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 vegetation of two pond types with different management, fishponds and storage ponds, in the Českobudějovická basin (South Bohemia) were compared. A selection of 99 relevés from fishponds and 99 relevés from storage ponds (small ponds used for the storage of marketable fish) from 2000–2004 was analysed with direct and indirect ordination, analysis of beta diversity and ANOVA statistics. The difference between storage ponds and fishponds was found to be more important than gradients correlated with temporal changes, soil moisture and mud depth. A significantly higher mean number of all species, number of bryophytes, archaeophytes and neophytes and beta-diversity was found in storage ponds. There were no significant differences in cover values, except for the moss layer which had significantly higher cover in storage ponds. Mean Ellenberg indicator values for light, continentality, moisture and nutrients were significantly higher in fishponds. For instance, *Oenanthe aquatica* and *Rumex maritimus* were determined as typical fishpond species and *Amblystegium humile* and *Eleocharis palustris* agg. as typical storage pond species. Because the pond type is defined by specific management, the management practices should be considered as the most important factor influencing the vegetation of the ponds. The management of storage ponds includes, in comparison to fishponds, more varied practices of different intensity. We assume that this management variability is a crucial factor which determines the species richness of these two similar habitat types.

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

Introduction

The vegetation of exposed pond bottoms can colonize various periodically flooded or waterlogged habitats with eliminated succession of competitively strong perennial herbs. The variability of habitat types is given by both environmental conditions and management. This habitat variability modifies vegetation structure and species composition, even within one and the same plant community. Large differences can be expected in vegetation of habitat types which are very distant in their physiognomy, environmental conditions and management, e.g. river alluvial deposits and fishponds. However, there are also habitats which seem to be similar, e.g. various types of ponds. Not infrequently, they are confused in their function in the landscape by biologists and nature conservationists. This can lead to misconceptions about biota and appropriate management of such habitats.

We tested the differences in species composition and vegetation characteristics of two similar pond types – fishponds and storage ponds. Both pond types are essential for fish farming, which has been developing in Central Europe since the 11th century (Andreska 1997), but they are used for different purposes. Therefore the management of fishponds and storage ponds is different. An old management practice, summer drainage of the pond, enables vegetation of pond bottoms to develop. This practice is employed in both pond types, but to a different extent.

The fishponds serve for fish breeding, especially for breeding the common carp (Čítek et al. 1998). The regime of flooding and exposure is rather regular. The phase of flooding is long, in comparison to the phase of exposure. The management further includes organic manuring, feeding the fish stock, occasionally liming etc. Fishponds are one of the most frequent habitats of annual hygrophilous vegetation in Central Europe. Their flora and vegetation were often documented in the past (e.g. Domin 1904, Klika 1935, Ambrož 1939, Pietsch 1963, Pietsch & Müller-Stoll 1968, Philippi 1968, Vicherek 1972). Recently, more studies dealing with the biological and ecological aspects of this vegetation type have been done (e.g. Müller-Stoll & Pietsch 1985, Lampe 1996, Pietsch 1999, Poschlod et al. 1999, Täuber 2000).

The storage ponds serve especially for storage of marketable fish (Čítek et al. 1998). Some irregularities in the regime of flooding and exposure are quite common. The phase of flooding is often shorter than the phase of exposure. Management of storage ponds is more diverse than 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, we studied localities of exposed pond bottoms throughout the Czech Republic. We have observed the differences in species composition of fishponds and storage ponds depending on different human impact (Šumberová 2003, Šumberová et al. 2005). For detailed comparison of both habitat types we have chosen the Českobudějovická basin (South Bohemia).

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

Material and methods

Environmental conditions in the study area

The Českobudějovická basin is situated in the central part of South Bohemia, SW Czech Republic. Its total area is 640 km^2 (Demek et al. 1987). A major part of the basin is a flat upland which in the southeastern part merges into a plain and in the northwest into rugged hilly countryside. Mean elevation of the basin ranges from 370 to 440 m (Culek 1996). River alluvia (Demek et al. 1987) and numerous fishponds, made by a man mainly in the 15th–16th centuries, are important forms of relief.

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

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

Fishponds and storage ponds and their management

Two pond types with different management – fishponds and storage ponds – were investigated.

The fishpond is an artificial water body, primarily intended for breeding fish. In the Czech Republic, most fishponds are carp ponds, i.e. they serve for breeding of common carp with low-level addition of other fish species with a market value, e.g. pike, pike-perch, tench, white amur. All fishponds in our study were carp ponds.

Fishponds are divided into main ponds and nursery ponds according to the age of fish. The nursery ponds serve for breeding of the youngest fish stages (up to the age of 1 or 2 years). Then fish are stocked into main ponds where they grow to marketable size (usually at 3 or 4 years of age) (Čítek et al. 1998).

In fishponds, the following management practices are used: feeding the fish stock with cereals, use of organic manure (dung, compost, etc.), occasional liming, elimination of aquatic and littoral vegetation by mowing or using herbicides, winter and summer drying. Summer drying enables mineralization of nutrients in the pond mud and reduces fish parasites and water macrophytes. This old management practice was regularly used in the past but it was limited in the last decades for economic reasons. At present, mostly partial summer drying or reduced summer drying is used, i.e. drying of the fishpond margins or only during part of the growing season. Regular summer drying is practised in nursery ponds yearly or every second year from March/April to May/June, before the stocking of the fingerlings. Nowadays, summer drying is used on the main ponds irregularly, e.g. in cases of dam reconstruction, water deficiency or removal of excessive mud.

Storage ponds are usually small ponds of square or oblong form. The walls of the storage ponds are built from stones, concrete panels, poured concrete, or they are not stabilised, and then are covered with grass or clay. The storage ponds are interconnected to a storage pond system via canals. The storage ponds serve for short-term storage of marketable fish between the fishing out from the main ponds and transporting them to consumers (Čítek et al. 1998). The fishponds are fished out mostly in autumn or partly in early spring. Therefore the storage ponds are most frequently used from autumn to spring. Nearly all storage ponds remain without water from March or April at the latest.

Similarly to fishponds, the management of the storage ponds includes summer drying. The periodicity and duration of the summer drying is, however, different from fishponds. Most storage ponds are dried each year for 6–10 months so as to eliminate parasites and diseases. Liming of the bottom or spraying with lime milk on the walls is used for the same reason. Before the storage of fish, vegetation is mown and biomass is raked out. Rarely, the fish farms use grazing, mostly by sheep. The low vegetation on the storage pond bottom positively influences the health of the stored fish. Recently, some fish farms have been using herbicides (usually Roundup) to various extents, to retard or eliminate vegetation growth in the growing season. Use of herbicide 1–2 times per year can reduce the frequency of mowing from 4–6 to 1–2 times per year without a considerable negative influence on the population of most species. The fish farms included in out study use herbicide for the storage pond bottoms extensively (1–2 times per year) or they do not use it at all.

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

A total of 31 fishponds (10 main ponds and 21 nursery ponds) and 51 storage ponds of 5 storage pond systems were included in our study. Currently 6 economic subjects, including four private fish farms, one school fish farm and one fishery research institution, farm the fishponds and the storage ponds.

Sampling design
We compiled a data set of 204 relevés of vegetation of exposed pond bottoms in the Českobudějovická basin; 102 relevés from storage ponds and 102 relevés from fishponds, recorded by authors in 2000–2004. The area of most relevés was 1 m^2, in tall stands predominated by *Bidentetea* species mostly 4 m^2. Besides common relevé header data (i.e. sampling date, cover of individual layers, locality etc.), data about moisture and type of substrate were recorded for each relevé. In both pond types, the relevés were gathered in an optimal phase of vegetation development and from places with various 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 with deviating floristic composition were excluded from the data set for current analyses. The outliers were extremely species-poor relevés, which were closely related to the vegetation of shallow still waters. The final data set includes 198 relevés; 99 relevés from storage ponds and 99 relevés from fishponds (Fig. 1) were used for analysis.

Data analysis
These explanatory variables were compiled for each relevé: pond type, season, moisture and mud depth. The variable "pond type" includes two categories, the fish ponds and the storage ponds which are characterized by different intensity of management practices. The variable "season" was derived from the date of recording. 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 data were arranged in the following way: in the case of taxonomically problematic taxa or species difficult to identify in the juvenile stage, we used species aggregates or determination to the genus level. For details on *Achillea millefolium* agg., *Eleocharis palustris* agg., *Equisetum arvense*, *Myosotis palustris* agg., *Taraxacum* sect. *Ruderalia* and *Verbascum* sp. see Šumberová et al. (2005). Further species were grouped as follows: (1) all records of *Brachythecium*, *Bryum* (excl. *B. argenteum*), *Physcomitrium*, *Populus*, *Salix*, *Typha* and *Vicia* on the genus level; (2) all records of *Batrachium* as *Batrachium aquatile* agg.; (3) all records of species of *Chenopodium album* agg. (excl. *C. ficifolium*) on 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, we split the whole data set into two groups. One group contained relevés from fishponds and the second one 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 pattern of beta-diversity variation between storage ponds and fish ponds (the mean difference in species composition among relevés), we calculated it as the mean Sørensen index of dissimilarity for all pairs of relevés in each group (1 – S, where S is Sørensen similarity; Magurran 1988, Koleff et al. 2003). Then we determined confidence intervals for beta-diversity in each group, using 100 bootstrap samples (Efron & Tibshirani 1993) taken from the relevés belonging to that group. This procedure was done in the JUICE 6.3 program (Tichý 2002).

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

To assess the overall variation patterns in species composition we subjected the whole data set to detrended correspondence analysis (DCA) from 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 of the first axis (3.27 SD units), we used the ordination methods which are more suitable for unimodal models.

We performed a series of partial canonical correspondence analyses (pCCA; Lepš & Šmilauer 2003) to detect the effect of each explanatory variable on species composition of vegetation of 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. Significances of the first canonical axes were again tested. Permutation tests with 999 permutations were always used to test significances of first canonical axes. The full model was performed for testing the effect of the pond type, while the other three variables were permuted independently of pond type 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 a single explanatory variable and the other three variables were used as covariables, we listed scores 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 of exposed pond bottoms between 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 in the storage ponds than in the fishponds. However, the differences in mean cover values of 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 a part of the characteristics were found. Mean Ellenberg indicator values for light, continentality, moisture and nutrients were significantly higher in fishponds than in storage ponds. The differences in Ellenberg indicator values for temperature and pH were not significant.

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

Gradients given by season, moisture and mud depth are less important. *Alisma plantago-aquatica*, *Eleocharis acicularis* and *Persicaria hydropiper* show a clear relationship to muddy substrate with high moisture, and without preference to any type of pond. On the opposite side of the diagram *Gnaphalium uliginosum*, *Juncus bufonius* and *Trifolium hybridum* represent a group of species growing on drier sands or sands with a thin mud layer.

Seasonal changes are closely related to pond type. The vegetation of fishponds, especially of the nursery ponds, reached its optimal phase earlier than the vegetation of storage ponds exposed at the same time. Additionally, most fishponds were flooded in early summer. The storage ponds were exposed until early autumn. In the graphs (Figs 3, 4), the relevés from storage ponds are ordered in the direction of the later season while the relevés from fishponds in the opposite direction.

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 and followed by season, moisture and mud depth. The explained variation attributable to net shared effect of 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 the other ones, is presented in Table 4, which shows that vegetation of fish ponds is characterised by species *Carex bohemica, Oenanthe aquatica*, *Phalaris arundinacea*, *Rumex maritimus* etc. Characteristic species of storage ponds are for example: *Amblystegium humile*, *Bryum argenteum, Eleocharis palustris* agg. and *Persicaria minor*.

Discussion

Although the fishponds and the storage ponds are similar habitat types, vegetation of their exposed pond bottoms differs significantly in several features (Table 2). The results of pCCAs and DCA (Figs 3, 4; Table 3) show that the variability of vegetation in our study is more related to the variable pond type than to any other. Although the variability explained by this variable was low, it was considerably higher than the variability explained by the other variables. This result is consistent with our observations of vegetation of exposed pond bottoms.

Because the storage ponds and fishponds are defined by their management, we assume that the knowledge in management practices is crucial for explanation of vegetation variability. However, in common fishpond management it is not possible to quantify exactly the intensity of individual practices. Especially in the storage ponds, the variability of management is high and the different management practices are used irregularly. There is often evidence of using herbicides, grazing, liming etc. In the fish farms, it is also possible to obtain information about practices used in fishpond and storage pond management. Nevertheless, the fish farms do not keep records about timing of most management practices, the amount of herbicides or lime used for individual storage ponds etc. Therefore, in this study we decided to use "pond type" as a variable which has two categories, fishpond and storage pond. We suppose that in each of these categories the influence of management practices on vegetation is summarised.

The complex of management practices on storage ponds obviously leads to higher variability of vegetation of exposed pond bottoms than the management of fishponds. It is reflected in a higher number of plant species, alien species and beta-diversity.

Mechanical disturbance and diversity

In many habitats with regular mechanical disturbances, the succession of perennial species and re-establishment of annual-dominated stands occur permanently. It results in a mosaic of more vegetation types with high species richness (Hobbs & Huenneke 1992). The second type of management, including one-time extensive disturbance, e.g. reed stands removal, or long-term flooding of the substrate, eliminates perennial herbs. Annual vegetation generally regenerates from the soil seed bank (e.g. Baldwin & Mendelssohn 1998, Bernhardt 1999, Poschlod et al. 1999) and is usually species-poor and structurally simple. In our study both management types are represented. Most storage ponds could be included into the first type, all fishponds and storage ponds drained for a short time into the second one. The intensity of mechanical disturbances on 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 ponds and fishponds. In general, the variability of disturbances is higher in the storage ponds than in fishponds.

The management of storage ponds often differs among individual fish farms. The period of exposure of the storage pond bottoms in this study ranged between 2 and 10 months. Different types of flooding and exposure periodicity led to stabilisation of both annual and perennial plant communities within one storage pond system (Šumberová et al. 2005).

According to substrate type, microtopography of the bottom and management, the perennial stands in long-term exposed storage ponds occur in mosaic with annual vegetation or form dense swards with limited possibility for survival of annuals. The first type represents storage ponds with uneven bottoms with frequent depressions, formed by various types of substrate. The vegetation is mown or additionally 1–2 times a year sprayed with herbicide. There are frequent annual weed 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 second type involves storage ponds with flat, usually loamy bottoms without depressions. The vegetation is regularly mown. There is frequent occurrence of species of wet meadows, e.g. *Leontodon autumnalis*, *Symphytum officinale, Trifolium hybridum*.

In fishponds, the periodicity of flooding and exposure does not differ considerably among the individual fish farms. All fish farms possess nursery and main fishponds; the fishponds within these categories are managed in the same way. Nursery fishponds are usually dried in summer each 1–2 years for 2–3 months. The main fishponds are dried in longer intervals, but often for a whole growing season. Therefore the species richness of 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. However, during summer drying of any fishpond type can not establish stands of perennial herbs.

Similarly to vascular plants, the bryophytes also sensitively respond to the periodicity of flooding and exposure. In the storage ponds, significantly higher species richness and cover of a moss layer was detected (Table 2). Horáková et al. (2005) refers to the differences in species spectrum and life forms of bryophytes in both pond types.

Other aspects of management and their influence on vegetation

Although the mechanical disturbances and periodicity of flooding and exposure have a large impact on vegetation of exposed pond bottoms, in many cases they particularly influence the quantity of individual species in the stands. The absence or presence of a number of species can not be explained by type and intensity of mechanical disturbance alone.

Manuring

Our analysis shows that species with higher mean Ellenberg indicator values for nutrients are related rather to fishponds than to storage ponds. Usage of organic manure is a widely used practice in fishponds. Manuring is not used in storage ponds. We suggest that the nutrient content in storage ponds is lower, which enables the occurrence of species considered to be sensitive to nutrients, especially nitrogen. These species, occurring nowadays in the region only in storage ponds, include e.g. *Pycreus flavescens* and *Tillaea aquatica* (Čeřovský et al. 1999). In the fishponds, the amount of nutrients in substrate is probably higher, which is suitable for species such as *Chenopodium ficifolium*, *C. rubrum, Ranunculus sceleratus*, *Rumex maritimus* etc., frequently occurring on fishpond bottoms.

Feeding the fish stock and alien plant species

Another common management practice in fishponds is feeding the fish stock with cereals; it is not used in storage ponds. Because the cereals also contain weed seeds, feeding the fish can contribute to import of weeds into the vegetation of exposed pond bottoms (Hejný 2000). Therefore a higher number of alien species, especially of archaeophytes, in fishponds was expected.

However, the results presented in Table 2 and Fig. 2, show a significantly higher number of archaeophytes in storage ponds, similarly as in the case of neophytes. Exact analysis of the archaeophytes found that the group of cereal weeds was represented to a low degree in the whole data set. Only *Apera spica-venti* is considered to be a species typical of weed communities in cereal fields. An essential part of the group of archaeophytes was formed by ruderal species (e.g. *Cirsium arvense*, *Lactuca serriola*, *Medicago lupulina*, *Polygonum aviculare*, *Tanacetum vulgare*) or species that frequently occur as weeds in root crops and also in ruderal vegetation (e.g. *Chenopodium polyspermum*, *Echinochloa crus-galli*, *Setaria pumila*, *Sonchus asper*, *Tripleurospermum inodorum*). Some of these species, e.g. *Echinochloa crus-galli*, have an affinity to moist substrate and grow on both pond types. They can form a persistent seed bank (Thompson et al. 1997), probably also in temporally flooded wetlands. Therefore their abundance in these habitats is often high. Other species of the archaeophyte group, e.g. *Erysimum diffusum, Geranium pusillum, Lactuca serriola* and *Polygonum aviculare*, are transported into storage ponds from the vegetation of storage pond walls. These species are casual in vegetation of annual hygrophilous herbs.

Neophytes are represented by similar ecological groups as archaeophytes. There were weeds of root crops (e.g. *Galinsoga ciliata*) and species 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 exposed substrates (pond margins, ditches and canals, river banks, etc.). The first two species are widely distributed throughout fishponds and storage ponds in the Czech Republic. *Lindernia dubia* currently has a few localities in the Czech Republic, but it has not yet been found in fishponds (Kurka 1990, Šumberová et al. 2005).

Transportation of the fish

Nowadays, the transportation of living fish throughout Europe is common and can contribute to the spread of wetland species over long distances. However, there was transportation of fish and thereby a possibility of seed dispersal also in the past (Andreska 1997). Transportation of diaspores with the fish can partly explain the variability in species composition of different pond types or individual ponds of one type. There are some studies considering ichthyochory as an important plant dispersal mechanism (e.g. Smits et al. 1989, Paula et al.1995, Vilella et al. 2002, Chick et al. 2003, Piedade et al. 2003), but plant species of exposed pond bottoms were not yet studied from this point of view. We assume the possibility of transportation both directly with the fish (epi- and endoichthyochory) and with the tools used in fishpond management.

The fishponds were the most probable source of diaspores for storage ponds before establishment of seed bank in storage pond bottoms. Nowadays, the storage ponds function as refuges of some species which occurred in the nearby fishponds in the past (Šumberová 2003). For example, in the first half of the 20th century, *Lindernia procumbens* and *Tillaea aquatica* were documented in several fishponds in the Českobudějovická basin (Jílek 1936, 1956). From these fishponds the marketable fish were transported to the storage ponds in Hluboká. Currently, the species have not been documented in the fishponds of the regions but they persist in rich populations in storage ponds.

Liming

Liming is used in both pond types. In fishponds, it should contribute especially to the stabilisation of pH in water and faster nutrient mineralization in sediment. The amount of lime used in fishponds probably does not change the pH considerably, as shown by the occurrence of plant species which are considered to be acidophilous, e.g. *Carex bohemica, Coleanthus subtilis*, *Elatine hydropiper* and *E. triandra* (Hejný 1960, 1969, Müller-Stoll & Pietsch 1985, Lampe 1996, Täuber 2000). We recorded these species rarely in storage ponds. *Coleanthus subtilis* did not occur there at all. In the storage ponds, liming is used as prevention of diseases and parasites. There was occurrence of species considered as basiphilous and calciphilous (e.g. *Centaurium pulchellum, Cyperus fuscus, C. michelianus*; Hejný 1960, Müller-Stoll & Pietsch 1985, Täuber 2000), which were very rare or absent in fishponds. However, in the storage ponds the species indicated as acidophilus, e.g. *Isolepis setacea, Peplis portula* and *Tillaea aquatica*, also grew (Lampe 1996). This is probably one of the reasons why significant differences were not detected in the Ellenberg indicator value for pH between the fishponds and the storage ponds. The variability in substrate chemism on different sites of the bottom within one pond, or even in different depth of substrate in one site (Filípková 2001), probably enables co-existence of species with different demands on pH and nutrients.

Removal of excessive mud

An excessive mud layer is regularly removed from both pond types. In deep mud, there are anoxic conditions where pathogens and parasites survive. These conditions are undesirable in ponds for fish farming. However, the acceptable depth of mud differs between the two types of ponds.

In general, the bottom of a storage pond should be sandy or loamy, without organic mud. In fishponds a mud layer of up to 30 cm (so called "active mud" and "lower mud"; Čítek et al. 1998) is useful, because of the nutrient content. In praxis, the mud in both pond types is usually deeper than desirable due to high expenses connected with mud removal; this fact could be 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 the species of muddy substrates, incl. hydrophytes *Alisma plantago-aquatica*, *Butomus umbellatus* etc., also occurred in storage ponds. Nevertheless, in fishponds the conditions for hydrophytes were more suitable. In the storage ponds, the spectrum of aquatic plant species in the phase of flooding is restricted by the high fish stock. In fishponds, terrestrial forms of floating macrophytes, surviving from the flooding phase, are quite common. This is consistent with a significantly lower mean Ellenberg indicator value for moisture in storage ponds (Table 2).

Temperature and light conditions of the ponds

Although the bottoms of both pond types are open to light, the storage ponds can be more shadowed due to their small size. The Ellenberg indicator value for light is significantly lower in storage ponds (Table 2). It can be explained by the occurrence of juveniles of trees (e.g. *Alnus glutinosa*, *Salix* spp.), forest herbs (e.g. *Scrophularia nodosa*) or wetland species growing also in forested wetlands (e.g. *Lysimachia vulgaris*) in storage ponds.

Ellenberg indicator values for temperature did not significantly differ between fishponds and storage ponds. However, we expected a higher mean Ellenberg indicator value for temperature in storage ponds, 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 in fishponds in our data set. They are more frequent in warmer regions, for example in South-Eastern Europe, Central and South-Eastern Asia etc. (Lampe 1996). In the past, they also occurred in South Bohemian fishponds, but with low frequency (Ambrož 1939, Hejný 1969). Maintenance of these species in storage ponds could also be caused by the specific temperature regime. The area of the storage pond is small and closer to the air convection; therefore higher summer temperatures can be expected.

In winter, the exposed bottoms of storage ponds are probably better frost protected, also due to permanent water flow in the central stream. This allows some perennial or facultative annual wetland species, e.g., *Eleocharis acicularis*, *Juncus articulatus, Leersia oryzoides* and *Peplis portula*, to survive the winter in their green state. These species have Atlantic or Subatlantic distribution. The species with 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 corresponds with the lower Ellenberg indicator value for continentality.

"Fishpond species" and "storage pond species" – interpretation of pCCA

The division of species in pCCA into groups of "storage pond species" and "fishpond species" (Table 4) reflects our field experience. It is also supported by results of DCA (Fig. 3). However, the analysis does not take rare species into account. The fit value, i.e. the measure of habitat impact on occurrence of the individual species, is influenced by the number of occurrences of the species in the data set. The species which occurred rarely in the vegetation of one pond type, show low fit values similarly to species unrelated to habitat type. Rare "storage pond species" include e.g. *Centaurium pulchellum, Cyperus flavescens, Gypsophila muralis, Lindernia procumbens* and *Tillaea aquatica*. We never found these species in fishponds of the region. The species *Chenopodium rubrum, Coleanthus subtilis*, *Elatine triandra*, and *Spergularia echinosperma* occurred, with sporadic exceptions, only in the fishponds, but their frequency in the data set was low. High affinity of *Coleanthus subtilis* to fishponds is visible in Fig. 3.

Can results be transferable to other regions?

Our study shows the situation only in one model region, the Českobudějovická basin. We assume that the results of analyses would be similar for the regions with analogous environmental conditions (cf. Šumberová 2003).

According to our observations, similar analyses could give different results for vegetation in warm regions with occurrence of calcareous substrates. The warm and dry summers together with higher pH and calcium content in 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 warm regions is restricted to fishponds. On the other hand *Bidens tripartita, Cyperus fuscus*, *Plantago uliginosa* occur on the fishpond and storage pond bottoms of these regions with approximately the same frequency. 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 Českobudějovické pánvi. Sádky a rybníky představují podobná stanoviště, která se liší svým využitím a obhospodařováním. Analyzovaly jsme 99 fytocenologických snímků z rybníků a 99 snímků ze sádek z let 2000–2004. Snímky jsme podrobily analýze přímou a nepřímou ordinací, analýze beta-diverzity a statistickému hodnocení metodou ANOVA. Nejvýznamnější ekologický gradient byl korelován s rozdíly mezi sádkami a rybníky, které jsou dány typem hospodaření. 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, mechorostů, 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. Protože oba typy vodních nádrží, sádky i rybníky, jsou charakterizovány specifickým obhospodařováním, soubor hospodářských zásahů je třeba považovat za nejdůležitější faktor, který ovlivňuje vegetaci těchto stanovišť. 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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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	more than 10 cm
moisture	drying plot	usually moist	waterlogged	shallowly flooded; to 5 cm	flooded; more than 5 cm

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

	fish ponds			storage ponds				
	mean value	min	max	mean value	min	max	F	p
species richness								
number of all species	16.51	5	29	20.86	7	37	23.427	p<0.0001
number of archaeophytes	1.13	0	4	2	0	7	24.5755	p<0.0001
number of neophytes	0.44	0	2	1.2	0	4	39.9864	p<0.0001
number of mosses	0.88	0	4	2.11	0	9	25.7436	p<0.0001
beta-diversity								
Sørensen index of dissimilarity	0.62	0.59	0.65	0.66	0.62	0.68	486.8344	p<0.0001
plant cover								
cover total	73.08	15	100	72.68	1	100	0.014	n.s.
cover of herb layer	67.17	10	100	65.06	1	100	0.349	n.s.
cover of moss layer	5.18	0	70	14.64	0	90	15.98209	p<0.0001
cover of algae	9.29	0	60	9.78	0	90	0.03985	n.s.
mean Ellenberg indicator values								
Light	7.47	7	7.9	7.28	6.8	7.7	43.5	p<0.0001
Temperature	6	5.6	6.4	5.98	5.6	6.3	0.8	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

Table 3. – Percentage variation in species data explained by particular environmental variables. Gross effects include the total variation explained by the particular variables. Net effects include variation explained by the particular variables except for variation 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 the 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 relation to individual pond types. The measure of the effect of pond type on the occurrence of each species is given by fit value. Scores indicate the relationship to storage ponds (negative values) or fishponds (positive values). The species are arranged according to increasing score value. Only species with the highest fit are shown.

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

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

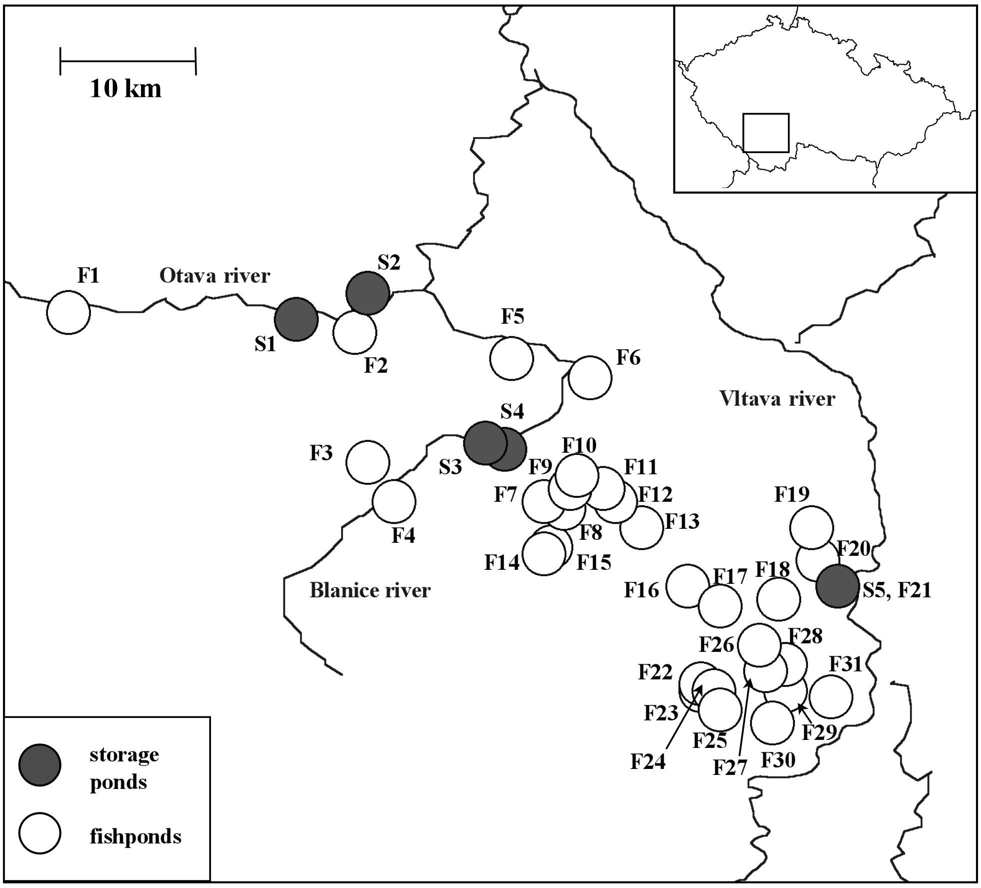


Fig. 2. – Box-and-whisker plots of the values: (a) number of species; (b) Sørensen index of dissimilarity; (c) number of archeophytes; (d) number of neophytes.

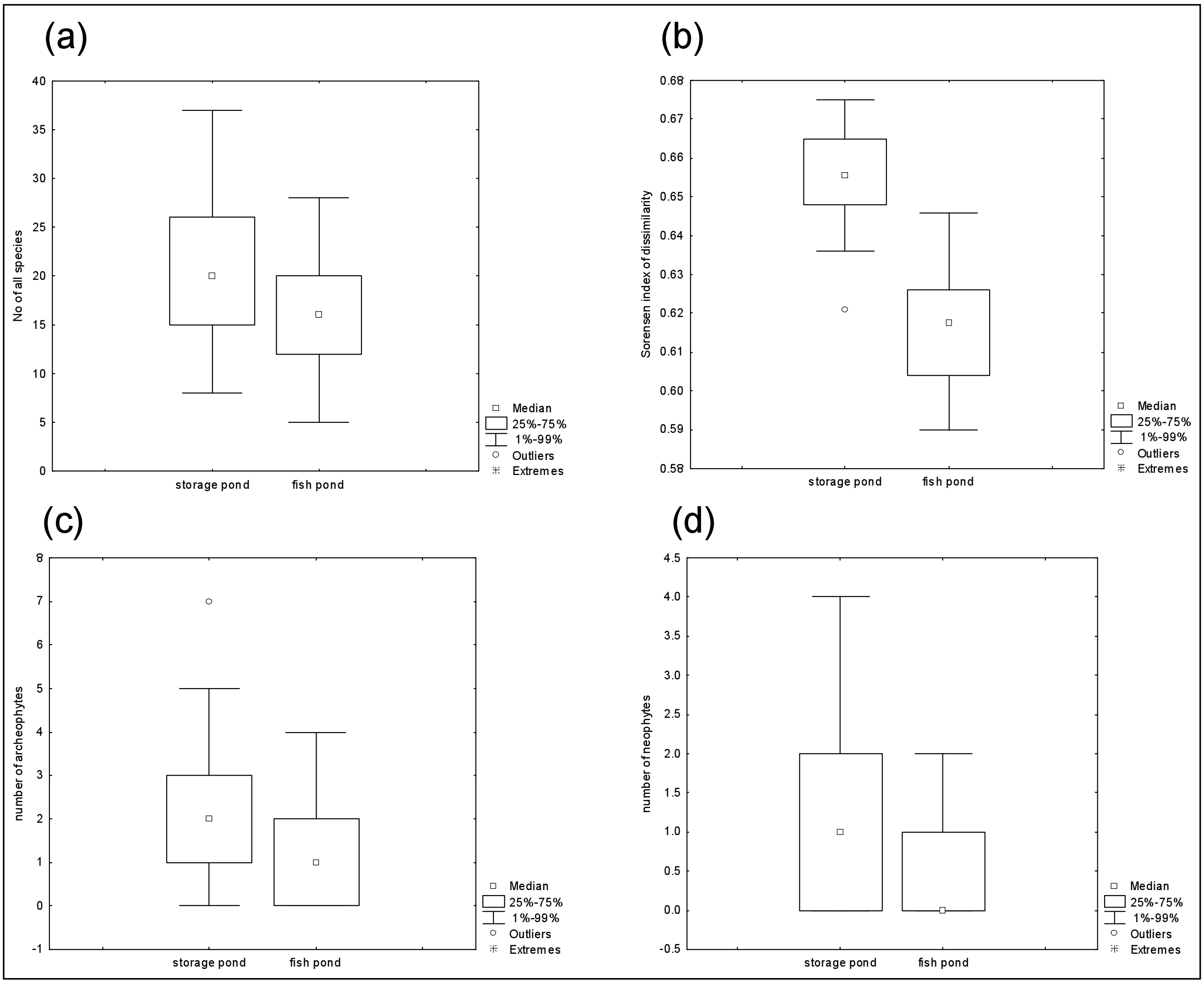


Fig. 3. – Detrended correspondence analysis (DCA) diagram of species with passively projected explanatory variables for vegetation of exposed fishpond and storage pond bottoms. Only species with high weight in the analysis are shown.

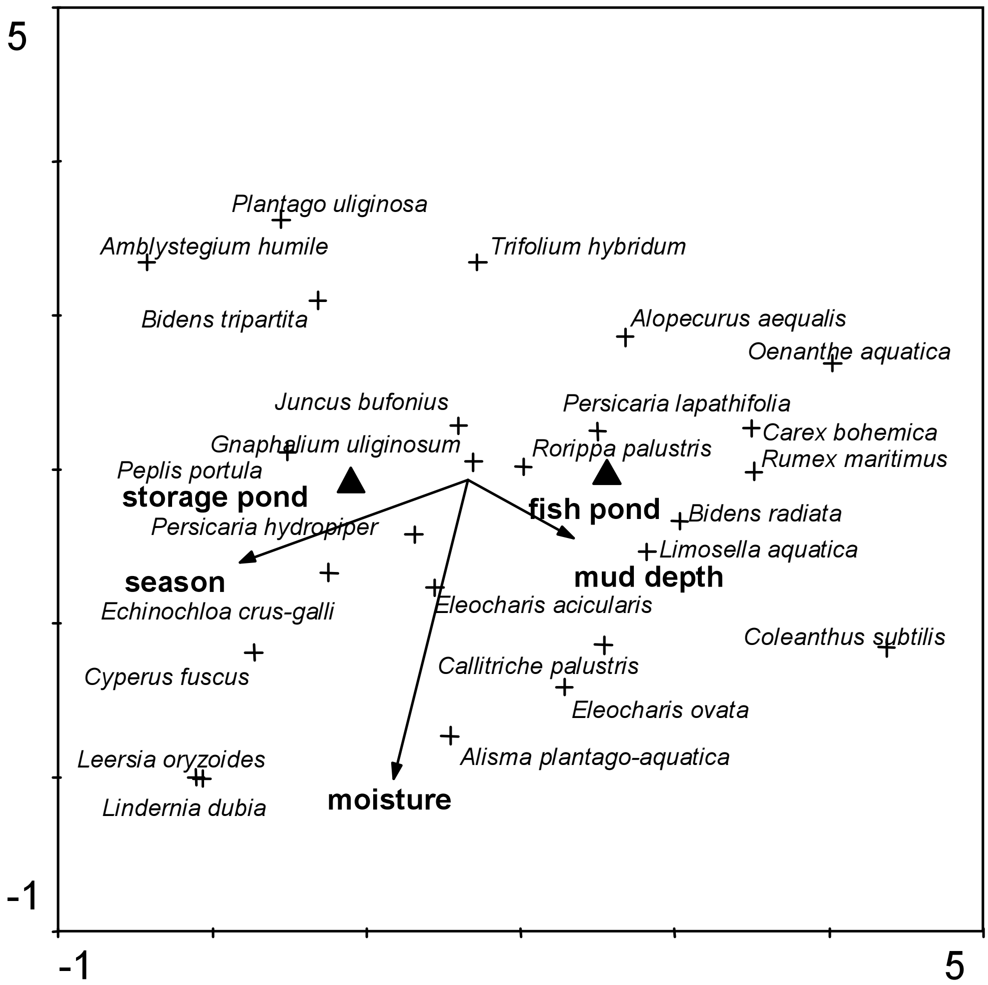
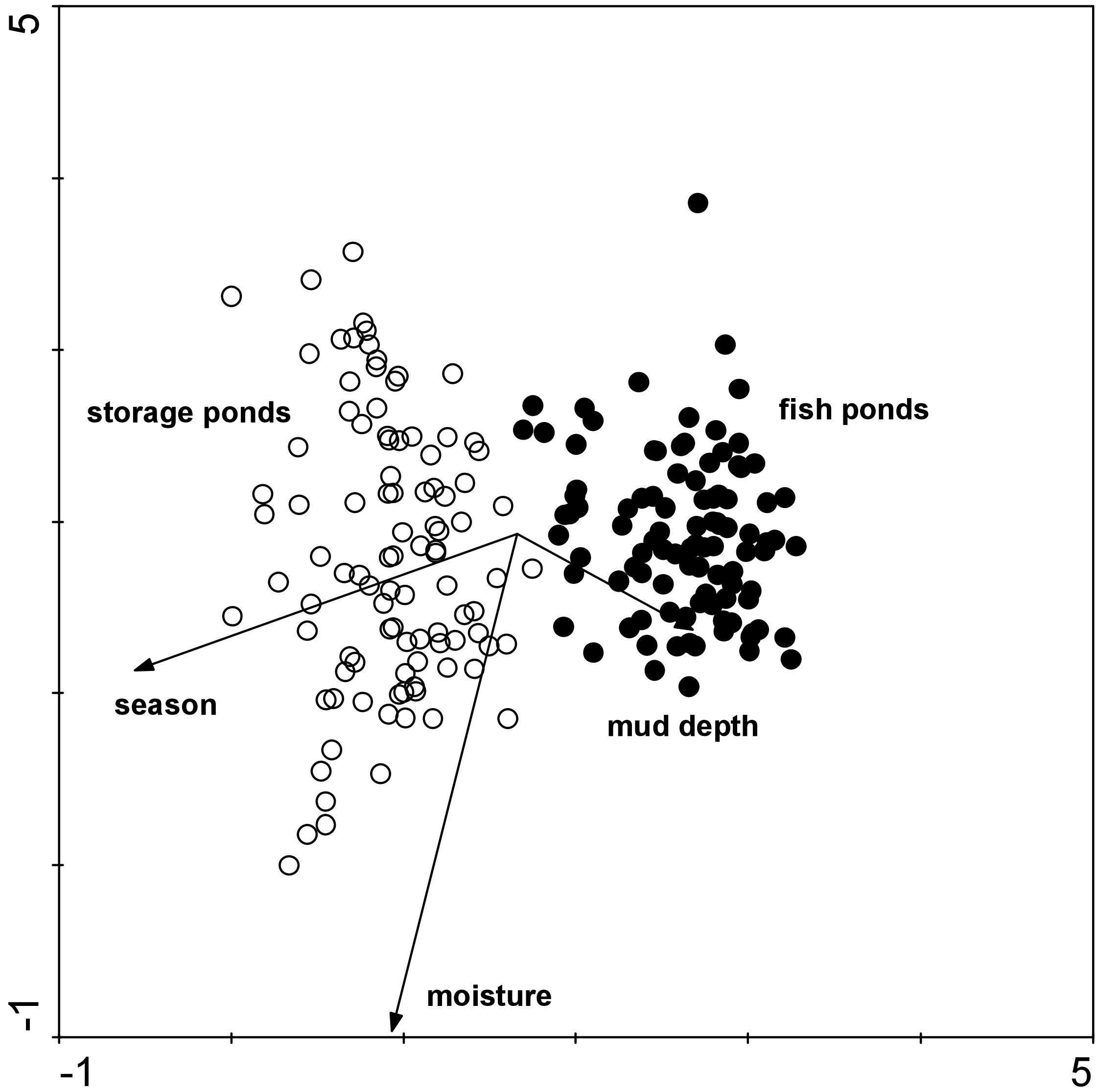


Fig. 4. – Detrended correspondence analysis (DCA) diagram of plots with passively projected explanatory variables for vegetation of exposed fishpond and storage pond bottom.



Appendix 1. – List of study sites

The list of storage ponds and fishponds includes in the first place the pond's name and its location. Further data are: **storage ponds** – use of herbicides (H), regular liming (L) and grazing (G); **fishponds** – marked as main ponds (MP) or nursery ponds (NP), grouped according to sub-regions. The numbers correspond with the numbers of localities in the map (Fig. 1).

Storage ponds

S1. Čejetice storage ponds – Čejetice, 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 – Vodňany, north part of the town, 0.6 km SW of the railway station; L.
S5. Hluboká storage ponds – Hluboká nad Vltavou, in the south 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 – Sudoměř, 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. Švarcemberský fishpond – Protivín, 2.7 km ESE of the railway station; NP
F7. Kuchyňka fishpond – Černěves, 0.3 km N of the village; NP
F8. Černěveský fishpond – Černěves, 1 km SE of the village; MP
F9. Bukový fishpond – Újezd, 2 km ESE of the village; MP
F10. Velký Černoháj fishpond – Strpí, 1 km SW of the village; MP
F11. Radomilický fishpond – Radomilice, south-western margin of the village; MP
F12. Jezero fishpond – Radomilice, 1.3 km S of the railway station; MP
Protivín, 2.7 km ESE of the railway station; NP
F7. Kuchyňka fishpond – Černěves, 0.3 km N of the village; NP
F8. Černěveský fishpond – Černěves, 1 km SE of the village; MP
F9. Bukový fishpond – Újezd, 2 km ESE of the village; MP
F10. Velký Černoháj fishpond – Strpí, 1 km SW of the village; MP
F11. Radomilický fishpond – Radomilice, south-western 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 south 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 České 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, south margin of the town, opposite the storage pond system; NP
F22. Čakovec Starý fishpond – Čakovec, 0.6 km NE of the village; NP
F23. Bojiště fishpond – Čakovec, 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 – Čejkovice, 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 north-eastern part of the village; NP
F30. Závratský fishpond – Závraty, 0.4 km N of the village; NP
F31. Šindlovský fishpond – Šindlovy Dvory, on the southern margin of the village; MP