and fish storage ponds, localities with various periods and lengths of summer drainage were included. Fish farming equipment and rubber boots were usually roughly washed before sampling.

For each object to be sampled, sub-samples of sediment were randomly collected from different parts of the object. The number of sub-samples varied according to the substrate type and the size of object to be sampled, for example, but it usually ranged between 20 and 30. After their careful homogenization we obtained a mixed sample. Coarse particles (stones, wood pieces, roots, etc.) were removed. The volume of each standard homogenized sediment sample was 450–500 ml. In some cases the amount of sediment had to be reduced due to the time-consuming sampling design (e.g. rubber boots) or the absence of larger amounts of appropriate sediment (e.g. fish farming equipment). In addition, the first samples from the fishponds were smaller because the volume was only approximately estimated in the field. Later on it was measured precisely. For the accurate volumes of each sample containing *Lindernia* see Chapter 4.3.

The seedling emergence method (e.g. GROSS 1990, TER HEERDT & al. 1996, THOMPSON & al. 1997) was used to analyse the soil propagule bank. The samples were stored for 2–3 weeks (spring samples) or 4–6 months (autumn samples) in the refrigerator at 4–5 °C. Following this the samples were prepared for cultivation. To achieve the highest possible germination rate, each large sample was divided into several sub-samples. At the beginning of our research in 2008 we used sub-samples of 100 ml; in 2009 we reduced the volume to 50 ml. Each sub-sample was diluted with tap water and discharged in a thin layer (2–6 mm) into a plastic cultivation container (12 × 19 × 11 cm) filled with about 4–6.5 cm of cultivation substrate. The substrate was a mixture of fine sand, silty loam and peat (2:2:1), and had been sterilized for 3 h at 100 °C. In the samples collected in 2008 and spring 2009, the majority of the sub-samples of each sample were kept moist (terrestrial variant), and the rest were shallow flooded (submerged variant; water level ranged between 2 and 5 cm) in the first year of cultivation. Very small samples (about 10–20 ml) were not divided into sub-samples and only the terrestrial variant was used for cultivation. In one sample (D1 in Table 3), we tried to concentrate the propagules in the sediment before cultivation, according to TER HEERDT & al. 1996. However, manual sieving of sediment (i.e. without an automatic sieve system) is very time-consuming; therefore, we did not use this approach further on. The first results from the analysis of the propagule content in the sediments showed that this would not be even appropriate due to the very high seedling density in most of the samples.

The cultivation of each sample continued from March or April until mid-August or September in the first growing season (see Chapter 4.3. for details on individual samples). During the winter, the samples were allowed to dry and in the next growing season the terrestrial and submerged treatments were interchanged. After the second growing season, or in some cases during it (i.e. in June or July), cultivation was finished. In the samples collected in autumn 2009 and spring 2010 and cultivated during the growing season of 2010, the moist and submerged variants in each sample were interchanged after about 4 months of cultivation. According to our experiences in 2008 and 2009, most of the species of each variant emerged in the first 2–3 month of cultivation and after this none or only sporadic germination was observed. Therefore, and also because of the end of project funding in 2010, the cultivation experiments that started in 2010 were restricted to only one growing season.

The containers were protected against the influx of propagules from the vicinity using fine unwoven fabric. Cultivation took place in the greenhouse without temperature or daylight regulation, simulating natural germination conditions. The temperatures ranged between 5 and 35°C. All seedlings that emerged were identified, counted and then removed from the container. For species that were difficult to determine, some of the seedlings were transplanted and cultivated in separate pots (e.g. *Lindernia* species). Some seedlings died before determination. In these cases, only an approximate identification is given or they are included as "indet." (see Table 3).

In order to detect possible differences in the germination rate between *Lindernia dubia* and *L. procumbens*, we performed a germinability pilot test. We used 2×50 seeds of each species and cultivated them on the same substrate and under the same conditions as the sediment samples of the terrestrial variant (see above). The seeds used in this test were obtained from dry herbarium specimens, collected during the previous growing season.

Explanation of the abbreviations in Table 1:

1) Management: RSD = reduced summer drainage (only occasional summer drainage of some ponds, usually for less than 2 month), SSD = short summer drainage (i.e. summer drainage for 2–4 months), LSD = long summer drainage (i.e. summer drainage for 5 or more months), H = herbicide application (number of applications per year is given in the parentheses), G = grazing (including domestic birds), M = mowing, L = disinfection liming of the bottom or walls, W – manual weeding of vegetation (each year before the stocking period), 0 – without management. In the case that the management changed during the time from when the last species was found and the last visit to the locality, the relevant years are indicated in parentheses.
2) Sources of the data: A = Kurka 1990, B = Lepší & Douda 2005, C = Chán 1999, D = Míchal & Kurka 1991, E = Filípková 2001, F = Šumberová 1999, G = own unpublished data (for full citations see the reference list).
3) Population size: >10 = tens of individuals, >10–100 = between tens and hundreds of individuals, <10–100 of individuals = up to 10–100 of individuals, etc.; ?? – exact data are missing, the population size was estimated on the basis of soil seed bank density; e.y. = every year.

Table 1. Recently confirmed and newly found localities of *Lindernia dubia* and *L. procumbens*. Localities where only *L. dubia* was found are marked in black, the localities where both species were found are marked in grey and the localities where only *L. procumbens* was found are white. The numbers and levels of grey listed in the second column correspond to Figure 1.

	locality no.	Locality (town/village)	habitat	coordinates	altitude (m a.s.l.)	year	management	available data	number of individuals	source
Lindernia dubia	1	Čejkovice	system of small fry ponds	49°00'30" N 14°22'54" E	385	2009, 2010	mainly SSD, G	flora & vegetation	> 10	G
	2	Hluboká nad Vltavou	muddy river deposit of the Vltava River	49°03'17" N 14°26'36" E	380	2003	0	flora	< 100	G
	3	Hluboká nad Vltavou	muddy river deposit of the Vltava River	49°03'49" N 14°26'46" E	380	2003	0	vegetation	< 100	B
	4	Veselí nad Lužnicí	muddy river bank on confluence of the Lužnice and Nežárka rivers	49°11'49" N 14°42'09" E	410	1989	0	vegetation	> 100	A
	5	Žišov	muddy river deposit of the Lužnice River	49°11'55" N 14°42'26" E	410	2003	0	vegetation	2	B
both species	6	Čejetice	fish storage ponds	49°15'01" N 14°01'20" E	390	2001–2003, 2005, 2008; 2010 in seed bank	mainly LSD, M, L	flora, vegetation & seed bank	**L. d.:** 2003 – 2 2005 – 6 2008 > 1000 **L. p.:** < 10–100 e.y.	G
	7	Kestřany	fish storage ponds	49°16'16" N 14°04'19" E	375	2001, 2003–2005, 2006, 2008	SSD–LSD, M, L	flora & vegetation	**L. d.:** 2004 – 2 2005 – 8 2008 > 200 **L. p.:** < 100–1000 e.y.	G
	8	Hluboká nad Vltavou	fish storage ponds	49°02'43" N 14°25'56" E	380	1997; 2001–2010	SSD–LSD, H (1–2), M, L	flora, vegetation, seed bank & seed dispersal	**L. d.:** > 10 000 e.y. **L. p.:** > 100–1000 e.y.	C; G

	9	Dobronice near Bechyně	muddy river deposit of the Lužnice River	49°20'01" N 14°29'52" E	370	2003	0	vegetation	**L. d.**: 1 **L. p.**: 1	B
Lindernia procumbens	10	Blatná	fish storage ponds	49°25'26" N 13°52'52" E	430	2001, 2003	LSD, M, L	flora & vegetation	< 20 e.y.	G
	11	Vodňany	fish storage ponds of town Vodňany	49°09'11" N 14°10'35" E	395	2001, 2004	SSD–LSD, M, L, G	flora & vegetation	< 20 e.y.	G
	12	Hrbov	fish storage ponds	49°01'20" N 14°09'15" E	460	2010 (only seed bank)	LSD, M, L	flora, vegetation & seed bank	?? > 1000	G
	13	Šaloun, near Lomnice nad Lužnicí	fish storage ponds	49°04'08" N 14°42'43" E	425	1988–1991, 1999	SSD (1999)–RSD (2002), L	flora & vegetation	< 20 e.y.	D; E; G
	14	Třeboň, near Opatovický mlýn	fish storage ponds	48°59'18" N 14°46'52" E	435	1999	SSD (1999)–RSD (2008), L	flora & vegetation	< 100	G
	15	Třeboň, near Svět fishpond	fish storage ponds	48°59'47" N 14°46'17" E	435	2008; 2010 in seed bank	RSD–SSD, W, L	flora & seed bank	3	G
	16	Stříbřec	fish storage ponds	49°01'55" N 14°52'25" E	445	2002	LSD, W, L	flora	1	G
	17	Štiptoň near Nové Hrady	fish storage ponds	48°48'03" N 14°46'54" E	465	2008	SSD–LSD, H (0–1), M, L	flora & vegetation	< 20	G
	18	Telč	fish storage ponds	49°11'18" N 15°26'51" E	520	2008	RSD–SSD (rarely), L	flora	4	G
	19	Bohdaneč	fish storage ponds	50°04'59" N 15°39'55" E	215	2002; 2009 in seed bank	LSD, M, L	flora, vegetation & seed bank	< 20	G
	20	Lanžhot, confluence of the Morava and Dyje Rivers (4 localities)	borrow pit, sand pits, water-logged road	48°40'29" – 48°39'27" N 16°56'19" – 16°57'09" E	150	1994–1996	0	vegetation	< 20 e.y.	F
	21	Studénka	fish storage ponds	49°43'02" N 18°03'58" E	230	2002	SSD, M, L	flora & vegetation	> 100	G

2.3. Data Processing and Analysis

2.3.1. Floristic Data and Population Size

Floristic lists for the individual localities were computerized and stored in an Excel format. For the purpose of this study, we selected all data on *Lindernia dubia* and *L. procumbens*. The data was completed by adding recent records from other authors (KURKA 1990, MÍCHAL & KURKA 1991, CHÁN 1999, FILÍPKOVÁ 2001, LEPŠÍ & DOUDA 2005). On the basis of this data, we compiled a table to summarize the recent occurrence of both *Lindernia* species and the size of their populations, amongst other parameters (Table 1). The coordinates of the localities were taken from digital maps <www.mapy.cz>.

Data from the Hluboká fish storage pond system collected in 2002–2010 were used to compare fluctuations in the population size of both *Lindernia* species. In this pond system, where we performed long-term investigations of pond bottom vegetation, both *Lindernia* species are well established. We used presence/absence data collected separately for each of 48 ponds in the system. For each *Lindernia* species, we calculated the number of ponds in which the species occurred in individual years and then the sum of ponds with at least one occurrence of a particular species during the whole investigation period. The results obtained were compared with the total number of investigated ponds, which varied between the years.

2.3.2 Vegetation Data

The phytosociological relevés were stored in the Czech National Phytosociological Database (CHYTRÝ & RAFAJOVÁ 2003) using the database software TURBOVEG (HENNEKENS & SCHAMINÉE 2001); 634 phytosociological relevés contained at least one of the two *Lindernia* species. This number only includes our own unpublished data. To avoid oversampling some localities, we randomly chose only two relevés from each pond. This subset of 103 relevés, including 39 relevés with *L. dubia*, 22 relevés with *L. procumbens* and 42 relevés with both species was used for subsequent analyses.

The differences in the species composition on habitats colonized by either invasive *L. dubia* or native *L. procumbens* are summarized in a synoptic table (Table 2). This table shows the percentage frequencies of plants in the relevés occupied by either *L. procumbens* or *L. dubia*, or by both *Lindernia* species. Diagnostic species for each column of the phytosociological table were determined using fidelity, i.e. the association between a species and a particular habitat/vegetation type. The phi coefficient was used as a measure of this association; its statistical significance was checked by Fisher's exact test ($P < 0.05$) according to CHYTRÝ & al. 2002. Plants with phi > 0.20 were considered as diagnostic for either of the columns containing one of the *Lindernia* species or for the column containing both of them. Fidelity calculations and table preparations were carried out using the JUICE program (TICHÝ 2002).

The ecological requirements of both *Lindernia* species were compared using Ellenberg indicator values for vascular plants (ELLENBERG & al. 1992). Ellenberg indicator values are simple ordinal classes of vascular plants with a similar realized ecological niche along a studied gradient. They contain values for light (9 categories), temperature (9 categories), continentality (9 categories), moisture (12 categories), soil reaction (9 categories) and nutrients (9 categories). For both species studied, we analysed the probability of their occurrence with respect to the ecological gradients expressed as mean Ellenberg indicator values, calculated for individual relevés.

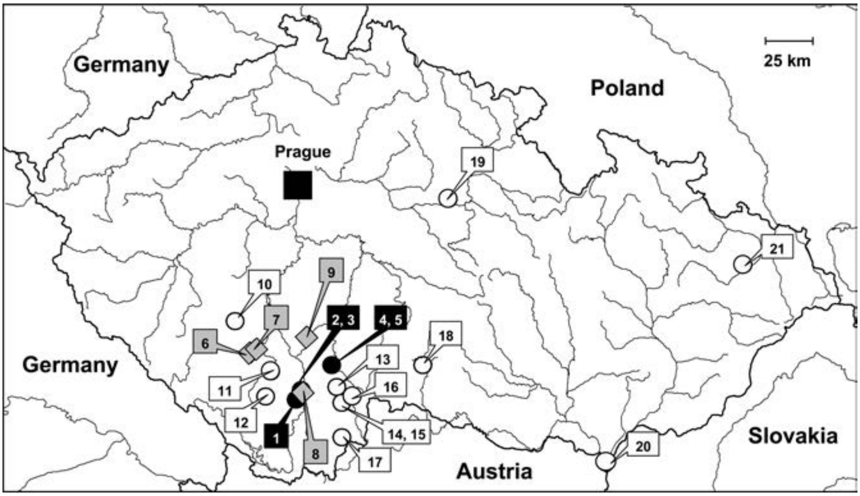

Fig. 1. Recent distribution of *Lindernia dubia* and *L. procumbens* in the Czech Republic. – Occurrence of *L. dubia* (black circles): 1 Čejkovice. – 2, 3 Hluboká nad Vltavou (alluvium). – 4, 5 Veselí nad Lužnicí; Žíšov. – Both *Lindernia* species (grey squares): 6 Čejetice. – 7 Kestřany. – 8 Hluboká nad Vltavou (fish storage ponds). – 9 Dobronice near Bechyně. – *L. procumbens* (white circles): 10 Blatná. – 11 Vodňany. – 12 Hrbov. – 13 Šaloun, near Lomnice nad Lužnicí. – 14, 15 Třeboň. – 16 Stříbřec. – 17 Štiptoň near Nové Hrady. – 18 Telč. – 19 Bohdaneč. – 20 Lanžhot, confluence of the Morava and Dyje Rivers (four localities). – 21 Studénka. – For further details see Table 1.

Species response curves were used to determine differences in the ecological demands of both species. The species response curves were derived using generalized linear models (GLM; Austin 1980) with binomial distribution and the logit link function in CanoDraw version 4.0. Differences between the ecological characteristics of the species studied, expressed as mean Ellenberg indicator values calculated for the relevés, were further analysed using t-tests. These analyses were carried out using Statistica 9 software <www.statsoft.com>.

To assess the main patterns of species composition of the different vegetation types, detrended correspondence analysis (DCA) was carried out using the Canoco program (ter Braak & Šmilauer 2002). In order to interpret the DCA results, the mean Ellenberg indicator values calculated for the plots were passively projected onto the ordination diagram.

In order to characterize the relationship between *L. dubia* and *L. procumbens* and the different durations and timing of pond bottom exposure, we classified each of the 103 relevés into one of three categories. As the majority of the ponds were exposed at least for part of the vegetation period, with the end of exposure in September/October, the following categories for the start of exposure in a current year were used: (1) December–March, (2) April–May, (3) June–August. The ponds that were exposed later and those that were exposed for a very short period (less than 1 month) were considered as being flooded during the vegetation period. The proportion of individual exposure categories in the subsets of plots containing *L. dubia, L. procumbens* and both species was calculated and visualized in pie charts.

2.3.3. Data on Soil Seed Bank and Seed Dispersal

All data from the samples where any *Lindernia* species was detected are summarized in Table 3 (see Chapter 4.3. for more detail about the sampling design). For each of the taxa included in the table we computed the number of seedlings per litre of sediment. With the exception of the *Lindernia* species, situated at the top of the table, all of the taxa were ranked in descending order according to the cumulative number of seedlings per litre. Taxa with a cumulative number of seedlings <50/litre are not displayed in the table. They are only represented in the total number of seedlings and total number of taxa as a group of other species/taxa with a low seedling density (see Table 3). The species with a seedling density >100/litre of sediment in a sample are highlighted. Although bryophytes occurred in most of the samples, they were not included in the table due to their problematic quantification and, in some cases, still incomplete species determination.

The taxonomy and nomenclature of all vascular species in this paper follow the Key to the Flora of the Czech Republic (Kubát & al. 2002). The taxonomy and nomenclature of the bryophytes was unified according to the Check- and Red List of Bryophytes in the Czech Republic (Kučera & Váňa 2003). Most of the algae were not determined; the only exception in this paper is *Nostoc commune* Vaux ex Born. & Flach.

3. Current State of Knowledge

3.1. *Lindernia dubia*

Lindernia dubia is a North American species native to catchments of the Mississippi River. It has also been recorded in other parts of the USA, Canada and South America. However, occurrences in these regions are probably secondary (Meusel & al. 1978, Casper & Krausch 1981). This species colonizes wet habitats, particularly on the shores and muddy banks of rivers, ponds and lakes (Mack & Boerner 2004, Deil 2005). It was introduced to Europe in the middle of the nineteenth century, probably through shipping traffic. The first European records came from southern France. Further records have followed from central and northern Italy, Spain, Portugal, Germany (Casper & Krausch 1981, Wisskirchen 1995), Romania (Ciocarlan & Costea 1994), Bulgaria (Markova 1995, Tzonev & Šumberová 2004, Stojchev & Chesmedziev 2005), Slovenia (Trpin & al. 1995), the Czech Republic (Kurka 1990, Lepší & Douda 2005, Šumberová & al. 2005), Poland (Drobnik & Buchalik 2004) and Serbia (Ranđelović & al. 2005, Tomović & al. 2007). *Lindernia dubia* has successfully colonized new places in warm temperate zones in Europe and in temperate to tropical zones in Asia. In this secondary distribution range, the species has invaded similar habitat types as in its native regions. In addition, it has been reported as being abundant in paddy fields in the southern parts of Europe and Asia (Koch 1954, Markova 1995, Yoshino & al. 2006). This species has been designated as being potentially expansive in Europe and its spread into new areas has already been predicted by Wisskirchen 1995 and Tzonev & Šumberová 2004.

In the Czech Republic, *L. dubia* was observed for the first time in 1989 in ephemeral vegetation on the muddy bank of the Lužnice River (southern Bohemia; KURKA 1990). More recently, it has colonized new localities in southern Bohemia (LEPŠÍ & DOUDA 2005, ŠUMBEROVÁ & al. 2005, 2006). Stream water and waterfowl are considered to be the most probable dispersal vectors of this species (WISSKIRCHEN 1995, BURKART 2001). However, in southern Bohemia, where traditional fish farming takes place, dispersal via the equipment and vehicles used in fishpond management and directly with the fish (ichthyochory) may also be important (ŠUMBEROVÁ 2005). The transport of live marketable fish throughout Europe may contribute to diaspore dispersal, not only on the local scale but also on the continental scale. In the second half of the twentieth century the import of fry from other countries was also quite common.

3.2. *Lindernia procumbens*

The congeneric species *Lindernia procumbens* is native to the temperate to tropical zones of Eurasia (VON LAMPE 1996). It primarily occurs on periodically flooded natural habitats in river floodplains (BURKART 2001). *L. procumbens* has also colonized anthropogenic habitats, for example sand pits and the exposed bottoms of artificial ponds used in fish farming (CASPER & KRAUSCH 1981, CHÁN 1999, ŠUMBEROVÁ 2003, ŠUMBEROVÁ & al. 2005, 2006). However, intensive human impacts and land use changes may directly lead to habitat loss by destruction (e.g. river regulations) or by faster succession as a consequence of eutrophication. Nowadays, *L. procumbens* is a threatened taxon in the majority of European countries and is protected by the Bern Convention and by the EU Habitats Directive (PROCHÁZKA 2001). In the Czech Republic, this species is listed as a critically endangered species (HOLUB & PROCHÁZKA 2000, PROCHÁZKA 2001), with only a few recently discovered localities. This species was also rare historically (AMBROŽ 1939, CHÁN 1999, HEJNÝ 1999), and only a small number of its historical localities have been confirmed in recent decades. Changes in fishpond management are thought to be the probable cause of the decline in this species (PROCHÁZKA & al. 1999). Nevertheless, in recent years botanical investigations of periodically flooded habitats have identified new localities of this species (e.g. ŠUMBEROVÁ 1999, 2003, LEPŠÍ & DOUDA 2005). The majority of them are situated in fish storage pond systems, which are comprised of several small ponds for the short-term storage of marketable sized fish. This habitat type was not sufficiently studied until the last decade (ŠUMBEROVÁ 2003, 2005, ŠUMBEROVÁ & al. 2005, 2006).

The life forms and ecological preferences of the two *Lindernia* species are similar. They are short-lived annuals that reproduce entirely by small, dust-like seeds and colonize riverbanks and periodically exposed bottoms of small ponds (CASPER & KRAUSCH 1981, KURKA 1990, KŘÍSA 2000, STOJCHEV & CHESMEDZIEV 2005, BOJŇANSKÝ & FARKAŠOVÁ 2007). High substrate moisture is important for seed germination (von Lampe 1996). In unsuitable conditions, i.e. deep submersion, a dry substrate or dense cover by perennial vegetation, they probably survive in a persistent soil seed bank. This has been documented in numerous papers that have reported the occurrence of these species in the same locality after long periods of unsuitable conditions, and papers that compared the actual vegetation and soil seed banks of wetlands (e.g. Capers 2003, Nishihiro & al. 2004, 2006, Deil 2005, Šumberová 2005, Liu & al. 2006, Tomović & al. 2007). However, exact data on the seed longevity of the two *Lindernia* species are not yet available.

4. Results

4.1. Recent Occurrences of *Lindernia dubia* and *L. procumbens* in the Czech Republic

The localities of the two species, either confirmed or newly found, during the last two decades in the Czech Republic are displayed in Fig. 1. For more details about the localities and populations of both species, see Table 1. The number of recently identified localities of the native *L. procumbens* was about twice as high as the number of localities with the invasive *L. dubia*. However, *L. dubia* generally had much larger populations than *L. procumbens* and showed a tendency for a rapid increase in population size (Table 1).

In Hluboká nad Vltavou (loc. 8 in Fig. 1 and Table 1), where we carried out long-term investigations of flora and vegetation, *L. dubia* was documented in 48 out of a total of 49 fish storage ponds. The size of the population was found to be stable and includes thousands of individuals in most of the ponds. Fig. 2 shows that this species was documented in nearly all of the ponds investigated in a particular year. The number of ponds where *L. dubia* was not confirmed markedly increased only in the years 2006, 2009 and 2010. Native *L. procumbens* was recorded in 37 ponds during the years 2001–2010, i.e. in 77% of the total number of investigated ponds. However, the proportion of ponds with records of *L. procumbens* greatly varied among the years (Fig. 2). In some ponds only several individuals of this species were found, and this only occurred once during the whole investigation period.

4.2. Habitat and Vegetation Preferences

Both *Lindernia* species were mainly documented in fish storage ponds. Some other localities were reported in muddy river deposits, and *L. procumbens* was also found in sand pits and on forest tracks.

The vegetation types containing *Lindernia* species significantly differed in species composition. The synoptic table (Table 2) presents species with constancy values >20 % in at least one of the three columns. The species are sorted according to decreasing phi coefficient. The shaded species are those with a phi coefficient of association > 0.2, calculated for equally sized groups. The non-shaded species had no diagnostic value but occurred with a frequency > 20 % in the data set. Both *Lindernia* species occurred in stands with the diagnostic species *Elatine hydropiper, Gnaphalium uliginosum, Bolboschoenus maritimus* s. l. and *Cyperus michelianus*. *L. procumbens* was amongst vegetation containing wetland annuals, for example *Coleanthus subtilis* and *Elatine triandra*, wetland perennials, for example *Carex acuta* and *Lycopus europaeus*, the ruderal plants *Tanacetum vulgare* and *Taraxacum* sect. *Ruderalia*, and juveniles of wind-dispersed *Salix* species. *L. dubia* invaded both drier pond bottoms with annual ruderal weeds such as *Sonchus arvensis* and *S. asper*, and flooded plots dominated by *Lemna* species. However, there were also many

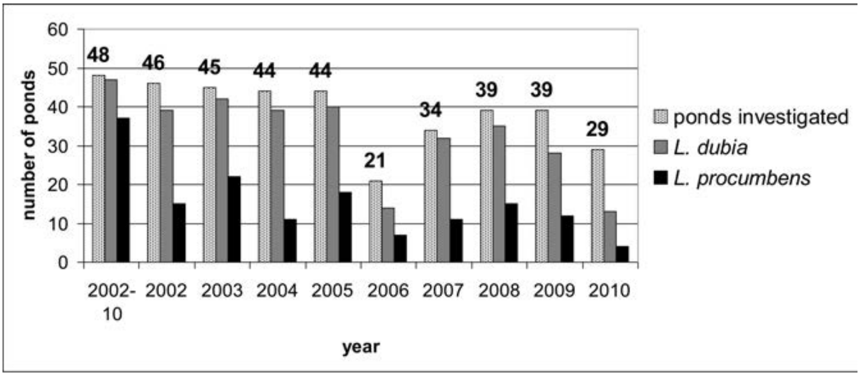

Fig. 2. Occurrence of *Lindernia dubia* and *L. procumbens* in fish storage ponds in Hluboká nad Vltavou in 2002–2010. The columns show the numbers of all ponds investigated in each year and the number of ponds with records of *L. dubia* and *L. procumbens*. A summary of the whole research period (the left part of the graph) shows the total number of ponds investigated and the number of ponds with at least one record of *L. dubia* and *L. procumbens* during 2002–2010.

species that were shared with a similarly high frequency by all three relevé groups. Like both *Lindernia* species, the majority of these accompanying species were wetland annuals, for example *Cyperus fuscus, Eleocharis ovata* and *Juncus bufonius* (Table 2).

The ordination diagram of the detrended correspondence analysis (Fig. 3) shows that the positions of the plots colonized by *L. dubia* or *L. procumbens* or both largely overlap. However, some differences in the relationships of both *Lindernia* species to individual ecological factors, as expressed by the means of the Ellenberg indicator values, are obvious. The gradient related to the first ordination axis is between nutrient- and base-rich plots preferably colonized by the alien *L. dubia* (right side of the diagram) and several plots with more thermophilous and continental vegeta-

Table 2. Synoptic table. Species composition of the plots occupied by both *Lindernia* species, only by *L. procumbens* and only by *L. dubia*. Numbers are the percentage frequencies of species occurrence. Dot indicates absence.

No. of relevés summarised	42	22	39
Lindernia procumbens	100	100	0
Lindernia dubia	100	0	100
Diagnostic species			
E_1			
Elatine hydropiper	14	.	3
Gnaphalium uliginosum	79	64	38
Bolboschoenus maritimus s. l.	50	9	38
Cyperus michelianus	14	5	.
Rorippa palustris	83	73	54
Taraxacum sect. Ruderalia	5	41	15
Juncus compressus	.	18	3
Coleanthus subtilis	.	14	.
Salix fragilis	5	18	.
Elatine triandra	2	18	3
Salix cinerea	2	18	3
Lythrum salicaria	14	32	8
Lycopus europaeus	.	9	.
Carex acuta	.	9	.
Tanacetum vulgare	.	9	.
Bidens radiata	7	27	10
Plantago uliginosa	31	59	36
Sonchus arvensis	.	.	13
Butomus umbellatus	2	.	15
Lemna minor	36	9	49
Sonchus asper	10	.	21
Frequent species			
E1			
Cyperus fuscus	88	77	79
Peplis portula	81	82	44
Callitriche palustris s. l.	76	68	62
Leersia oryzoides	71	64	62
Echinochloa crus-galli	71	50	67
Juncus bufonius	57	73	44
Eleocharis ovata	57	41	38
Limosella aquatica	52	41	23
Alisma plantago-aquatica	45	45	64
Eleocharis acicularis	43	41	49
Persicaria lapathifolia	40	59	51
Spirodela polyrhiza	31	9	36
Juncus articulatus	29	9	23
Rumex maritimus	29	32	13
Persicaria hydropiper	24	45	44
Bidens tripartita	24	23	15
Ranunculus sceleratus	12	27	15
Trifolium hybridum	12	27	26
Sagina procumbens	5	23	10
Carex bohemica	7	23	8
Persicaria minor	14	18	26
Myosotis caespitosa	12	18	23
Eleocharis palustris s. l.	17	18	21
E_0			
Nostoc commune	55	32	44
Bryum argenteum	19	9	28
Amblystegium humile	26	9	31
Riccia cavernosa	17	23	8

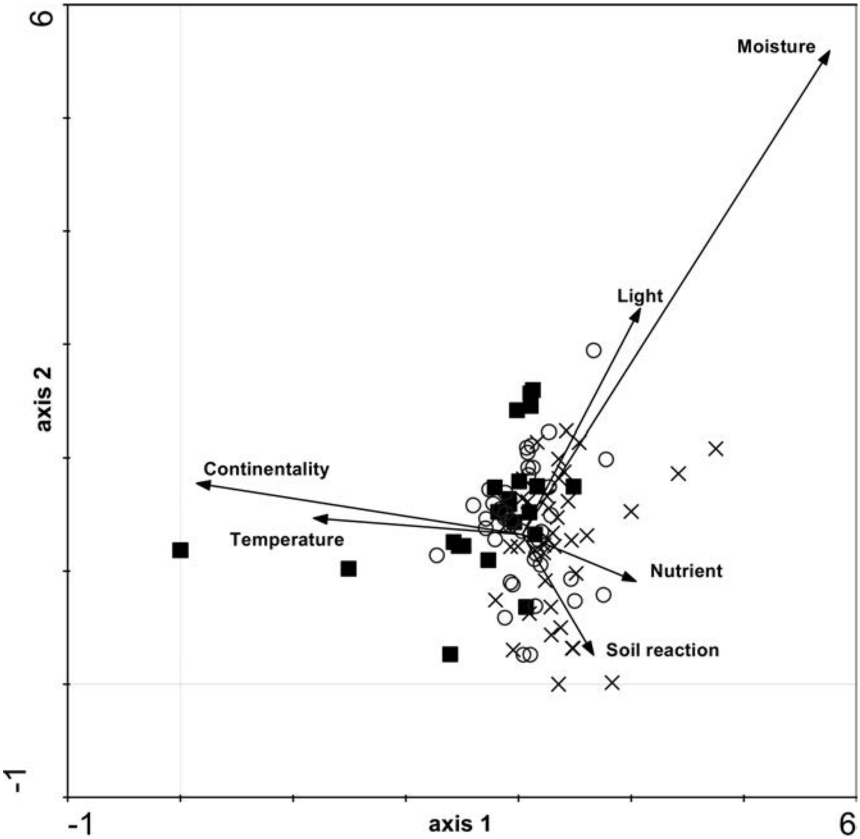

Fig. 3. Diagram of the detrended correspondence analysis of the data set of phytosociological relevés containing *Lindernia dubia, L. procumbens* or both. The first ordination axis (eigenvalue 0.478) and the second ordination axis (eigenvalue 0.295) are shown.

■ plots with Lindernia procumbens
× plots with Lindernia dubia
○ plots with both Lindernia species

tion occupied by native *L. procumbens* (the left side of the diagram). The second gradient is related to the second ordination axis and refers to plots in order of moist and open stands (upper part of the diagram) to relatively dry stands with shade-tolerant species (bottom part of the diagram).

According to the t-tests (results not displayed), temperature and continentality were the most important factors reflected in the differences between species composition of stands containing *L. dubia* and *L. procumbens*, respectively. However, although the differences related to these two factors were found to be significant, they were very small.

The species response curves show more or less important differences in the ecological demands of both species (Figs 4a–f). For the Ellenberg indicator values for light (Fig. 4a) and continentality (Fig. 4b), both species have similar optima; however, the curves of the alien *L. dubia* are flat in comparison to the curves of *L. procumbens*. This shows that increasing levels of light and continentality do not have a very important influence on the occurrence of *L. dubia*, but they have a highly positive impact on the occurrence of *L. procumbens*. Along the temperature, moisture and nutrient gradients, the response curves of *L. procumbens* show a relatively narrow ecological niche compared to the response curves of *L. dubia*. In comparison to *L. dubia, L. procumbens* finds its optimum in plots with lower temperature (Fig. 4c), higher moisture (Fig. 4d) and lower nutrient levels (Fig. 4e). *L. dubia* has its optimum in the driest plots, although the response curve shows a relatively high probability of its occurrence in shallow flooded plots (Fig. 4d). Both species show clearly opposing responses along the soil reaction gradient: whereas *L. dubia* shows an affinity for relatively base-rich plots, *L. procumbens* occurs more frequently on plots with a lower pH (Fig. 4f).

Further analysis of our data set also showed that *Lindernia procumbens* prefers habitats with a short duration of exposure (Fig. 5a), while *L. dubia* also frequently grows on habitats with a long duration of exposure (Fig. 5b). Most of the plots where both species occurred together belonged to the category of shortest bottom exposure (Fig 5c). Plots where only *L. procumbens* grew originated from larger parts of the localities where there were no established populations of *L. dubia*.

4.3. Basic Characteristics of the Sediment Samples

The results of the seed bank and seed dispersal analysis (see Chapter 4.4. and Table 3) could have been influenced by various factors such as the sampling date, the cultivation period and the type of substrate, for example. Therefore, in this part we present detailed information on all of the samples from which at least one seedling of either *Lindernia* species emerged.

The information is given in the following order: sample code, locality name, locality number (in parentheses), substrate type, habitat type or object (i.e. dispersal vector), special storage or preparatory conditions (if applicable), sampling date, sowing date, end of cultivation and total size of sample. Codes: D = ditches, V = vehicles, R = rubber boots, P = puddles on roads in fish storage pond complexes, FSP = fish storage pond bottom sediments, Dr = drifts.

D1 – Hluboká nad Vltavou, fish storage pond complex (loc. 8), muddy bottom sediment from small supply ditch (= a branch of the main supply ditch), propagules in sample concentrated by sieving before cultivation; 17. 3. 2008, 5. 4. 2008, 8. 8. 2009, 500 ml (= the volume before sample concentration).

D2 – Hluboká nad Vltavou, fish storage pond complex (loc. 8), muddy bottom sediment from small supply ditch (= a branch of the main supply ditch, same parts as in D1); 17. 3. 2008, 5. 4. 2008, 8. 8. 2009, 300 ml.

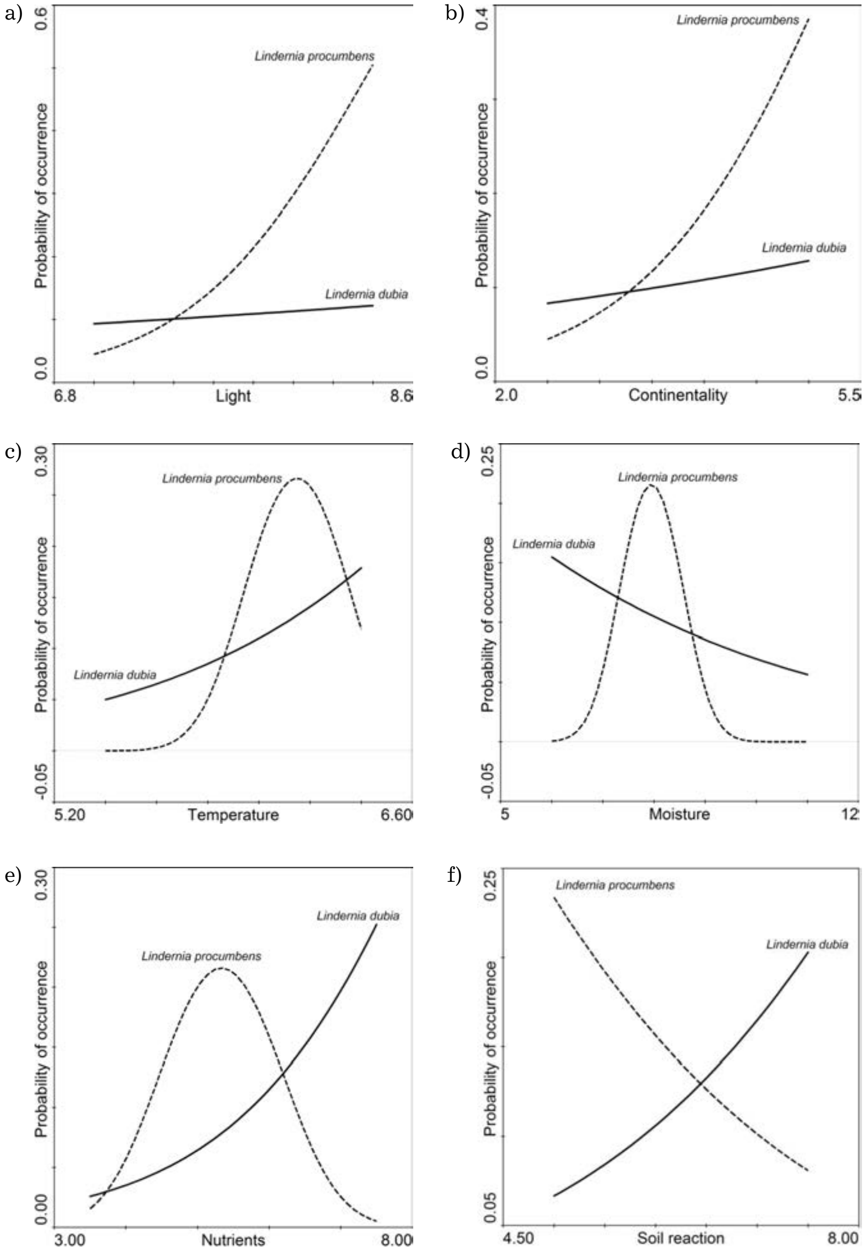

Fig. 4. Species response curves for *Lindernia dubia* and *L. procumbens* with respect to the mean Ellenberg indicator values for light (a), continentality (b), temperature (c), moisture (d), nutrients (e) and soil reaction (f), as derived from generalized linear models with binomial distribution.

D3 – Hluboká nad Vltavou, fish storage pond complex (loc. 8), muddy bottom sediment from the lower drainage channel (main drainage channel in the fish storage pond complex); 16. 3. 2009, 28. 3. 2009, 21. 9. 2010, 450 ml.

D4 – Hluboká nad Vltavou, fish storage pond complex (loc. 8), muddy bottom sediment from middle drainage channel (drains the upper and middle parts of the fish storage pond complex and flows into the lower drainage channel); 16. 3. 2009, 28. 3. 2009, 21. 9. 2010, 450 ml.

FSP1 – Hluboká nad Vltavou, fish storage pond complex (loc. 8), muddy bottom sediment from fish storage pond no. 26 (drained each year, usually from December to March and from June to October); 18. 4. 2008, 30. 4. 2008, 9. 8. 2009, 475 ml.

FSP2 – Hluboká nad Vltavou, fish storage pond complex (loc. 8), muddy bottom sediment from fish storage pond no. 18 (deeply flooded each year from October to December, shallow flooded or partly exposed from December until the end of September or October); 18. 4. 2008, 30. 4. 2008, 9. 8. 2009, 475 ml.

FSP3 – Lázně Bohdaneč, fish storage pond complex (loc. 19), muddy bottom sediment from fish storage ponds nos. 22–24 (usually only flooded for about 3–4 weeks each year, the bottoms are overgrown with perennial wetland vegetation, sediment collected from below the perennial stands); 16. 4. 2009, 28. 4. 2009, 21. 9. 2010, 450 ml.

FSP4 – Třeboň, fish storage pond complex (loc. 15), sandy and muddy bottom sediment from fish storage pond no. 10 (exposed irregularly, i.e. in some years during the growing season, in other years only from winter to early spring); 31. 3. 2010, 9. 4. 2010, 20. 9. 2010, 450 ml.

FSP5 – Čejetice, fish storage pond complex (loc. 6), muddy bottom sediment from fish storage pond no. 9 (drained each year, usually from winter or early spring to autumn, sediment collected from below the perennial stands); 1. 4. 2010, 9. 4. 2010, 20. 9. 2010, 450 ml.

FSP6 – Hrbov, fish storage pond complex (loc. 12), sandy and muddy bottom sediment from fish storage pond no. 10 (drained each year, usually from winter or early spring to autumn, sediment collected from below the stand of *Carex gracilis*); 1. 4. 2010, 8. 4. 2010, 20. 9. 2010, 450 ml.

Dr1 – Hluboká nad Vltavou, fish storage pond complex (loc. 8), drift floating on the water surface of fish storage pond no. 41 (mainly contained biomass of uprooted *Tillaea aquatica*; stored in a paper bag in a refrigerator during the winter); 9. 11. 2008, 17. 3. 2009, 21. 9. 2010, 475 ml.

R1 – Hluboká nad Vltavou, fish storage pond complex (loc. 8), dry sandy and muddy sediment from seven pairs of rubber boots used by employees of the fish farm when working in the fish storage ponds; 21. 3. 2008; 6. 4. 2008; 8. 8. 2009; 50 ml.

R2 – Hluboká nad Vltavou, fish storage pond complex (loc. 8), wet sandy and muddy sediment from two pairs of rubber boots. The whole sample was collected by designed sampling, i.e. repeated walking through drained fish storage pond no. 26 (see also FSP1), rough washing of the rubber boots and collection of the rest of sediment from the soles of the boots; 18. 4. 2008, 30. 4. 2008, 9. 8. 2009, 475 ml.

R3 – Hluboká nad Vltavou, fish storage pond complex (loc. 8), liquid muddy sediment from two pairs of rubber boots. The whole sample was collected by designed sampling (see R2) in shallow flooded fish storage pond no. 18 (see also FSP2); 18. 4. 2008, 30. 4. 2008, 9. 8. 2009, 220 ml.

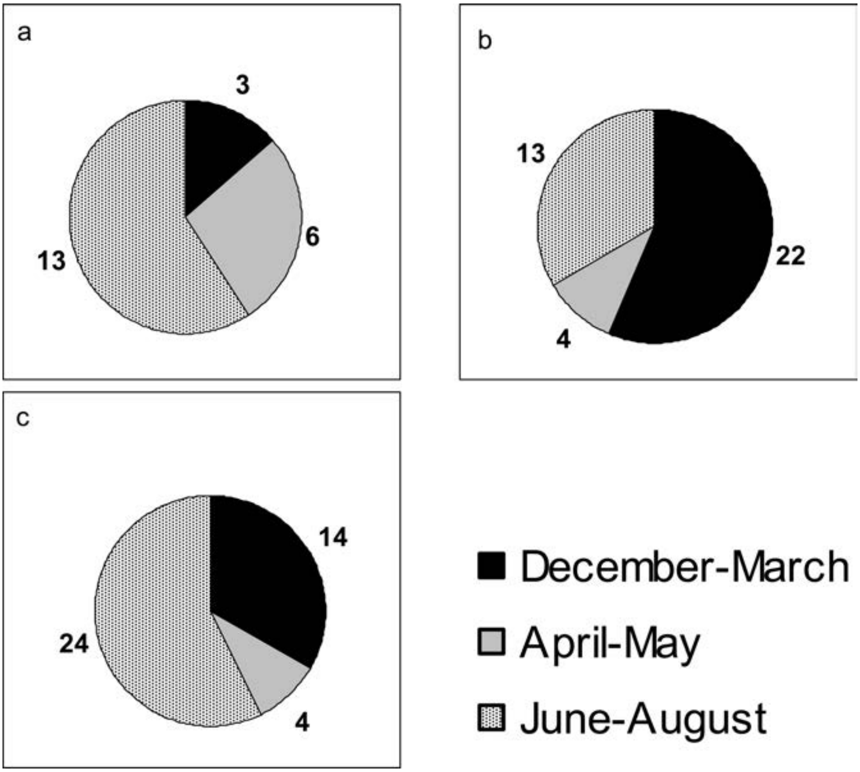

Fig. 5. Occurrence of *Lindernia procumbens* and *L. dubia* on habitats where the start of substrate exposure began at different times (the end of the exposure occurred in September-October in all habitats): a) relevés with only *L. procumbens*; b) relevés with only *L. dubia*; c) relevés with both species. In the graphs the numbers of relevés in each exposure category are displayed.

V1 – Hluboká nad Vltavou, fish storage pond complex (loc. 8), mixture of clay, sand and organic mud from the bottom parts of a tractor used during fishing out of the fishpond Šnekl near Hluboká nad Vltavou (16 km from the fish storage pond complex; collected on the day of fish harvesting: only the new layer of wet sediment); 16. 3. 2009, 30. 3. 2009, 28. 6. 2010, 450 ml.

V2 – Hluboká nad Vltavou, fish storage pond complex (loc. 8), mixture of clay, sand and organic mud from the bottom parts of a lorry used during fishing out of the fishpond Malešický near Malešice village (5 km from fish storage pond complex; collected on the day of fish harvesting: both older dry and new wet layers of sediment); 18. 3. 2009, 28. 3. 2009, 21. 9. 2010, 450 ml.

V3 – Hluboká nad Vltavou, fish storage pond complex (loc. 8), mixture of wet to dry clayey and loamy mud and coarse sand from the bottom parts of a lorry (used for transporting fish long distances; sediment collected during fish loading, part of the sediment had obviously originated in puddles between the ponds; 18. 3. 2009, 30. 3. 2009, 21. 9. 2010, 450 ml.

P1 – Hluboká nad Vltavou, fish storage pond complex (loc. 8), mixture of dry clay and coarse sand from puddles on the road between the ponds; 14. 4. 2008, 2. 5. 2008, 9. 8. 2009, 475 ml.

4.4. Seed Bank and Dispersal of *Lindernia* Species in the Pond Systems

At least one *Lindernia* species was detected in 16 of a total of 87 sediment samples. This number included six samples from undisturbed fish storage pond bottoms with various periods of flooding and exposure, four samples of bottom sediment from connecting and drainage ditches, three samples from rubber boots, three samples from vehicles, one sample from puddles on the road between the fish storage ponds and one drift sample from a fish storage pond (Table 3 and Chapter 4.3.). No seeds of *L. dubia* or *L. procumbens* were found in any sample from the fishpond and fish farming equipment.

L. dubia was mainly found in sediment samples collected from ponds and propagule dispersal vectors (i.e. ditches, rubber boots and vehicles) in the Hluboká nad Vltavou fish storage pond system where a large population of this species is documented. The species was also detected in sample no. FSP5, originating from the Čejetice fish storage pond system (loc. 6 in Table 1). This locality was probably invaded by *L. dubia* in 2002 and it already forms large populations in several ponds of this pond system. Although we did not observe *L. dubia* in the vegetation of the particular pond where sediment was collected for analysis, the seed bank of this species was very dense. The number of emerged seedlings of *L. dubia* in sample FSP5 was the highest for this species within the whole data set: 1152 seedlings in 450 ml of sediment (i.e. 2560 seedlings/litre; see Table 3). It is likely that the invasion of *L. dubia* in Čejetice accelerated between the last floristic and vegetation data recording on the locality in the growing season of 2008 and the sediment sampling in early spring in 2010.

Propagules of native *L. procumbens* were found in sediments from a higher number of the localities than *L. dubia*, which corresponds to the currently higher number of floristic records. It is remarkable that the number of emerged seedlings of *L. procumbens* in all samples is much lower in comparison to the neophytic *L. dubia* (Table 3). The germination rates of both species in our pilot test were similar: 76 and 78 % for *L. procumbens* and 74 and 84 % for *L. dubia*. Therefore, it can be assumed that the numbers of emerged seedlings more or less reflected the real differences in soil seed bank density or the number of transported seeds of both *Lindernia* species.

L. procumbens was also found in soil seed banks in localities where only very small populations of this species were observed (see sample FSP4 in Table 3 and loc. 15 in Table 1) and in locations where it was not found at all during the last few years. For example, sample FSP3 originates from the Lázně Bohdaneč fish storage pond complex (loc. 19 in Table 1) where *L. procumbens* was only documented in 2002 after the reconstruction of a particular pond. In Čejetice (FSP5, loc. 6), the population of *L. procumbens* was regularly confirmed during each visit in late summer (lastly in 2008). However, in the pond used for sediment sampling, *L. procumbens* was only found in vegetation in 2001. In FSP6, from Hrbov (loc. 12), the highest number of emerged seedlings of *L. procumbens* was found: 129 in a 450 ml sample (i.e. 287/l). In this locality, neither recent nor historical records of this species exist. The vegetation currently consists of perennial species, for example *Carex gracilis* and *Lysimachia nummularia*. In the sediment sample from Blatná (loc. 10), no *L. procumbens* seeds were found, although a small population of the species was observed there in 2001 and 2002.

Regarding propagule dispersal vectors, for *L. procumbens* we confirmed dispersal via water (see samples D3 and D4 in Table 3) and rubber boots (samples R2 and R3). We did not find this species in the samples from vehicles or puddles on roads between the ponds, where the neophytic *L. dubia* was detected.

Table 3 also summarizes other abundant species that emerged from the sediment samples. Most of them were wetland annual or short perennial species native to Central Europe that usually grow in vegetation together with both *Lindernia* species (compare this table with the synoptic table – Table 2). This list also includes several non-native species (e.g. neophyte *Gratiola neglecta*), ruderal plants (e.g. *Polygonum aviculare* agg.) and aquatic macrophytes (e.g. *Spirodela polyrhiza*).

L. dubia was one of the species for which the highest total number of seedlings was found, as well as the highest number of emerged seedlings from individual samples. Only three other species, *Tillaea aquatica, Cyperus fuscus* and *Juncus articulatus*, showed higher seedling numbers in individual samples (Table 3). *Tillaea aquatica* had also a higher total number of seedlings. However, the sample with an exceptionally high number of emerged seedlings of *Tillaea* (8127 in 475 ml, i.e. 17,109/l) did not include the bottom sediment but included the drift floating in the flooded fish storage pond (sample Dr1 in Table 3).

In samples cultivated for two years, most of the seedlings of all species, including both *L. dubia* and *L. procumbens*, had already emerged in the first year of cultivation (data not shown). Germination in the second cultivation year continued, especially in the sub-samples that were flooded in the first year. Although both *Lindernia* species showed an ability to germinate in shallow water, the number of seedlings of *L. dubia* that emerged for the terrestrial variant was usually 1.5–2.5 $\times$ higher than the submerged variant. For *L. procumbens*, the difference between the number of seedlings for the terrestrial and submerged variants was smaller. In some cases, even more seedlings of this species emerged for the submerged variant than for the terrestrial one (data not shown).

Table 3. Analysis of soil seed bank and seed dispersal vectors – results of cultivation. Only the samples where either *L. dubia* or *L. procumbens* were found are displayed. For the number of all seedlings, the unidentified seedlings are also included. Only in those samples for which no individuals were identified to the species level was genus level identification (or, if genus level identification was impossible, family level) included in the total number of identified taxa. The numbers of emerged seedlings for individual species and their recalculation

species	number of															
	D1		D2		D3		D4		FSP1		FSP2		FSP3		FSP4	
	s	1l	s	1l	s	1l	s	1l	s	1l	s	1l	s	1l	s	1l
Lindernia dubia (incl. cf.)	2	4	2	7	464	1031	361	801	1070	2253	355	747	0	0	0	0
Lindernia procumbens (incl. cf.)	0	0	0	0	7	16	3	7	0	0	8	17	52	116	1	2
Lindernia sp.	0	0	0	0	3	7	40	89	0	0	0	0	0	0	0	0
Tillaea aquatica	0	0	0	0	58	129	2	4	0	0	0	0	0	0	0	0
Cyperus fuscus	5	10	3	10	346	768	73	163	104	219	88	185	744	1653	15	33
Juncus articulatus (incl. cf.)	0	0	0	0	44	97	8	18	2	4	52	109	154	342	2436	5413
Callitriche palustris	1	2	1	3	283	629	88	195	253	533	206	434	2	4	9	20
Juncus bufonius (incl. cf.)	2	4	3	10	122	270	47	104	498	1048	35	74	77	171	17	38
Plantago major / uliginosa	1	2	0	0	5	11	0	0	1	2	0	0	62	138	0	0
Peplis portula	0	0	0	0	11	24	14	31	33	69	2	4	0	0	4	9
Gnaphalium uliginosum	0	0	0	0	13	29	6	13	23	48	0	0	20	44	0	0
Epilobium ciliatum	15	30	4	13	1	2	7	16	9	19	0	0	0	0	169	376
Juncus compressus (incl. cf.)	0	0	0	0	0	0	0	0	2	4	0	0	4	9	0	0
Elatine hydropiper (incl. cf.)	0	0	0	0	7	16	3	7	0	0	81	171	0	0	0	0
Limosella aquatica	1	2	2	7	73	162	29	65	0	0	1	2	10	22	1	2
Echinochloa crus-galli	0	0	1	3	5	11	2	4	3	6	0	0	0	0	0	0
Lemna minor / gibba	0	0	0	0	24	54	9	20	1	2	56	118	2	4	7	16
Eleocharis acicularis	0	0	0	0	11	24	1	2	4	8	13	27	0	0	0	0
Rorippa palustris	0	0	0	0	20	44	9	20	10	21	10	21	8	18	0	0
Lythrum salicaria	0	0	0	0	0	0	0	0	0	0	0	0	69	153	0	0
Juncus filiformis (incl. cf.)	0	0	0	0	0	0	0	0	0	0	0	0	70	156	0	0
Persicaria lapathifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	35
Ranunculus sceleratus	0	0	0	0	2	4	2	4	24	51	13	27	0	0	2	4
Gratiola neglecta	0	0	0	0	0	0	0	0	0	0	0	0	72	160	0	0
Poa annua	2	4	1	3	1	2	0	0	1	2	0	0	0	0	0	0
Sagina procumbens	0	0	0	0	0	0	0	0	2	4	0	0	32	71	0	0
Juncus effusus	0	0	2	7	3	7	4	9	3	6	7	15	1	2	26	58
Alisma plantago-aquatica	0	0	0	0	5	11	1	2	10	21	16	34	3	7	0	0
Eleocharis ovata	0	0	0	0	18	40	1	2	6	13	19	40	2	4	3	7
Spirodela polyrhiza	3	6	3	10	26	58	3	7	0	0	4	8	0	0	0	0
Najas minor	0	0	0	0	3	7	2	4	0	0	18	38	0	0	0	0
Polygonum aviculare agg.	0	0	0	0	0	0	1	2	0	0	1	2	0	0	0	0
Leersia oryzoides	0	0	0	0	5	11	3	7	1	2	7	15	0	0	0	0
Persicaria minor	1	2	1	3	2	4	0	0	0	0	14	29	1	2	4	9
Elatine triandra (incl. cf.)	0	0	0	0	12	26	4	9	0	0	8	17	0	0	0	0
Alopecurus geniculatus	0	0	0	0	0	0	0	0	0	0	27	57	0	0	0	0
Chenopodium ficifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potamogeton pusillus	0	0	0	0	2	4	3	7	0	0	12	25	0	0	0	0
Veronica anagallis-aquatica	1	2	2	7	1	2	0	0	0	0	0	0	11	24	3	7
not precisely determined taxa (high propagule density)																
Juncus sp.	0	0	0	0	9	20	4	9	9	19	5	11	49	109	66	147
Elatine sp.	0	0	0	0	0	0	0	0	0	0	74	156	0	0	0	0
Epilobium sp.	4	8	0	0	5	11	0	0	2	4	1	2	2	4	32	71
Poaceae indet.	1	2	0	0	4	8	1	2	1	2	6	13	0	0	0	0
other species (low propagule density)	7	14	4	12	43	94	28	62	10	20	5	10	65	141	7	15
not precisely determined taxa (low propagule density)	2	4	0	0	3	6	0	0	0	0	1	2	1	2	1	2
unidentified	4	8	4	13	21	46	6	13	36	76	56	118	41	91	1	2
number of seedlings in samples	52	104	33	110	1662	3693	765	1700	2118	4459	1201	2528	1554	3453	2820	6267
identified taxa in samples	18	–	16	–	44	–	34	–	36	–	29	–	43	–	20	–

on 1 l of sediment are given for each sample. Values higher than 1000 seedlings on 1 l, 500 seedlings on 1 l and 100 seedlings on 1 l are highlighted in the levels of a black-grey scale. The species where some of the individuals were not identified with 100% certainty are indicated with “incl. cf.” in parentheses. The species (excluding *Lindernia*) are ranked in descending order according to the cumulative number of seedlings on 1 l (see the last column); species with a lower value than 50 are not displayed.

seedlings																							
FSP5		FSP6		Dr1		R1		R2		R3		V1		V2		V3		P1		total	
s	1l	s	1l	s	1l	s	1l	s	1l	s	1l	s	1l	s	1l	s	1l	s	1l	all s	cum. on 1 l
1152	2560	0	0	25	53	0	0	927	1952	97	440	1	2	3	7	1	2	29	61	4489	10024
32	71	129	287	0	0	0	0	3	6	3	14	0	0	0	0	0	0	0	0	238	536
0	0	0	0	0	0	1	20	0	0	0	0	0	0	0	0	0	0	0	0	44	116
0	0	21	47	8127	17109	1	20	0	0	0	0	0	0	0	0	0	0	0	0	8209	17309
2396	5324	510	1133	0	0	2	40	32	67	37	168	1	2	0	0	0	0	1	2	4357	9777
0	0	0	0	0	0	0	0	3	6	16	72	1	2	0	0	0	0	1	2	2717	6065
32	71	127	282	0	0	1	20	73	154	54	245	0	0	14	31	0	0	12	25	1156	2648
78	173	111	247	0	0	2	40	94	198	8	36	3	7	9	20	2	4	1	2	1109	2448
230	511	131	291	0	0	8	160	0	0	0	0	20	44	25	56	1	2	6	13	490	1230
109	242	298	662	0	0	0	0	8	17	4	18	0	0	1	2	0	0	0	0	484	1078
95	211	112	249	0	0	0	0	8	17	1	5	0	0	0	0	0	0	0	0	278	616
4	9	1	2	0	0	0	0	2	4	0	0	1	2	0	0	0	0	0	0	213	473
91	202	111	247	0	0	0	0	0	0	0	0	2	4	1	2	0	0	0	0	211	468
0	0	0	0	0	0	0	0	0	0	40	181	0	0	1	2	0	0	0	0	132	377
30	67	20	44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	167	373
138	307	2	4	0	0	0	0	1	2	1	5	0	0	1	2	0	0	1	2	155	346
4	9	0	0	0	0	0	0	3	6	22	100	0	0	0	0	0	0	0	0	128	329
78	173	11	24	0	0	0	0	0	0	2	9	0	0	0	0	0	0	0	0	120	267
39	87	12	27	1	2	0	0	1	2	3	14	1	2	1	2	0	0	0	0	115	260
0	0	27	60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	96	213
6	13	18	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	94	209
60	133	9	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	86	190
0	0	0	0	1	2	0	0	26	55	6	27	1	2	0	0	0	0	0	0	77	176
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	72	160
0	0	0	0	0	0	3	60	0	0	0	0	15	33	19	42	0	0	0	0	42	146
19	42	11	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	64	141
0	0	0	0	0	0	0	0	0	0	0	0	7	16	4	9	0	0	2	4	59	133
0	0	0	0	0	0	0	0	18	38	3	14	0	0	0	0	0	0	0	0	56	127
0	0	0	0	0	0	0	0	3	6	0	0	0	0	0	0	0	0	0	0	52	112
0	0	0	0	0	0	0	0	0	0	4	18	0	0	0	0	0	0	0	0	43	107
0	0	0	0	0	0	0	0	0	0	12	55	0	0	0	0	0	0	0	0	35	104
0	0	2	4	0	0	2	40	0	0	0	0	15	33	5	11	0	0	1	2	27	94
1	2	17	38	0	0	0	0	0	0	4	18	0	0	0	0	0	0	0	0	38	93
1	2	8	18	1	2	0	0	0	0	5	22	0	0	0	0	0	0	0	0	38	93
0	0	3	7	0	0	0	0	0	0	0	0	0	0	12	27	0	0	0	0	39	86
0	0	0	0	0	0	0	0	0	0	3	14	0	0	0	0	0	0	0	0	30	71
26	58	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26	58
0	0	0	0	0	0	0	0	0	0	4	18	0	0	0	0	0	0	0	0	21	54
0	0	0	0	0	0	0	0	0	0	0	0	4	9	0	0	0	0	0	0	22	51
151	336	72	160	0	0	0	0	2	4	0	0	2	4	0	0	0	0	0	0	369	819
0	0	0	0	0	0	0	0	0	0	34	155	0	0	0	0	0	0	0	0	108	311
8	18	0	0	0	0	0	0	2	4	0	0	0	0	0	0	0	0	0	0	56	127
6	13	1	2	0	0	0	0	3	6	4	18	1	2	6	13	0	0	2	4	36	85
24	52	52	113	11	22	1	20	4	8	4	19	23	48	45	97	2	4	6	12	340	771
0	0	3	6	0	0	1	20	0	0	0	0	1	2	2	4	0	0	0	0	16	50
177	393	21	47	1	2	1	20	23	48	21	95	10	22	9	20	0	0	1	2	433	1016
4987	11082	1840	4089	8167	17194	23	460	1236	2602	392	1782	109	242	158	351	6	13	64	135	**27187**	–
30	–	36	–	10	–	10	–	19	–	22	–	30	–	29	–	5	–	15	–	**109**	–

5. Discussion

The stands in which both *Lindernia* species grew were mainly assigned to the class *Isoëto-Nanojuncetea* Br.-Bl. & Tüxen ex Br.-Bl. & al. 1952, which comprises vegetation of wetland annuals (Deil 2005). *L. dubia* was also more frequently documented in the vegetation predominated by wetland perennials, especially in short reeds, for example *Eleocharitetum palustris* Savič 1926 and *Leersietum oryzoidis* Eggler 1933 associations.

Regarding the results of our vegetation data analysis, the relevés with *L. procumbens* were richer in diagnostic species, i.e. the species with a significantly higher concentration in the group of *L. procumbens*-relevés, than the two remaining groups. This probably reflects the fact that in the relevés with only *L. procumbens*, a larger number of localities and various habitats was represented than in the relevés with *L. dubia* or both species.

It should be taken into account that the neophytic *L. dubia* has not yet developed the full potential of its distribution. The comparison of habitat preferences of both *Lindernia* species showed that whilst the ecological niches of these species overlap, the niche of *L. dubia* is broader than that of *L. procumbens*. While *L. procumbens* was particularly found to flourish in the habitats with higher moisture and a shorter period of exposure (and lower coverage by perennial herbs), *L. dubia* is successful in habitats with different periods of exposure (and therefore in both annual and perennial stands). The overlap of the ecological niches of both species was obvious not only from our analysis but also from the fact that in a large part of the analysed relevés both *Lindernia* species occurred together. The majority of the plots with *L. procumbens* but without *L. dubia* were found in localities where *L. dubia* still occurred in a small amount or where it did not occur at all. In the Hluboká fish storage ponds, neophytic *L. dubia* was usually present, in small numbers at least, admixed in all stands with native *L. procumbens*. However, *L. procumbens* was often lacking, not only in the stands with *L. dubia*, but also in many of the ponds with apparently suitable conditions; these were only colonized by *L. dubia*.

Regarding the species response to environmental factors, expressed as Ellenberg indicator values, important differences were found, for example in the factor moisture. *L. dubia* was found to occur under a wider range of moisture conditions than *L. procumbens*, which had an optimum in plots with higher moisture levels. This was also visible from the diagnostic species of the vegetation with both *Lindernia* species. The alien *L. dubia* occurred together with the aquatic macrophyte *Lemna minor* on one side, and with ruderal weeds on the edges of dry fish storage ponds on the other. On the contrary, species of exposed pond bottoms, such as *Coleanthus subtilis* and *Elatine hydropiper*, with an optimum on wet muddy substrata, were found in the stands with *L. procumbens*. Although both *Lindernia* species can germinate and develop in shallow water (e.g. Willis & Mitsch

1996, von Lampe 1996, Abernethy & Willby 1999), according to field investigations by Nishihiro & al. 2006, *L. dubia* tolerates deeper submersion and, at the same time, a greater decrease in the water level below the soil surface than *L. procumbens*. It was interesting that, in some of our cultivation samples, the submerged variant of *L. procumbens* seemed to germinate better than the terrestrial variant; this did not apply to *L. dubia*. However, the overall relatively small number of *L. procumbens* seedlings does not allow any generalization. Thus, further experimental cultivations under various moisture conditions, including repeated substrate flooding and exposure, are necessary in order to determine the details of the demands on the hydrological regime of both species.

A similar situation as for the moisture factor applied for the nutrients factor. According to the results of our analysis and also to our field experiences, the ecological niche of *L. dubia* regarding the amount of nutrients is much broader than that of *L. procumbens* and *L. dubia* has its optimum on more nutrient-rich habitats than *L. procumbens*. However, further cultivation experiments are necessary to explain the role of nutrients in the growth of both species. It is likely that interspecific competition, which is usually much stronger on nutrient-rich substrata, is more important than the amount of nutrients alone. The different competitive ability of *L. dubia* and *L. procumbens* was also reflected in the response of both species to light.

Our results and field observations partly contradict each other regarding the factor of temperature. The results of the DCA and t-tests of both *Lindernia* species indicate that *L. procumbens* is more thermophilous than *L. dubia*. Additionally, according to our observations in Hluboká (see below), the germination of *L. procumbens* proceeds during periods with higher temperatures than the germination of *L. dubia*. For *L. procumbens*, we also found large inter-annual fluctuations in the size of its population, which were also, at least partly, dependent on temperature. The most numerous populations of *L. procumbens* were observed in extremely warm years; similar results were also reported by Nobis & al. 2010 from Poland. However, the species response curves show higher optimum temperatures for *L. dubia* than for *L. procumbens*. Part of the problem here may be that whilst in the Ellenberg indicator values macroclimatic factors are considered, for the germination of seeds and seedling recruitment the microclimate is more important (Fenner & Thompson 2005). Thus, microclimatic conditions, especially the temperatures of the soil surface and the air several centimetres above it, are probably more important for the occurrence of both *Lindernia* species and also for other wetland annuals than macroclimatic conditions. Secondly, for the factor of temperature, but also continentality and soil reaction, the results may have been partly influenced by the fact that the alien *L. dubia* currently has a more restricted distribution in the Czech Republic than the native *L. procumbens*. The localities documented by relevés with *L. dubia* were concentrated in relatively warm parts of southern Bohemia, formed by slightly acidic to slightly basic substrata and only rarely originated from regions with a relatively cold climate and predominantly acidic substrata. Thus, in the case of further invasion of *L. dubia*, an analysis performed on new data may show different results for three of the abovementioned factors than the analysis presented in the current study. Nevertheless, it is likely that our data represent at least part of the ecological optimum of *L. dubia*, as demonstrated by its numerous populations.

We also found important differences in the seed bank densities of *L. dubia* and *L. procumbens*. Although in literature sources *L. dubia* is often reported as one of the most abundant species in the soil seed banks analysed, in most published papers (e.g. McFarland & Rogers 1998, Kenow & Lyon 2009) the number of emerged seedlings ranged between tens and hundreds on 1 m^2 (1 l of sediment comprises 0.1 $m^2 \times 1$ cm depth). Only Leck 2003 found seed bank densities comparable with our results for *L. dubia* in a river marsh in north-eastern America, where in some parts of the marsh there were even approximately 60,000 seeds on 1 m^2 of the surface substrate layer (depth 0–3 cm; corresponding to 30 l of sediment on 1 m^2 and 2000 seedlings on 1 l of sediment). Seed bank densities for *L. procumbens* were also published by Liu & al. 2006, for example, and they were similar to our results. Unfortunately, data regarding seed longevity are lacking for both species. In our study *L. procumbens* showed an ability to survive in a soil seed bank for at least 7–9 years, without occurring in recent vegetation. It is possible that in some localities, for example in Hrbov (loc. 12 in Table 1), the time between the last occurrence of the species and its detection in soil seed banks or its appearance in the locality after mechanical disturbance was even longer, but due to the absence of historical data we cannot make reliable conclusions regarding this matter.

The most surprising finding for us was the large population size and seed bank density of *L. dubia* in Čejetice (loc. 6), where the invasion of this neophyte began just several years ago. During the first visits to this locality in 2001 and 2002 we did not find any *L. dubia* plants. The propagules were probably unintentionally transported on the rubber boots of the first author who, in 2002, regularly visited the fish storage ponds in Hluboká and also occasionally visited other pond systems in southern Bohemia. Besides the new locality in Čejetice, in 2003 *L. dubia* also appeared in Kestřany (loc. 7). This case and also the results of our later research of dispersal vectors suggest the large potential of *L. dubia* to spread and colonize new habitats. Although this species is regarded as potentially invasive in warmer parts of Europe, exact records about its possible speed of invasion are lacking.

Fish storage ponds offer good conditions for the development of both *Lindernia* species and thus this habitat type functions as an important source of propagules of these species for the surrounding landscape. For example, the Hluboká fish storage pond system is drained by a system of channels that empties into the Vltava River. Two new localities of *L. dubia* were discovered in 2003 in Vltava downstream from the fish storage pond system (LEPŠÍ & DOUDA 2005). However, a much more frequent occurrence can be expected due to the continual supply of propagules from the source population in the fish storage ponds. As we found, the sediments on the bottom of the drainage ditches contain a high number of propagules and *L. dubia* is the most abundant species there.

Native *L. procumbens* also occurred in the sediment samples from the drainage ditches, but at much lower densities. The dispersal of a higher number of propagules by a greater variety of vectors for *L. dubia* than *L. procumbens* is probably only related to the much higher number of propagules of *L. dubia* in the bottom sediments of fish storage ponds rather than to specific dispersal adaptations. The most abundant plant species with small propagules has the greatest probability of being dispersed not only via water streams but also via more complicated dispersal routes. For instance, the seeds can be transported on the rubber boots of fish farmers out from the ponds and deposited in the depressions on roads between the ponds. We confirmed a relatively large number of *L. dubia* seeds in one sample from a puddle on the road. From there, vehicles, which were probably "infected", moved between the fish storage pond system in Hluboká and the surrounding fishponds (V1 and V2, Table 3) and even transported live fish to other European countries (V3, Table 3).

According to our data, vehicles contribute to the dispersal of many wetland, ruderal and grassland species, both perennial and annual. At the fishponds, cars can drive right up to the edge of the fishponds, sometimes even into shallow water. In such a way, some sediment containing plant propagules could easily be washed down from the car into the fishpond. NEFF & BALDWIN 2005 also confirmed for *L. dubia* seed dispersal by birds. This dispersal mechanism is also possible to some extent in our localities.

Despite the fact that appropriate means of dispersal of *L. dubia* exist, this species was not found in the fishponds in the vicinity of Hluboká. The only exception was the system of small fry ponds near Čejkovice (loc. 1), which has a similar regime as the fish storage ponds, i.e. these ponds are regularly left without water in the summer. Most fishponds in this region are only dry from March/April to May/June, which is not sufficient for the reproduction of thermophilous annual plants, including both of the *Lindernia* species. For example, in Hluboká, we observed the first seedlings of *L. dubia* in the first half of May and the seedlings of *L. procumbens* 3–4 weeks later; in colder years germination was delayed even further. For comparison, many other mudflat species have already germinated in March–April, for example *Juncus bufonius, Callitriche palustris* and *Limosella aquatica* (VON LAMPE 1996, ŠUMBEROVÁ & al. 2005). In some fishponds, summer drainage continues throughout the vegetation period each year. In these fishponds, *Lindernia* species may be limited by the lower level of substrate moisture in the later phase of pond bottom exposure, or by the dense stands of other herbs that germinate earlier (HEJNÝ 1999, ŠUMBEROVÁ & al. 2005). Thus, we conclude that later substrate exposure and/or management (e.g. mowing or herbicide use) favour both *Lindernia* species by eliminating strong competitors. Nevertheless, the alien *L. dubia* is much more successful under such suitable conditions than the native *L. procumbens* and, at the same time, it tolerates the competition of other herbs better.

It should be emphasized that the wider ecological niche of *L. dubia* can probably only partly explain the large invasive potential of this species. Because the plants of *L. dubia* are usually larger than those of *L. procumbens*, when under the same conditions, it is possible that they also produce more flowers and fruit. Our unpublished data, collected from a limited number of plants from Hluboká, suggest that *L. dubia* really is more productive and that the numbers of flowers and fruit increase on wet muddy substrata. However, the plants were collected during one growing period and their size could have been influenced by specific factors in a particular locality. Therefore, further studies of seed biology and productivity, including the cultivation of both *Lindernia* species under controlled conditions, are necessary.

The behaviour of plant species can strongly vary according to climatic conditions. This applies also to *Lindernia*: although the more thermophilous *L. procumbens* is threatened in Central Europe, in warmer parts of the world both *Lindernia* species have been listed as dangerous weeds of rice following the development of herbicide-resistance (OLOFSDOTTER & al. 2000, SHIBAYAMA 2001, YOUNG SON & RUTTO 2002, YOSHINO & al. 2006).

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