

Variability of vegetation of exposed pond bottoms in relation to management and environmental factors

Variabilita vegetace obnažených den ve vztahu k obhospodařování a faktorům prostředí

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Species composition, structure and ecological characteristics of the vegetation of two pond types with different management, fishponds and storage ponds, in the Českobudějovická pánev basin (South Bohemia), were compared. A selection of 99 relevés from fishponds and 99 from storage ponds (small ponds used for the storage of marketable fish) made in 2000–2004 were analysed using direct and indirect ordination and ANOVA. The difference between storage ponds and fishponds was found to be more important than gradients correlated with temporal changes, soil moisture and mud depth. Storage ponds had a significantly higher mean number of species, bryophytes, archaeophytes and neophytes and beta-diversity. There were no significant differences in cover values, except of moss layer, which had significantly higher cover in storage ponds. Fishponds had significantly higher mean Ellenberg indicator values for light, continentality, moisture and nutrients. *Oenanthe aquatica* and *Rumex maritimus* are typical fishpond species and *Amblystegium humile* and *Eleocharis palustris* agg. typical storage pond species. The management of storage ponds is more varied and of different intensity than that of fishponds. It is assumed that management is a crucial factor determining the species richness and influencing the vegetation of these two habitats.

Key words: beta-diversity, Czech Republic, fishpond, ordination, species richness, storage pond

Introduction

The species that colonize the exposed bottoms of ponds occur in periodically flooded or waterlogged habitats, in which competitively strong perennial herbs do not become established (Hejný 1960, Hejný & Husák 1978, Deil 2005). Variability in this type of habitat is determined by both environmental conditions and management, which modify vegetation structure and species composition, even within one and the same plant community. Large differences can be expected in vegetation in habitats that differ in physiognomy, environmental conditions and management, e.g. river alluvial deposits and fishponds. However, there are habitats, which seem to be similar, e.g. various types of ponds. Not infrequently, their function in the landscape is not distinguished by biologists and nature conservationists, which lead to misconceptions and inappropriate management.

In this study differences in species composition and vegetation characteristics of two similar types of pond, fishponds and storage ponds, were determined. Both are essential for fish farming, which has been practised in central Europe since the 11th century (Andreska 1997). The ponds are used for different purposes and their management differs. An old management practice, summer drying of the ponds, results in vegetation growing on the exposed bottoms. Both types of ponds are subjected to this practice, but to different extents.

Fishponds are used for rearing fish, especially of common carp (Čítek et al. 1998). The regime of flooding and draining is rather regular, but they are flooded for longer than they are drained. Management also includes organic manuring, feeding of the fish stock, occasionally liming etc. The exposed bottoms of fishponds in central Europe are commonly colonized by annual hygrophilous vegetation. This vegetation was well documented in the past (Domin 1904, Klika 1935, Ambrož 1939, Pietsch 1963, Pietsch & Müller-Stoll 1968, Philippi 1968, Vicherek 1972). Recently, the biological and ecological aspects of this vegetation has been studied (Hroudová 1981, Müller-Stoll & Pietsch 1985, Prach et al. 1987, Lampe 1996, Pietsch 1999, Poschlod et al. 1999, Täuber 2000).

The storage ponds are used to store marketable fish (Čítek et al. 1998). Some irregularities in the regime of flooding and exposure are quite common; they are flooded for shorter periods than they are drained. The management of storage ponds is more diverse than that of the fishponds, including the use of herbicides, mowing, regular liming etc. Their flora and vegetation were rarely studied (Míchal & Kurka 1991, Chán 1999, Filípková 2001).

In 2000–2004, the exposed bottoms of ponds at different localities throughout the Czech Republic were studied. The differences in the stands of plants that colonize fish and storage ponds subject to different human impact are recorded (Šumberová 2003, Šumberová et al. 2005). For a detailed comparison of both habitats the Českobudějovická pánev basin (S Bohemia) was chosen.

The following questions are addressed: (1) Are there significant differences in the species composition and vegetation characteristics (vegetation cover, species number, etc.) of fish and storage ponds? How can these differences be explained? (2) What are the main gradients in the species composition of the vegetation that grows on exposed bottoms of ponds?

Material and methods

Environmental conditions

The Českobudějovická pánev basin is situated in the central part of S Bohemia, SW Czech Republic. Its total area is 640 km² (Demek et al. 1987). A major part of the basin is a flat upland, surrounded by hilly countryside of the Blatenská pahorkatina upland and Šumavské podhůří foothills on the northwest and west, the Táborská pahorkatina upland on the north and east and the Novohradské podhůří foothills and Třeboňská pánev basin on the southeast and south (Chábera 1998). Mean altitude of the basin ranges from 370 to 440 m (Culek 1996). River alluvia (Demek et al. 1987) and numerous fishponds, made by man mainly in the 15th–16th centuries, are important features of the terrain relief.

The Českobudějovická pánev basin is a tectonic depression filled mostly by unstabilized non-calcareous freshwater sediments. Soils consists of pseudo-clays and clays on the plain, cambisols on the ridges and fluvisols in river alluvia (Culek 1996).

The climate in the Českobudějovická pánev basin is temperately warm. The mean annual temperature is 7.8 °C (České Budějovice). The sum of annual precipitation is 620 mm in the centre (České Budějovice) and decreases towards the northwest to 570 mm (Vodňany) and 596 mm (Protivín) (Culek 1996). The region is one of the most continental in the Czech Republic, due to extreme temperatures in winter and summer. The highest and lowest temperatures recorded are + 40 °C and – 42.2 °C, respectively (Culek 1996). This area is in the catchment basin of the Vltava river. The fish and storage ponds are fed by small streams. The Českobudějovická pánev basin is a cultural landscape, formed of a mosaic of arable land, grasslands, forests and wetlands. Study sites were located throughout the whole area, with most in the southern and central part of the basin (Fig. 1).

Management of fish and storage ponds

A fishpond is an artificial water body, primarily intended for rearing fish. In the Czech Republic, most fishponds serve for rearing common carp plus smaller numbers of other marketable fish, e.g. pike, pike-perch, tench, white amur. All fishponds studied were carp ponds.

Fishponds are divided into main ponds and nursery ponds according to the age of the fish. The nursery ponds are used to rear the youngest fish (up to 1 or 2 years old). Then fish are put in the main ponds where they grow to marketable size (usually 3 or 4 years old) (Čítek et al. 1998).

The fishponds are subjected to addition of cereal feed for fish, organic manure (dung, compost, etc.) and occasional liming, the elimination of aquatic and littoral vegetation by mowing or application of herbicides, and are dried in winter or summer. The effect of drying in summer is to increase mineralization of nutrients in the pond mud, and to reduce fish parasites and water macrophytes (Hejný 1978, Hejný et al. 2000). This old management practice was regularly used in the past but less so now for economic reasons. At present, mostly partial summer drying is used, i.e. exposure of the fishpond margins by lowering the water level, or drying for only part of the growing season. Regular summer drying of nursery ponds occurs yearly or every second year from March/April to May/June, before they are stocked with fingerlings. Nowadays, summer drying of the main ponds occurs irregularly, e.g. in cases of dam reconstruction, shortage of water or removal of mud.

Storage ponds are usually small and of square or oblong form. The walls of these ponds are made of stones, concrete panels, poured concrete, or are covered with grass or clay. The ponds are interconnected with one another via canals. They serve for short-term storage of marketable fish collected from the main ponds (Čítek et al. 1998). Fish are collected from the fishponds mostly in autumn, or occasionally early spring. Therefore, the storage ponds are most frequently used from autumn to spring. Nearly all storage ponds are drained in March or April at the latest.

The periodicity and duration of the summer drying of the storage ponds differs from that of fishponds. Most storage ponds are dry for 6–10 months each year, which eliminates parasites and diseases. Liming of the bottom or spraying the walls with lime milk achieves the same purpose. Before they are used to store fish, the vegetation at the pond bottom is mown and raked out, or more rarely grazed, mostly by sheep. The presence of cropped vegetation on bottoms of storage ponds positively influences the health of the stored fish. Recently, some fish farms have used herbicides (usually Roundup) to retard or eliminate

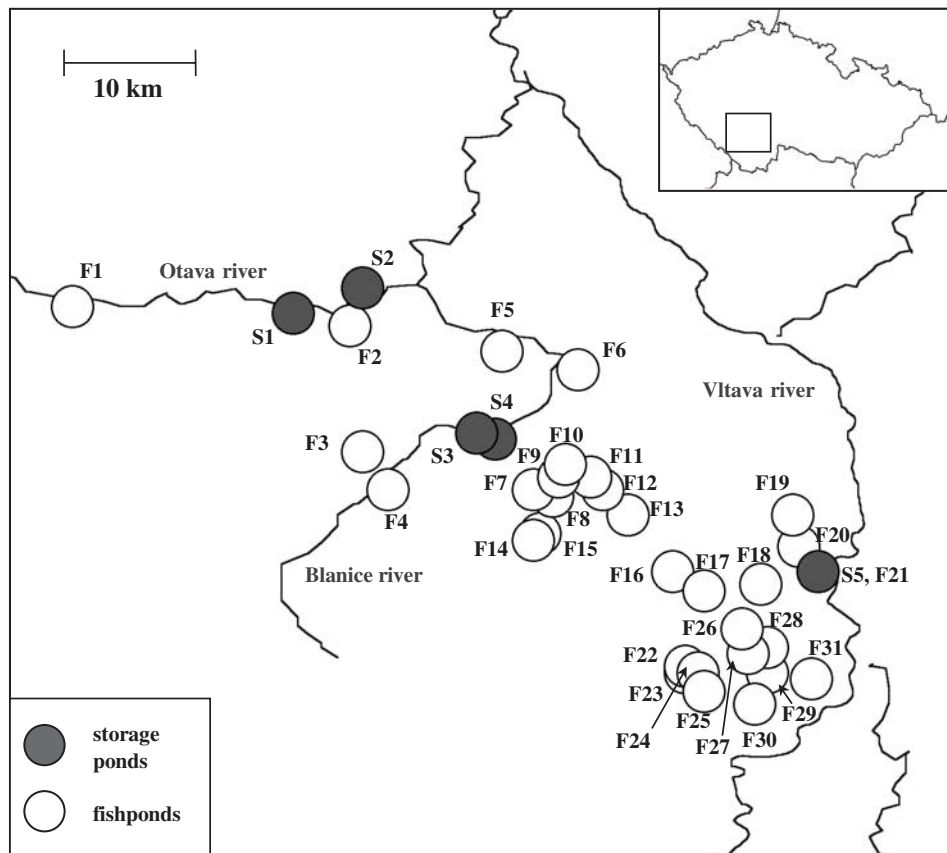


Fig. 1. – Map of the study area. Numbers of the localities correspond with the numbers used in the list of study sites in Appendix 1.

the vegetation. The application of herbicide, 1–2 times per year, reduces the need for mowing from 4–6 to 1–2 times per year and does not seriously affect the survival of most plant species. The fish farms included in this study sprayed herbicide on the exposed bottoms of drained storage ponds, 1–2 times per year, or not at all.

Study sites

The location of the study sites are shown on the map (Fig. 1). The list of study sites with their numbers is included in Appendix 1. More detailed information on some of the localities can be found in Horáková et al. (2005) and Šumberová et al. (2005).

A total of 31 fishponds (10 main and 21 nursery ponds) and 51 storage ponds in five storage pond systems were included in this study. These ponds are farmed by four private fish farms, one school fish farm and one fishery research institution.

Table 1. – Scales for variables mud depth and moisture used in the analyses.

Variable / scale	1	2	3	4	5
Mud depth	pure sand	up to 1 cm	1–3 cm	3–10 cm	> 10 cm
Moisture	dry	usually wet	waterlogged	shallowly flooded; to 5 cm	flooded; > 5 cm

Sampling

In total, 204 relevés of the vegetation colonizing exposed pond bottoms in the Českokobudějovická pánev basin were recorded by the authors in 2000–2004; 102 from storage ponds and 102 from fishponds. The area of most relevés was 1 m², but in tall stands dominated by *Bidentetea* species, mostly 4 m². In addition to data on sampling date, cover of individual layers, locality etc., moisture and type of substrate were recorded for each relevé. For both pond types, the relevés were made when the vegetation was at its maximum and from places of different moisture and mud depth. The relevés are currently stored in TURBOVEG format in the Czech National Phytosociological Database (Hennekens & Schaminée 2001, Chytrý & Rafajová 2003).

Six relevés of abnormal floristic composition were excluded from the data set for the current analyses. They were extremely species-poor and more closely related to the vegetation of shallow still waters. The data set used in this analysis set includes 198 relevés; 99 from storage and 99 from fishponds (Fig. 1).

Data analysis

These explanatory variables were compiled for each relevé: pond type, season, moisture and mud depth. The variable “pond type” includes two categories, fish and storage ponds, which are characterized by different management. The variable “season” was derived from the date. This variable was measured on an ordinal scale as the number of half-month intervals from the beginning of the year. The variables “moisture” and “mud depth” were scaled according to Table 1.

Before the analysis, the species were arranged in the following way: taxonomically difficult taxa, or those not easily identifiable in the juvenile stage, were placed in aggregates or determined to generic level. For details of the *Achillea millefolium* agg., *Eleocharis palustris* agg., *Equisetum arvense*, *Myosotis palustris* agg., *Taraxacum* sect. *Ruderalia* and *Verbascum* sp. see Šumberová et al. (2005). Other species were grouped as follows: (1) all records of *Brachythecium*, *Bryum* (excl. *B. argenteum*), *Physcomitrium*, *Populus*, *Salix*, *Typha* and *Vicia* at the generic level; (2) all those of *Batrachium* as *Batrachium aquatile* agg.; (3) all of species of *Chenopodium album* agg. (excl. *C. ficifolium*) at the aggregate level. To decrease the effect of the most abundant species, species percentage covers were square-root transformed. Alien species were classified according to Pyšek et al. (2002). The algae and blue-green algae were not determined, with the exception of *Botrydium granulatum* Grev. and *Nostoc commune* Vauch ex Born. et Flach. Nomenclature of vascular plants and bryophytes follows Kubát et al. (2002) and Frey et al. (1995).

To characterize ecological differences between the vegetation of fishponds and storage ponds, the whole data set was split into two groups. One contained relevés from fishponds

and the other from storage ponds. The mean Ellenberg indicator values were calculated for individual relevés and then for individual relevé groups. Similarly the mean species number, cover of individual layers, presence of alien species and other basic vegetation characteristics were calculated (Table 2). In order to assess the variation in the pattern of beta-diversity between storage and fish ponds (the mean difference in species composition among relevés), the mean Sørensen index of dissimilarity for all pairs of relevés in each group were calculated ($1 - S$, where S is Sørensen similarity; Magurran 1988, Koleff et al. 2003). Then the confidence intervals for beta-diversity in each group were determined, using 100 bootstrap samples (Efron & Tibshirani 1993) taken from the relevés belonging to that group. This procedure was done using the JUICE 6.3 program (Tichý 2002).

The above values for both pond types were compared by one-way ANOVA. Box and whisker plots were constructed for those characteristics that differed most between the two pond types. The statistical analyses and the box-and-whiskers graphs in this study were computed using the STATISTICA 7.1 program (StatSoft 2001).

To assess the overall patterns in variation in species composition the whole data set was subjected to detrended correspondence analysis (DCA) in the CANOCO 4.5 package (ter Braak & Šmilauer 2002). For interpretation of DCA results in terms of environmental gradients, four explanatory variables (pond type, season, moisture and mud depth) were passively projected on the ordination scatter plot. As this analysis revealed a rather long gradient on the first axis (3.27 SD units), ordination methods more suitable for unimodal models were used.

A series of partial canonical correspondence analyses were performed (pCCA; Lepš & Šmilauer 2003) to detect the effect of each explanatory variable on the species composition of the vegetation growing on exposed pond bottoms. Gross effects were tested using separate CCAs with a single explanatory variable, followed by permutation tests for the first canonical axis. Net effects of particular variables, after partialling out the effects shared with the other three variables, were tested using partial CCAs, each with a single variable and another three variables used as covariables. Significance of the first canonical axes were again tested. Permutation tests using 999 permutations were always used to test the significance of the first canonical axes. The full model was used to test the effect of pond type, while the other three variables were permuted independently of its effect. The ratio of particular canonical eigenvalues to the sum of all eigenvalues (total inertia) was used to measure the proportion of explained variation (Borcard et al. 1992). For the partial CCA, in which the pond type was the only explanatory variable and the other three variables were covariables, the scores were listed along the first canonical axis for species with the highest fit in the analysis. The resulting species order reflected the vegetation change along the gradient of the explanatory variable, after partialling out the effects of the other variables.

Results

Table 2 and Fig. 2 show the differences in characteristics of vegetation colonizing the exposed pond bottoms of fish and storage ponds. The mean numbers of all species, bryophytes, archeophytes and neophytes and beta diversity, measured by Sørensen index of dissimilarity, were significantly higher for storage than fishponds. However, the differ-

Table 2. – Comparison of Ellenberg indicator values and important characteristics of the vegetation of fish and storage ponds. Results of one-way ANOVA are shown.

Characteristics	Fish ponds			Storage ponds			F	p
	Mean	Min	Max	Mean	Min	Max		
Number of species:								
Total	16.51	5	29	20.86	7	37	23.43	p < 0.0001
Archaeophytes	1.13	0	4	2	0	7	24.56	p < 0.0001
Neophytes	0.44	0	2	1.2	0	4	39.98	p < 0.0001
Mosses	0.88	0	4	2.11	0	9	25.74	p < 0.0001
Beta-diversity:								
Sørensen index of dissimilarity	0.62	0.59	0.65	0.66	0.62	0.68	486.83	p < 0.0001
Plant cover (%):								
Total	73.08	15	100	72.68	1	100	0.01	n.s.
Herb layer	67.17	10	100	65.06	1	100	0.35	n.s.
Moss layer	5.18	0	70	14.64	0	90	15.98	p < 0.0001
Algae	9.29	0	60	9.78	0	90	0.04	n.s.
Ellenberg indicator values:								
Light	7.47	7	7.9	7.28	6.8	7.7	43.50	p < 0.0001
Temperature	6	5.6	6.4	5.98	5.6	6.3	0.80	n.s.
Continentality	4.37	3.3	5.1	3.94	3.3	4.5	110.51	p < 0.0001
Moisture	8.27	6.9	9.3	7.72	6.2	9.4	49.73	p < 0.0001
pH	5.84	4.5	7.3	5.81	4.3	6.8	0.15	n.s.
Nutrients	6.26	4.6	7.5	6.1	4.8	7.7	4.17	p < 0.05

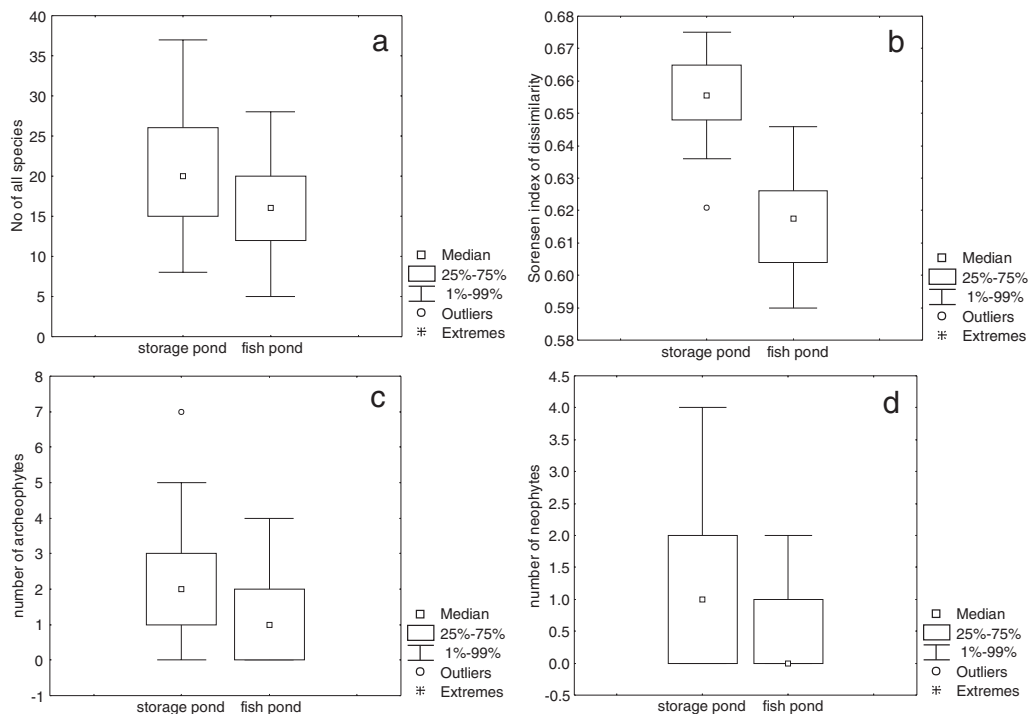


Fig. 2. – Box-and-whisker plots of the values: (a) number of species; (b) Sørensen index of dissimilarity; (c) number of archaeophytes; (d) number of neophytes.

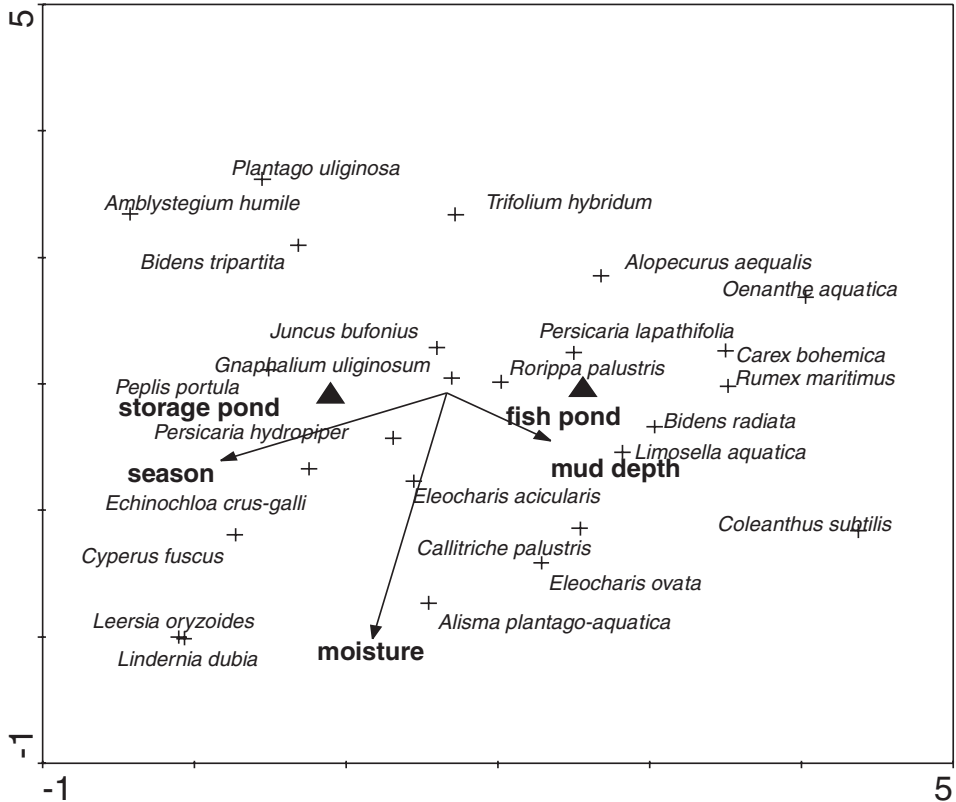


Fig. 3. – Detrended correspondence analysis (DCA) diagram of species with passively projected explanatory variables for the vegetation growing on the exposed bottoms of fish and storage ponds. Only species with high weight in the analysis are shown.

ences in mean cover values for the two pond types were not significant. Only the cover of the moss layer was significantly higher in storage ponds. As for the ecological features of significant species, expressed as Ellenberg indicator values, differences in some characteristics were found. Mean Ellenberg indicator values for light, continentality, moisture and nutrients were significantly higher for fishponds than storage ponds. The differences in Ellenberg indicator values for temperature and pH were not significant.

Detrended correspondence analysis (Figs 3, 4) shows the importance of sampling time, moisture, mud depth and pond type for the species composition. The most important differences were related to pond type. Species occurring mostly in fishponds, for example, were *Carex bohemica*, *Oenanthe aquatica* and *Rumex maritimus* and storage ponds, *Cyperus fuscus*, *Echinochloa crus-galli* and *Peplis portula*.

Gradients associated with season, moisture and mud depth are less important. *Alisma plantago-aquatica*, *Eleocharis acicularis* and *Persicaria hydropiper* are closely associated with very wet muddy substrates independent of type of pond. On the opposite side of the

diagram *Gnaphalium uliginosum*, *Juncus bufonius* and *Trifolium hybridum* form a group of species growing on drier sands or sands covered with a thin layer of mud.

Seasonal changes are closely related to pond type. The vegetation of fishponds, especially nursery ponds, reached its maximum development earlier than that of storage ponds exposed at the same time. In addition, most fishponds were flooded in early summer and storage ponds in early autumn.

The amount of variation in species data explained by net effects of particular variables, as detected by partial CCAs (Table 3), was highest for pond type, followed by season, moisture and mud depth. The explained variation attributable to the shared net effects of these three variables was negligible. All variables together explained 4.4% of the total variation in species data. In spite of the low percentage of explained variation, the effects of each of these variables on species composition were highly significant. Variation in species composition between fishponds and storage ponds, after partialling out effects of other variables, is presented in Table 4, which shows that vegetation of fish ponds is characterized by the species *Carex bohemica*, *Oenanthe aquatica*, *Phalaris arundinacea*, *Rumex maritimus* etc. and of storage ponds, for example, by *Amblystegium humile*, *Bryum argenteum*, *Eleocharis palustris* agg. and *Persicaria minor*.

Discussion

Although fish and storage ponds are similar habitats, the vegetation that colonizes their exposed bottoms differs significantly in several features. The variability in vegetation is more related to pond type than to any other factor. Although the variability explained by pond type was low, it was considerably higher than that explained by the other variables.

Table 3. – Percentage of the variation in species present explained by particular environmental variables. Gross effects include the total variation explained by particular variables. Net effects include variation explained by particular variables except for that shared with other variables. F-values of the permutation tests of first canonical axes are shown for partial CCAs, which were used to determine the net effects. The full model was performed for testing the effect of pond type; season, moisture and mud depth were permuted independently of pond type effect.

	Gross effects (%)	Net effects (%)	F-value of permutation test
Pond type	4.35	3.85	8.052***
Season	1.56	1.06	2.216***
Moisture	1.35	1.23	2.563***
Mud depth	1.11	0.94	1.973***
Shared effect of:			
pond type and season		0.55	
pond type and moisture		0.26	
pond type and mud depth		0.35	
season and moisture		0.15	
season and mud depth		0.27	
moisture and mud depth		0.12	
All explanatory variables	4.37	4.37	

Table 4. – Species with the highest association with pond type. The measure of the effect of pond type on the occurrence of each species is given by fit values. Scores indicate an association with storage (negative values) or fishponds (positive values). The species are arranged according to decreasing score value. Only species with the highest fit are shown.

Species	Axis 1 score	Fit
<i>Phalaris arundinacea</i>	1.16	0.10
<i>Oenanthe aquatica</i>	1.01	0.24
<i>Rumex maritimus</i>	0.80	0.37
<i>Carex bohemica</i>	0.79	0.25
<i>Ranunculus sceleratus</i>	0.68	0.12
<i>Limosella aquatica</i>	0.67	0.11
<i>Alopecurus aequalis</i>	0.47	0.13
<i>Persicaria lapathifolia</i>	0.35	0.09
<i>Echinochloa crus-galli</i>	–0.54	0.19
<i>Peplis portula</i>	–0.61	0.11
<i>Plantago uliginosa</i>	–0.64	0.15
<i>Cyperus fuscus</i>	–0.67	0.18
<i>Bidens tripartita</i>	–0.67	0.09
<i>Lindernia dubia</i>	–0.77	0.09
<i>Leersia oryzoides</i>	–0.79	0.13
<i>Sagina procumbens</i>	–0.79	0.10
<i>Bryum argenteum</i>	–0.81	0.12
<i>Persicaria minor</i>	–0.91	0.10
<i>Amblystegium humile</i>	–1.01	0.18
<i>Eleocharis palustris</i> agg.	–1.07	0.10

Because storage and fishponds are defined by the way they are managed, a knowledge of the management practices is crucial for understanding the reason for this variation in vegetation. However, it is not possible to quantify the intensity of individual practices involved in fishpond management. This is especially so for storage ponds, where the variability is high as the different management practices are used irregularly. There is often evidence of the effect of using herbicides, grazing, liming etc. For fish farms, it is possible to obtain detailed information on fish and storage pond management, but they do not keep records of when or the amount of herbicide or lime applied to individual storage ponds. Therefore, in this study “pond type” was used as a variable, with two categories, fish and storage pond. It is assumed that the influence of management practices on vegetation is included in each of these categories.

The more diverse management of storage ponds accounts for the higher variability of vegetation growing on their exposed pond bottoms compared to fishponds. It is reflected in a higher number of plant species, alien species and beta-diversity.

Mechanical disturbance and diversity

In many habitats, experiencing regular mechanical disturbances, periods of colonization by perennial species alternate with those of re-establishment of annuals, resulting in a mosaic of various vegetation types and high species richness (Hobbs & Huenneke 1992). On the other hand, an extensive single disturbance, e.g. removal of stands of reed, or flooding, eliminates perennial herbs. Annual vegetation generally regenerates from the soil seed

bank (Baldwin & Mendelssohn 1998, Bernhardt 1999, Poschlod et al. 1999) and is usually species-poor and structurally simple (Hejný & Husák 1978). In our study both these types of management are represented. The management of most storage ponds is of the first type, and fishponds and those storage ponds drained for a short time the second. The intensity of mechanical disturbance of the vegetation and soil surface (mowing, use of herbicides, grazing, filling up of the depressions, activity of fish stock, etc.), and the periodicity of flooding and exposure, are the most evident differences in the management of storage and fishponds.

The management of storage ponds often differs among fish farms. The period of exposure of the bottoms of storage ponds recorded in this study ranged from 2 to 10 months. This can result in the stabilization of both annual and perennial plant communities within one storage pond system (Šumberová et al. 2005).

Dependent on substrate type, microtopography of the bottom and management, the perennials growing on the bottoms of storage ponds exposed for long periods either occur in a mosaic with annual vegetation or form dense swards, which limits the survival of annuals. In our study, the vegetation in storage ponds with uneven bottoms and frequent depressions, and of various substrates was mown and/or sprayed with herbicide 1–2 times a year. This vegetation often includes annual weeds and ruderal species, e.g. *Chenopodium album* s.l. and *Lamium purpureum*, and seedlings of non-wetland perennials and phanerophytes, e.g. *Lactuca serriola* and *Salix* spp. The vegetation of storage ponds with flat, usually loamy bottoms without depressions is regularly mown and includes species of wet meadows, e.g. *Leontodon autumnalis*, *Symphytum officinale* and *Trifolium hybridum*.

The periodicity of flooding and draining of fishponds does not differ markedly among fish farms. All fish farms have nursery and main fishponds; the fishponds within each category are managed in the same way. Nursery fishponds are usually dried in summer every 1–2 years for 2–3 months. The main fishponds are dried at longer intervals than the nursery ponds, often for a whole growing season. Therefore the species richness of the vegetation that develops in nursery fishponds is very low and includes mainly species with extremely short life cycles, e.g. *Coleanthus subtilis*, or species with the ability to mature in shallow water, e.g. *Callitriche palustris*. In the main fishponds annual species with longer life cycles, e.g. *Carex bohemica* or *Eleocharis ovata* also frequently occur. Similarly, the bryophytes are also sensitive to the periodicity of flooding and exposure. In storage ponds, there was a significantly higher species richness and cover of the moss layer (Table 2). Horáková et al. (2005) refer to the differences in species spectrum and life forms of bryophytes in both types of ponds.

Other aspects of management and their influence on vegetation

The mechanical disturbance and periodicity of flooding and exposure mostly influence the abundance of particular species, but can not explain the presence or absence of certain species. There are other aspects of management that influence the vegetation, for example manuring. Our analysis shows that species with a high mean Ellenberg indicator value for nutrients occur more in fish than storage ponds. Application of organic manure to fishponds is widely practised. Manure is not added to storage ponds. Thus it is likely that the nutrient content of storage ponds is lower, which enables species considered to be sensitive to nutrients, especially nitrogen, to survive. These species, now occurring only in storage ponds in

this region, include e.g. *Pycreus flavescens* and *Tillaea aquatica* (Čeřovský et al. 1999). In fishponds, the nutrients content of the mud is probably high, which is suitable for species such as *Chenopodium ficifolium*, *C. rubrum*, *Ranunculus sceleratus*, *Rumex maritimus* and accounts for their frequent occurrence on exposed bottoms.

Another common management practice is the feeding of fish stock with cereals, but not in storage ponds. This feed contains weed seeds (Hejný et al. 2000) and could be the source of alien species, especially archaeophytes (Lososová 2004, Chytrý et al. 2005). However, significantly more species of archaeophytes and neophytes were found in storage ponds. Of the typical archaeophytes found in cereal crops only *Apera spica-venti* was represented. Most archaeophytes were either ruderal species (e.g. *Cirsium arvense*, *Lactuca serriola*, *Medicago lupulina*, *Polygonum aviculare*, *Tanacetum vulgare*) or weeds in root crops (e.g. *Chenopodium polyspermum*, *Echinochloa crus-galli*, *Setaria pumila*, *Sonchus asper*, *Tripleurospermum inodorum*). Some of these species, e.g. *Echinochloa crus-galli*, prefer moist substrates and colonize the exposed bottoms of both pond types. They form persistent seed banks (Thompson et al. 1997), probably also in temporarily flooded wetlands. Other archaeophytes, e.g. *Erysimum diffusum*, *Geranium pusillum*, *Lactuca serriola* and *Polygonum aviculare* grow in the walls of the storage ponds and only occur as casuals on exposed bottoms. Neophytes, like the archaeophytes, are weeds of root crops (e.g. *Galinsoga ciliata*); some are ruderal species of drier habitats, growing mainly on storage pond walls (e.g. *Conyza canadensis*). Three neophytes, *Bidens frondosa*, *Epilobium ciliatum* and *Lindernia dubia* are North American species typical of periodically drained substrates (pond margins, ditches and canals, river banks, etc.). The first two species are widely distributed in fish and storage ponds in the Czech Republic. *Lindernia dubia* currently occurs at a few localities in the Czech Republic but has not yet been found in fishponds (Kurka 1990, Šumberová et al. 2005).

Nowadays, the transport of living fish throughout Europe is common and can contribute to the spread of wetland species over long distances. However, this was also the case in the past (Andreska 1997). Transport of diaspores with fish can partly explain the variability in species composition of different pond types or individual ponds of one type. Some studies consider ichthyochory as an important plant dispersal mechanism (Smits et al. 1989, Vilella et al. 2002, Chick et al. 2003). It is likely that diaspores of plant species are transported both with the fish (epi- and endoichthyochory) and tools used in fishpond management. The fishponds were the most probable source of diaspores for storage ponds before the establishment of seed banks in the bottoms of storage ponds. Nowadays, storage ponds are refuges for some species, which occurred in nearby fishponds in the past (Šumberová 2003). For example, in the first half of the 20th century, *Lindernia procumbens* and *Tillaea aquatica* were recorded in several fishponds in the Českokobudějovická pánev basin (Jílek 1936, 1956). From these fishponds the fish were transported to storage ponds at Hluboká. Currently, these species are not recorded in the fishponds of the region but occur abundantly in storage ponds.

Lime is added to both types of ponds. In fishponds, it serves to stabilize the pH of the water and increase nutrient mineralization of the sediment. The amount of lime added to fishponds probably does not change the pH much, as acidophilous species occur there, e.g. *Carex bohemica*, *Coleanthus subtilis*, *Elatine hydropiper* and *E. triandra* (Hejný 1960, 1969, Müller-Stoll & Pietsch 1985, Prach et al. 1987, Lampe 1996, Täuber 2000). These species were rarely recorded in storage ponds and *Coleanthus subtilis* not at all. In the stor-

age ponds, liming is used to prevent disease and parasites. In these ponds there are basiphilous and calciphilous species (e.g. *Centaurium pulchellum*, *Cyperus fuscus*, *C. ichelianus*; Hejný 1960, Müller-Stoll & Pietsch 1985, Täuber 2000), which were very rare or absent in fishponds. However, some species considered to be acidophilous, e.g. *Isolepis setacea*, *Peplis portula* and *Tillaea aquatica*, also grow in storage ponds (Lampe 1996). This is probably why the Ellenberg indicator value for pH was not significantly different in fish and storage ponds. The spatial variability in the substrate chemistry of the bottoms of ponds, or even at different depths in the substrate at one site (Filípková 2001), probably enables species with different demands on pH and nutrients to co-exist.

Mud is regularly removed from the bottoms of both types of ponds. In deep mud, anoxic conditions develop where pathogens and parasites survive. However, the acceptable depth of mud differs in the two types of pond. In general, the bottom of a storage pond should be sandy or loamy, without organic mud. In fishponds a layer up to 30 cm (so called “active mud” and “lower mud”; Čítek et al. 1998) is useful, because of its nutrient content. In practice, the mud in both pond types is usually deeper than the optimum due to the great expense connected with mud removal; this was confirmed during our study. Sandy substrates and mud of various depths were represented in both pond types included in our data set (see Table 1). Therefore, species of muddy substrates, including the hydrophytes *Alisma plantago-aquatica*, *Butomus umbellatus* etc., also occurred in storage ponds. Nevertheless, in fishponds the conditions for hydrophytes were more suitable. In storage ponds, the spectrum of aquatic plant species in the flooded phase is restricted by the high number of fish. In fishponds, terrestrial forms of floating macrophytes, surviving from the flooded phase, are quite common. This is consistent with a significantly lower mean Ellenberg indicator value for moisture in storage ponds.

Temperature and light conditions in ponds

Although the bottoms of both pond types are exposed to light, the storage ponds can be more shadowed by their walls and surrounding vegetation due to their small size. The Ellenberg indicator value for light is significantly lower for storage ponds. This is due to the juveniles of trees (e.g. *Alnus glutinosa*, *Salix* spp.), forest herbs (e.g. *Scrophularia nodosa*) or forested wetland species (e.g. *Lysimachia vulgaris*) growing in storage ponds. Ellenberg indicator values for temperature did not significantly differ between fish and storage ponds. However, a higher mean Ellenberg indicator value for temperature of storage ponds was expected, because species considered as thermophilous occur there, e.g., *Cyperus flavescens*, *C. michelianus*, *Lindernia procumbens* and *Pulicaria vulgaris* (Hejný 1960, Ellenberg et al. 1992, Lampe 1996). These species were absent from fishponds in this study. They are more frequent in warmer regions, for example in SE Europe, Central and SE Asia etc. (Lampe 1996). In the past, they also occurred at a low frequency in S Bohemian fishponds (Ambrož 1939, Hejný 1969). It is likely these species occur in storage ponds because of their specific temperature regime. The area of storage ponds is small and more prevented from circulating air; therefore higher summer temperatures can be expected. In winter, the exposed bottoms of storage ponds are probably better protected from frost, due to the permanent flow of water in the central stream. This allows the vegetative growth of some perennial or facultative annual wetland species, e.g., *Eleocharis acicularis*, *Juncus articulatus*, *Leersia oryzoides* and *Peplis portula*, to survive over winter.

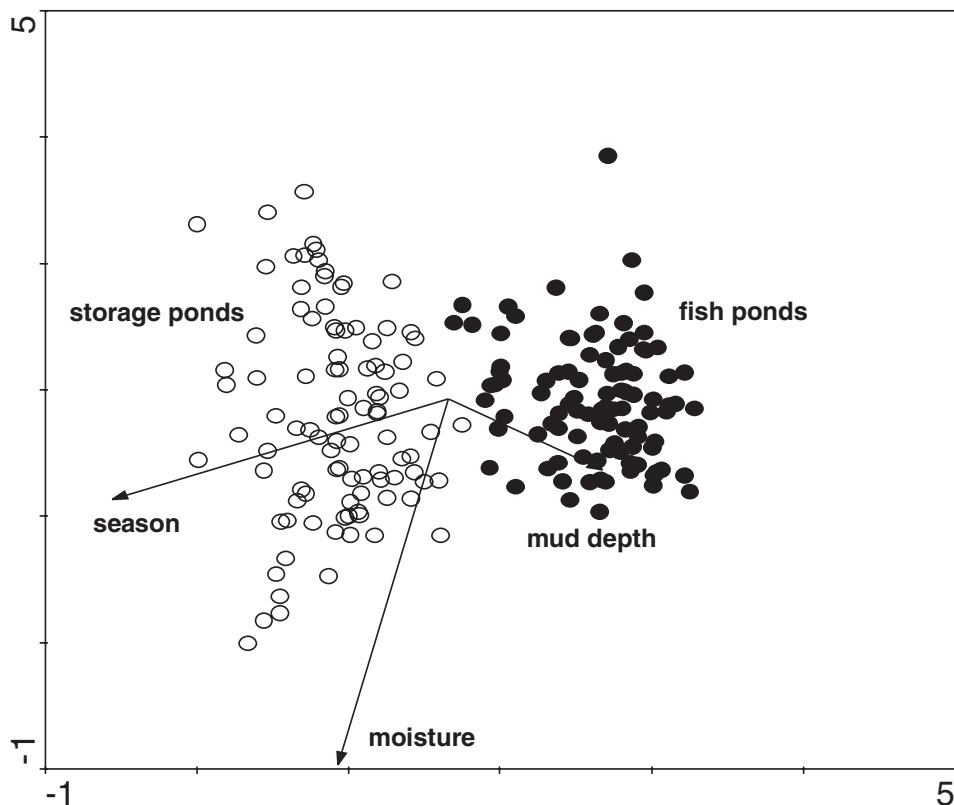


Fig. 4. – Detrended correspondence analysis (DCA) diagram of plots with passively projected explanatory variables for vegetation growing on the exposed bottoms of fish and storage ponds.

These species have an Atlantic or Subatlantic distribution. The species with an Atlantic affinity also include species of wet disturbed grasslands (e.g. *Alopecurus geniculatus*, *Glechoma hederacea* and *Potentilla reptans*) and species of nutrient-poor wet sands (e.g. *Isolepis setacea* and *Tillaea aquatica*) (Meusel et al. 1965, Lampe 1996). All these species groups were represented, mainly in storage ponds. This accounts for the lower Ellenberg indicator value for continentality.

“Fishpond species” and “storage pond species” – interpretation of pCCA

The division of species by pCCA into “storage pond species” and “fishpond species” (Table 4) reflects our field experience. It is also supported by the DCA (Fig. 3). However, this analysis does not take rare species into account. The fit value, i.e. the effect of habitat on the occurrence of individual species, is influenced by the number of occurrences of these species in the data set. The species that occurred rarely in one pond type show low fit values, as do species without relation to the pond type. Rare “storage pond species” include e.g. *Centaurium pulchellum*, *Cyperus flavescens*, *Gypsophila muralis*, *Lindernia procum-*

bens and *Tillaea aquatica*. These species were not found in fishponds in this study. *Chenopodium rubrum*, *Coleanthus subtilis*, *Elatine triandra* and *Spergularia echinospema* occurred, with sporadic exceptions, only in fishponds, but their frequency was low. The high affinity of *Coleanthus subtilis* for fishponds is illustrated in Fig. 3.

Do these results apply to other regions?

This study describes the situation in one region, the Českokobudějovická pánev basin. It is likely that similar results would be obtained for regions with similar environmental conditions (see Hroudová 1981, Prach et al. 1987, Šumberová 2003).

However, our study indicates that similar analyses could give different results for vegetation in warmer regions with calcareous substrates. Warm and dry summers together with a higher pH and calcium content of the substrate are probably the main limiting factors for some species, e.g. *Carex bohemica*, *Coleanthus subtilis*, *Elatine triandra*, *E. hydropiper* and *Eleocharis ovata*. The sporadic occurrence of these species in warmer regions is restricted to fishponds. On the other hand *Bidens tripartita*, *Cyperus fuscus* and *Plantago uliginosa* occur with approximately the same frequency on the exposed bottoms of fish and storage ponds of these regions. However, the effect of climatic and edaphic factors is modified by management.

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Souhrn

Studie srovnává druhové složení, strukturu a ekologické vlastnosti vegetace na obnažených dnech sádek a rybníků v Českokobudějovické pánvi. Sádky a rybníky představují podobná stanoviště, která se liší svým využitím a obhospodařováním. Analyzovaly jsme 99 fytoocenologických snímků z rybníků a 99 snímků ze sádek z let 2000–2004. Snímky jsme podrobily analýze příjmu a nepřímou ordinací a statistickému hodnocení metodou ANOVA. Nejvýznamnější ekologický gradient byl korelovan s rozdíly mezi sádkami a rybníky. Sezónní změny vegetace, vlhkost substrátu a hloubka bahna byly méně významné. Druhové složení a ekologické vlastnosti vegetace v sádkách a rybnících se významně liší. V sádkách byl detekován vyšší průměrný počet všech rostlinných druhů, mechorestů, archeofytů a neofytů a vyšší beta diverzita, vyjádřená jako Sørensenův index nepodobnosti. V hodnotách pokryvnosti byl zjištěn rozdíl pouze u mechového patra, které mělo signifikantně větší pokryvnost v sádkách. Při srovnání průměrných Ellenbergových indikačních hodnot jsme zjistily signifikantně vyšší hodnoty pro světlo, kontinentalitu, vlhkost a živiny pro rybníky. Ve výsledcích práce uvádíme druhy, které mají nejvýrazněji vyvinutou vazbu na jeden ze dvou typů zkoumaných stanovišť. Například druhy *Oenanthe aquatica* a *Rumex maritimus* byly zařazeny mezi typické druhy obnažených den rybníků, zatímco *Amblystegium humile* a *Eleocharis palustris* mezi druhy sádek. Obhospodařování sádek zahrnuje, ve srovnání s rybníky, více různých hospodářských zásahů o různé intenzitě. Domníváme se, že tato variabilita v obhospodařování je klíčovým faktorem, který určuje druhovou bohatost podobných stanovišť.

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Appendix 1. – The list of storage ponds and fishponds studied. H – use of herbicides; L – regular liming, G – regular grazing; MP – main pond; NP – nursery pond (NP). Sites are grouped according to sub-regions, the numbers correspond to those in Fig. 1.

Storage ponds: S1. Ťejetice storage ponds: Ťejetice, southwest margin of the village, between the railway and the Trnov fishpond; H (only on storage pond walls), L. – S2. Kestřany storage ponds: Kestřany, north part of the village, on the grounds of the castle; L, G. – S3. Storage ponds of the Research Institute of Fishery and Hydrobiology: Vodňany, northwest margin of the town, 1.6 km SW of the railway station. – S4. Storage ponds of the town of Vodňany: N part of the town, 0.6 km SW of the railway station; L. – S5. Hluboká storage ponds: Hluboká nad Vltavou, S part of the town; H, L.

Fishponds: **Strakonice sub-region** – F1. Pracejovický fishpond: Pracejovice, 0.5 km SW of the railway station; NP. – F2. Škaredý fishpond: Sudomeř, 1 km SE of the railway station; MP. **Protivín and Vodňany sub-region:** F3. Vítovský fishpond: Budyně, 0.4 km SSE of the village; NP. – F4. Blaňov fishpond: Bavorov, 1.8 km SSE of the railway station; NP. – F5. Skalský fishpond: Protivín, 2.1 km NW of the railway station; alternately NP and MP. – F6. Švarcemburský fishpond: Protivín, 2.7 km ESE of the railway station; NP. – F7. Kuchyňka fishpond: Ťerněves, 0.3 km N of the village; NP. – F8. Ťerněveský fishpond: Ťerněves, 1 km SE of the village; MP. – F9. Bukový fishpond: Újezd, 2 km ESE of the village; MP. – F10. Velký Ťernoháj fishpond: Strpí, 1 km SW of the village; MP. – F11. Radomilický fishpond: Radomilice, SW margin of the village; MP. – F12. Jezero fishpond: Radomilice, 1.3 km S of the railway station; MP. – F13. Novosedelský Dolní fishpond: Novosedly near Dívčice, on the S margin of the village, E of the road; NP. – F14. Rábinec fishpond: Holečkov (near Netolice), 0.5 km S of the railway station, W of the railway; NP. – F15. Novorábinec fishpond: Holečkov (near Netolice), 0.4 km S of the railway station, E of the railway; NP. – **Hluboká and Ťeské Budějovice sub-region:** F16. Knížecí fishpond: Pištín, 1 km WNW of the village; MP. – F17. Velký Pištínský fishpond: Pištín, 1.4 km SE of the village; NP. – F18. Bezdrev fishpond: Hluboká nad Vltavou, 3 km SW of church in the town, at more locations; MP. – F19. Šnekl fishpond: Hluboká nad Vltavou, 4.8 km NW of the church in the town; NP. – F20. Pěnský fishpond: Hluboká nad Vltavou, 2.5 km NW of the church in the town; NP. – F21. Podhradský fishpond: Hluboká nad Vltavou, S margin of the town, opposite the storage pond system; NP. – F22. Ťakovec Starý fishpond: Ťakovec, 0.6 km NE of the village; NP. – F23. Bojiště fishpond: Ťakovec, 0.5 km SE of the village; NP. – F24. Kvítkovický fishpond: Kvítkovice, 0.7 km NE of the village; MP. – F25. Panin fishpond: Lipí, 0.6 km WNW of the village; NP. – F26. Malý Machovec fishpond: Ťejkovice, 1.6 km SW of the village; NP. – F27. Vitín fishpond: Křenovice, 1.3 km ESE of the village; NP. – F28. Štičí fishpond: Haklovy Dvory, 1.3 km WSW of the village; NP. – F29. Městský fishpond: Třebín, next to the road junction in the NE part of the village; NP. – F30. Závratký fishpond: Závraty, 0.4 km N of the village; NP. – F31. Šindlovský fishpond: Šindlovy Dvory, on the S margin of the village; MP.