Early stadiums of floodplain forest succession in a wide river beds upon an example of Bečva

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ABSTRACT: In the years 1999–2001 early stadiums of succession development of a floodplain forest were monitored in the wide bed of the Bečva River formed during the floods in 1997. Changing site conditions were investigated and the vegetation of pebble beds was repeatedly mapped in detail. In dependence on the site conditions main types of biotopes were described. The vegetation data were evaluated in accordance with the life form and ecological claims of the identified species. The results indicated an increasing differentiation of the originally relatively homogeneous environment owing to fluvial processes and progress of vegetation. Generally hemicryptophytes and hemiheliophytes were thriving above all, the dominance of *Phalaris arundinacea* was still growing. As for the woody species, especially willows asserted themselves from the beginning, solitarily and weaker in vitality representatives of other genera were present at drier sites. The identified specimen of *Myricaria germanica* was probably planted artificially. As concerns neophytes, only R*eynoutria japonica* was spreading significantly but in a very uneven way. Generally, this development of similar communities only little documented in this region corresponds to STG *Saliceta fragilis inf.*

Keywords: succession; floods; pebble beds; *Myricaria*; *Salix*

Dynamics of succession development of floodplain ecosystems is widely suppressed in the existing conditions of the Central European cultural landscape. This fact is most obvious in the case of rivers where a wide floodplain has been exploited by human beings for ages and the natural development has been reduced to minimum. The original diversity of the dynamic fluvial succession series (Buček, Lacina 1994) was suppressed as well. Usually societies of hardwood floodplain forests predominate, most often STG *Ulmi-fraxineta carpini*. However, the given *status quo* can be disturbed by disastrous floods. During the extreme flood in 1997 wide overflowing occurred in many parts of Moravian rivers, bringing on the shaping of originally canalised river bed to a nearly natural status. Exceptionally extensive examples can be found on the river Spojená Bečva, where a new, over 100 m wide river bed was formed in some parts, each hundred meters long with a mosaic of riverine biotopes. As the river runs for the most part outside of any built-up area, it is possible to let it develop spontaneously even in the future. Thus we are given a unique opportunity to follow the natural development of societies of softwood floodplain forest from the very beginning.

HISTORY

The present river with large pebble beds flows in a very similar way as it did before its stream regulation. Then the Bečva was a tortuous stream with intensive processes of fluvial modelling, here and there even furcating into several arms. The motion of pebbles has always been very intensive there and pebbles traditionally used to be extracted directly from the bed. There were wide pebble areas with pools and detached arms situated in the river surroundings. In order to prevent floods and fertilise barren land man set about regulating the river. It was in 1895 for the part in question, with the final inspection coming through in 1935. The bed was straightened; newly it was of trapezoidal section, the slopes having a dip of 1:2 and the ground width being 35 m nearly in the whole length. Though small changes were in progress permanently, this shape remained stable both in the lengthwise and cross profile during the following 60 years (Havlík 1999).

In 1997 the Bečva, similarly like many other Moravian rivers, was affected by the biggest flood ever experienced there. At the culmination on 7th July 1997, 950 m^3/s flew through the bottom land in the Teplice profile, the flow rate being evaluated as a centennial one (Anonymus 1998). In extensive overflowing the water level rose up to 2.5 m over the ground level. Not only the attained flow rate but also its duration was extreme. As a result, some fundamental changes in the river bed and the adjacent floodplain came about. The riparian growths and the stone bank protection were snatched away at many places, by transposition of many tons of fluvial sediments the bedrock was denudated as well as the material buried for hun-

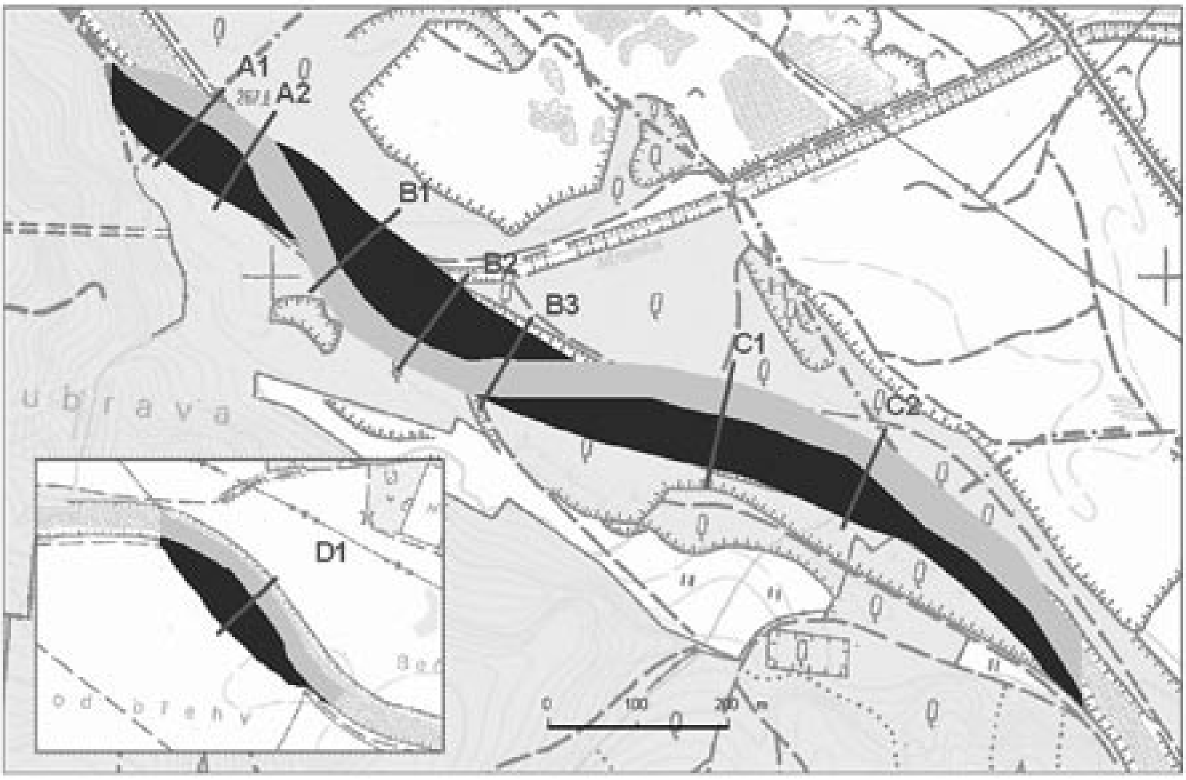


Fig. 1. Situation. The actual river bed, the areas of pebble beds and the observed transects are shown

dreds years. On the contrary, there were variedly thick layers of sand and pebble sediments or woody rubble deposited at many sites in the floodplain. The strongest changes could be found in locations where the originally straight channel was replaced by several bends with a morphologically varied over 100 m wide bed. A rich mosaic of biotopes originated in this way, including steep loam-sandy outer banks, variedly elevated pebble beds sometimes with alluviums of sand and silt, both torrential and calm water, protected lagoons, pools periodically watered by higher flow rates ...

METHODS

The monitoring of development in the floodplain was carried out in vegetation seasons in 1999–2001. This article deals with development of the newly formed river bed and its vegetation.

In order to investigate development at the newly established sites 8 transects were laid out across the wide river bed (Fig. 1). At the beginning and at the end of the period of observation a rough geodetic survey was performed in these cross profiles to recognise a general trend of the geomorphologic development. On transects, 10 m wide, the vegetation was mapped in summer months using series of phytocenological relevés. A uniform nomenclature was used (KUBÁT 2002). Depending on the extent of homogeneous growth the segment length for particular relevés of transects varied. The Braun-Blaquet combined scale of abundance and dominance modified by Zlatník (RANDUŠKA et al. 1986) was used. For the interpretation of the relevés the recorded data were converted into numerical values, assigning medians of intervals of the mentioned scale to each category, a sole specimen assessing as 0.001% and a solitary presence as 0.100%. When evaluating occurrence within a transect or a locality as the whole, weighted average of occurrence in particular segments was used. At the end of the period of observation, the horizontal structure of greens on the pebble beds was mapped as well. The focus was on general abundance and dominance of species, special attention was paid to the progress of woody species and invasive neophytes. On the basis of classification of species according to ecological requirements (ELLENBERG 1992), evaluation of spatial ordering and site conditions, some common trends of initial stadiums of local succession development could be defined. The numerical data processing was performed in the software environment of MS Access and MS Excel, spatial analysis and maps in Esri ArcView, the outputs were prepared using MS Word.

Natural conditions

Localisation

The area of interest is situated alongside the Bečva River between the towns of Valašské Meziříčí and Hranice na Moravě. The investigated pebble beds are parts of the wide river bed on river kilometre 52.497–54.551, approximately 2 km down the stream from Choryně, and river kilometre 56.200–57.130, by Lhotka nad Bečvou.

Geological and geomorphological conditions

The area is situated in the Valašskomeziříčská valley in the southwestern part of the Příbor bench land. The up to 2 km wide depressed area was created by Quaternary erosion. The accumulation relief of fluvial plain and relicts of river terraces are present there. The strath is composed of Quaternary stream-laid sediments (DEMEK 1987). The underlying rock of the area is composed of the massif of brunovistulicum with muscovite-biotite paragneiss with garnet and sillimanite. Devon limestones and group of beds of Carboniferous-Culm composed of conglomerates and sandstones are laid over the underlying rock. In the top wall there is an overfault of flysch rocks of the slezsky nappe (MÍSAŘ et al. 1983). The altitude at the focused places is approximately 263–278 m.

Hydrological conditions

The Bečva is a stream of the 3rd order, assessed as a pebble-bearing torrent. The area of the drainage basin for the profile at the junction with Juhyně is 1,161.74 km^2.

M-days flow rates, Pod Juhyní profile (m^3/s):

30	90	180	270	330	355	364
40.6	15.2	6.78	3.52	1.96	1.32	0.85

N-years flow rates, Pod Juhyní profile (m^3/s):

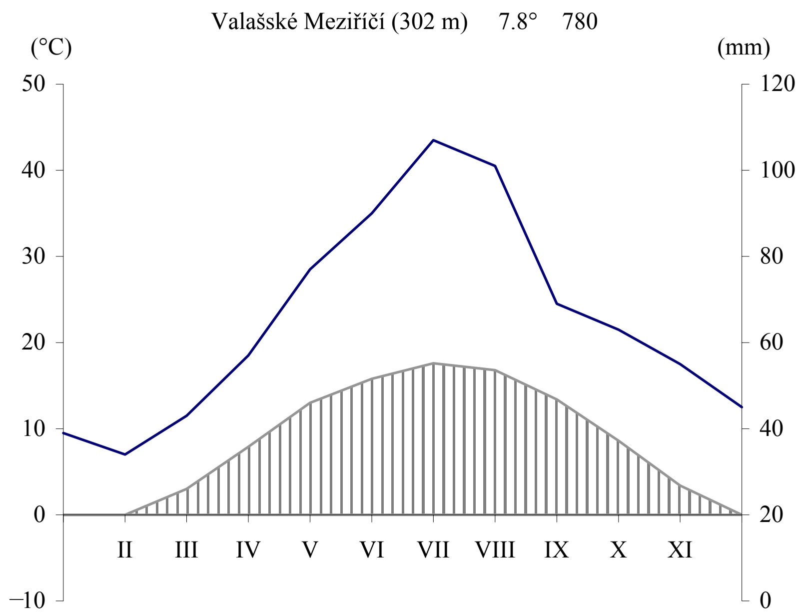
1	2	5	10	20	50	100
208	264	465	550	633	688	725

(Data by the Czech Institute of Hydrometeorology.)

Climatic conditions

Basic climatic characteristics from the meteorological station Valašské Meziříčí (altitude 302 m) in the period of 1901–1950 (ANONYMUS 1961).

	II	III	IV	V	VI	VII	VIII	IX	X	XI	
–3	–1.6	3	7.9	13	15.8	17.6	16.8	13.4	8.6	3.4	–0.4
39	34	43	57	77	90	107	101	69	63	55	45



Biogeographical conditions

According to the general biogeographical classification (CULEK et al. 1996) the followed region comes under Carpathian province, bioregion 3.4 Hranický. The nearness of mountain ranges of the Moravskoslezské Beskydy and Hostýnsko-vsetínská hornatina Mts. with Bečva being linked with them is of great significance for the genesis of local biota.

Floodplain forests *Pruno-Fraxinetum* locally in a complex with *Alnion glutinosae* represent the potential vegetation (NEUHÄUSLOVÁ et al. 1998) at the bottom land. Societies of *Carici pilosae-Carpinetum* and *Tilio-Carpinetum* follow up the slopes.

In the sense of Zlatník's geobiocenological typology (ZLATNÍK 1976) the floodplain belongs to STG 3 BC 5 *Alni glutinosae-saliceta sup.*, 3 BC-C (3)4 *Ulmi-fraxineta carpini sup.,* 3 C (4)5 *Ulmi-fraxineta populi sup.* and 3 BC-C 4 *Fraxini-querceta roboris-aceris sup.*

CHANGES IN THE RIVER BED AFTER THE FLOOD

Fluvial modelling processes

The bed created by the flood in 1997 remained roughly the same in the following years; nevertheless, the fluvial modelling processes are still under way. The most evident is the progressive bank erosion. All the time several hundred meters long sheer cut-banks have been refreshed. The progress of riparian crests in the most strained parts of the concave banks amounts on average to as much as several meters yearly (Fig. 2). Besides the bank material, i.e. flood loams with an underbed of fluvial pebble, the full-grown tree vegetation participates unreasonably on the speed of the progress. The undercut banks are not able to hold the weight of full-grown trees any more and subsequently fall breaking the shore. In addition the arisen turbulent streaming multiplies the destructive force of the stream. Thereby the course of the erosion is expedited. At places out of the active incidence of the stream the older cut-banks are gradually sliding down and overgrowing.

The bottom of the active river bed, i.e. the pebble deposits, is continually modified too. In the course of higher flow rates a great quantity of bed-load moves there. Above all the strongly represented pebble fraction is significant for the modelling. Thanks to erosion and sedimentation the surface of the parts of the bed situated lower in the cross profile is permanently fundamentally renewed and the stream in the frame of the wide river bed even

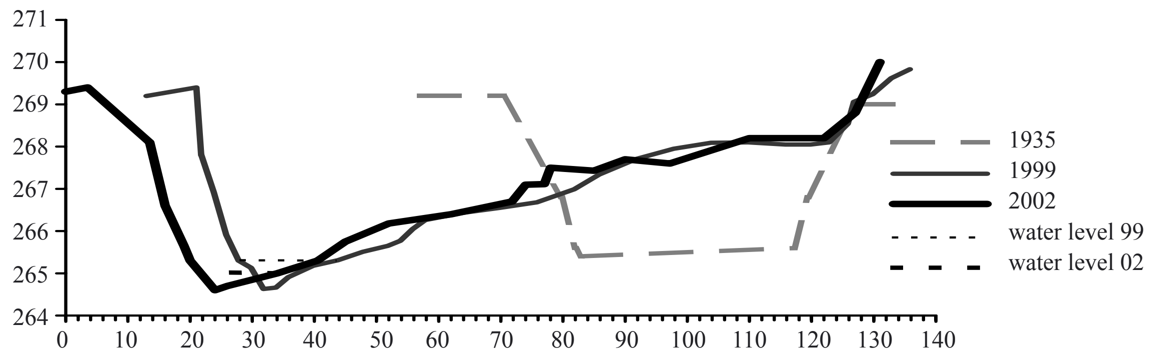


Fig. 2. Example of a cross profile (m). Situation at the beginning and at the end of monitoring compared with the year of final inspection (profile B2)

changes its course. The upper flood bed is inundated very rarely – from the time of its rise probably only once (in 1998).

The qualities of the substrate in the alluvium also gradually change. It was originally practically a pure pebble sometimes with sands. The amount of smaller fractions was minimal and only the lower flow rates in the following years allowed a gradual deposition of more fine-grained sediments. An important role is played by plants there. On the one hand, they supply the substrate with their detritus, on the other they notably affect the deposition just of the materials of fine fractions stripping them from the stream during inundation. So the character of the substrate is subsequently changed and the thereby enabled progress of vegetation even accelerates the course of its changes.

Development of vegetation

In the autumn 1997 the river bed transformed by the flood was only slightly overgrown, covering up to 1% of its dry parts, but frequently voiding the vegetation cover entirely. The first plants settled down mostly at the sites where rubbles and chesil of the pebble beds were immixed with a finer fraction or surfaced with a thin coat of flood silt. In the speciesless cover ruderal species were prevailing – *Urtica dioica, Galinsoga quadriradiata, Plantago major, Tanacetum vulgare, Tripleurospermum inodorum,*

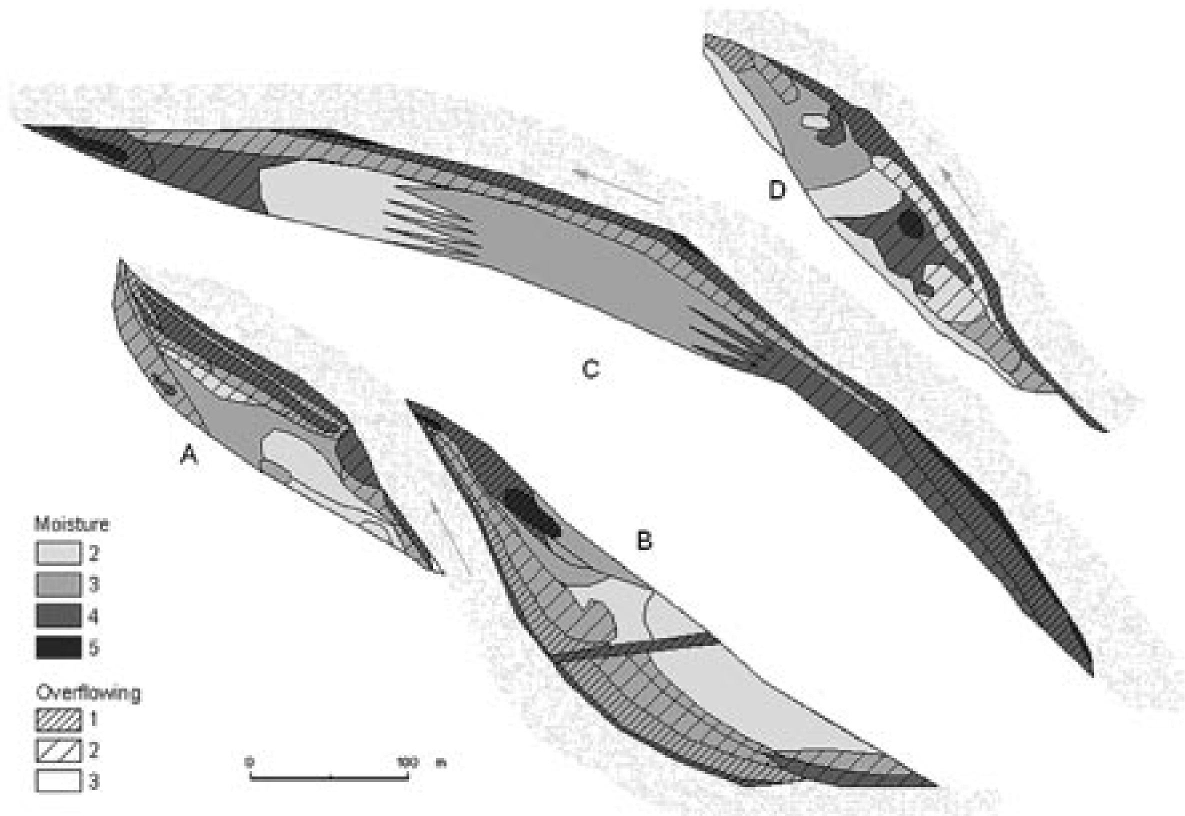


Fig. 3. Differentiation of habitat according to the main environmental factors. Moisture class 2 – limited, 3 – normal, 4 – enriched, 5 – wet; frequency of overflowing 1 – commonly, several times a year, 2 – regularly, at most once a year, 3 – very rarely. Note: The indistinct borders fluently verging on the bed C are schematically represented

Poa annua, etc. – the high frequency of the arable crops *Lycopersicon esculentum* and *Brassica napus* was remarkable. As for the species typical of the riverine biotope, only sporadically *Phalaris arundinacea* and *Myosoton aquaticum* occur. Woody plants were not found (LACINA 2002).

Depending on microtopical conditions particular sites were colonised with different swiftness by different species in the next years. The frequency and the way of floatation together with topical moisture conditions largely related to the soil fraction of the substrate seem to be the main factors influencing the course of colonisation.

Main factors of the environment

Frequency and way of floatation

The action of the surface water is logically an essential determining factor in the river bed. The limits consist in a repeated deficit of aerial oxygen owing to the inundation and in the case of Bečva especially in the mechanical action of the water course drifting the material of suspended load and shingle. According to the action of the surface water the following habitat types could be defined (Fig. 3):

Commonly inundated sites: They are the lowest parts of gently sloping beds. Only few species can endure the extreme conditions, above all the mechanical action of the stream. Most frequently *Persicaria lapathifolia, P. hydropiper, Barbarea vulgaris, Agrostis canina* were found. The individuals were isolated, often crooked, absolute majority of them emerging at the actual vegetation season. We cannot talk about a succession here, just ecesis. The cover was minimal, often even zero, in the cross-profile increasing with the growing elevation towards the edges of the bed. Higher covering could be seen close to boulders possibly to other obstacles in the river, where the plants are protected against the action of the stream. At these places *Phalaris arundinacea* appeared more frequently as well.

Sites regularly inundated during higher flow rates: A habitat type continuing in the one mentioned above in convex segments of shores, potentially in parts with distinct riparian crests building the inner edge of the riparian growth. The inundation comes several times a year, however, the strong destructive mechanical action of the water flow, above all the movement of pebbles, occurs only sporadically, less than approximately once a year. The trapping of fine-grained particles from the stream flowing through the vegetative growth applies primarily in this habitat type and thereby an amelioration of soil conditions proceeds.

Covering by vegetation was variable at these sites, recorded values ranged from 10 up to 100% in the last year of survey, above 50% routinely. *Persicaria lapathifolia, P. hydropiper, Phalaris arundinacea, Agrostis canina* often built wide polycormons there by propagating vegetatively. Some other species were found more often too – *Myosoton aquaticum, Mentha longifolia, Rumex crispus, Rorippa silvestris, Petasites hybridus,* but also *Urtica dioica, Lactuca serriola, Calamagrostis epigejos*, etc. Disappearance of *Veronica beccabunga* was interesting, being common in the first year of survey, it was found only sporadically in the following seasons. More favourable conditions also enable a renewal of willows – *S. alba, S. fragilis, S. × rubens.* The progressing succession was evident in this case; however, the recurrence of initial stadiums can be expected by higher flow rates. An exception was 5 m wide and high bands of willows – above all *Salix purpurea* – at some higher situated places along the upper boundary of the described habitat type, which was already able to endure even extreme flow rates. On the opposite, there were sites where the conditions prevented timely overcoming of the early succession stadiums. Stable growth that could resist the action of the flow and ensure stable ecological conditions never managed to grow during the period between floods. Regardless of the otherwise favourable conditions the development remained blocked and repeatedly only an ecesis proceeded here.

Sites out of regular inundation: The mechanical action of the water flow does not represent a limiting factor any longer in more elevated parts of the wide river bed. With respect to the character of the substrate – highly permeable pebble – availability of moisture is critical here.

Moisture conditions

Moisture conditions are in the wide bed of the Bečva River very heterogeneous (Fig. 3). The immediate nearness of water on one hand and the high permeable pebble bed on the other hand created a complete scale of moisture conditions. The permanently inundated sites are situated in the very neighbourhood of desiccating sites at the same time. Even a relatively slight elevation of the wavy surface represents a moisture handicap as the lower surroundings act like a drainage channel.

The potential for the capillary action of water and its retention is very limited in the coarse-grained material of pebbles. Extreme conditions reign particularly in upper layers of the immature substrate, especially when being fully insolated. Above all the chances for ecesis of newly created sites are very limited and so the colonisation proceeds very slowly. Owing to the pedogenetic process and sedimentation the amount of fine earth grows in the course of time, detritus from the arisen plants accumulates and prompts soil horizons to develop. More and more the surface is shadowed by the growth. The moisture conditions improve gradually. Rather than water percolating from the river bed the content of fine earth in the substrate plays therefore an important role on a considerable part of the surface. With progressing succession the portion of the fine earth rises and the original differences in the quality of soil gradually fade away. In initial stadiums, nevertheless, this is mediately one of the crucial factors.

Waterlogged and hydric sites: Besides the locations at the very edge of shores the surplus of water can be found in depressions of the upper part of the wide river bed, being supplied at least by percolating water. The greens prosper fine under such conditions. As soon as in the second year after the flood the cover exceeded 70% there, reaching 100% in the next seasons. Mostly *Phalaris arundinacea* dominated entirely being on the wettest, by fluctuating water level the most affected sites varied by *Agrostis canina, Persicaria lapathifolia, P. hydropiper,* in protected lagoons afloat even by *Typha latifolia* and *Lemna minor*. As for other species, *Calystegia sepium, Lysimachia vulgaris, Impatiens parviflora, Mentha longifolia, Lycopus europaeus*, etc. were found. As far as woody species are concerned, *Alnus glutinosa* reached the biggest growth, however, willows were prevailing – *Salix alba, S. fragilis, S. rubens, S. purpurea,* fewer *S. viminalis,* rarely *S. aurita.* At the end of observations approximately 80% of this habitat type area was overgrown with willows. Thus, the number of species decreased significantly. Thanks to deposition of fine-grained sediments and to accumulation of own detritus silting-up occurs and the topical edaphic conditions meliorate, resulting in further progress of vegetation.

Normal sites: The development of vegetation was decelerated by an extreme character of the pebble substrate at the beginning. Nevertheless, the general cover tended to 100% near the end of monitoring. Herbal vegetation was dominating, woody species occurred disseminated or sometimes in groups. *Calamagrostis epigejos* gradually predominated during the followed period, *Leucanthemum vulgare, Artemisia vulgaris, Tanacetum vulgare, Saponaria officinalis, Eupatorium cannabinum, Arrhenatherum elatior*, etc. occurred. The normal moisture conditions enabled woody species to prosper well in case they succeeded in overcoming the critical phase of ecesis on the immature substrate. The competition of the closed herb layer seems to be critical for further renewal. Till this time *Populus nigra, Populus tremula, Robinia pseudacacia, Salix alba, S. purpurea* have primarily been found. The tallest specimen reached the height of as much as 7 m.

Limited sites: As there are no repeated stream disturbances there, the general cover after 5 years, despite of the slower coming on of vegetation, was higher than in wetter but repeatedly denudated locations. Moreover, the above-mentioned process of succession, when the moisture conditions improve subsequently after the overcoming of the initial stadiums, played a special role. The local desiccating sites (with the exception of isolated outcrops) are therefore only temporary, changing into normal during the development. Intact by succession remain the exposed surfaces of progressing cut-banks or the elevated locations of pebble repeatedly denudated by higher flow rates.

The cover usually reached up to 10–20%. *Artemisia vulgaris* with *Melilotus albus, M. officinalis* and *Echium vulgare* were most often found there. *Calamagrostis epigejos* was also present, nevertheless, compared with the above-mentioned habitat type to a considerably smaller extent. *Verbascum chaixii, V. thapsus, Tanacetum vulgare, Leucanthemum vulgare* were frequent as well. The woody vegetation was practically missing, only a sporadic regeneration of *Populus nigra, Robinia pseudacacia* and *Salix alba* was registered.

Selected characteristics of vegetation

Cover

As early as at the beginning of the observations, i.e. the third year after the flood, differences in colonisation

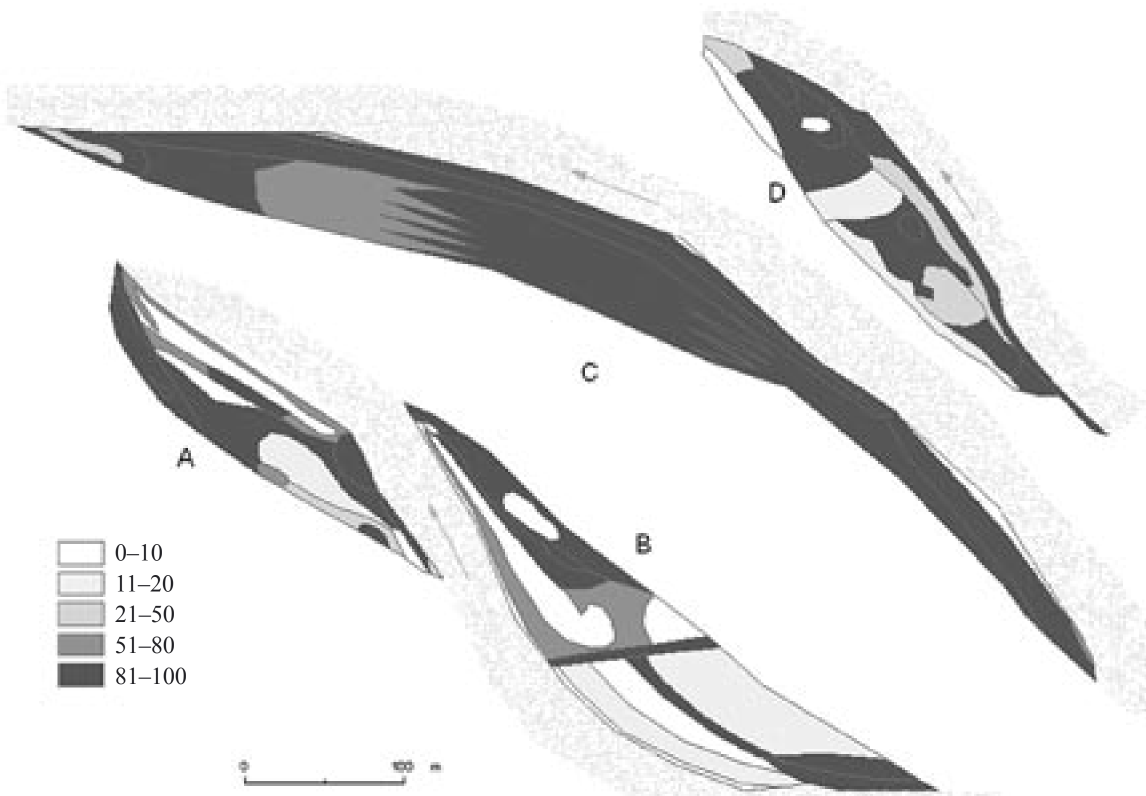
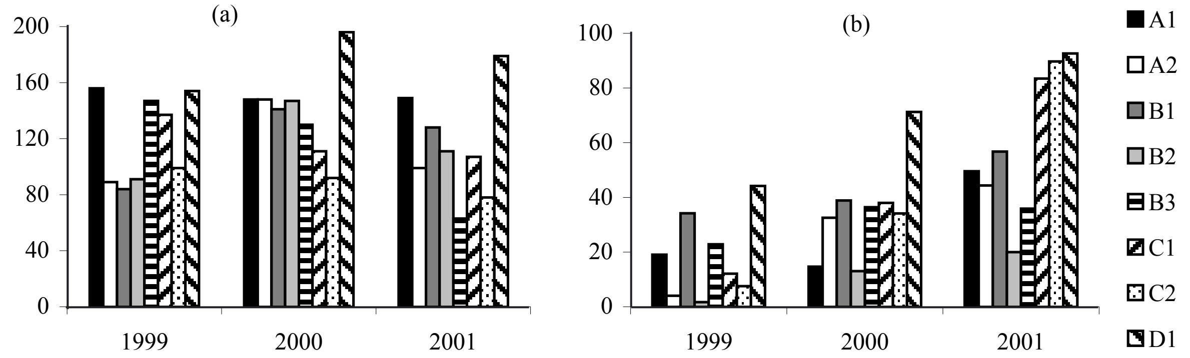


Fig. 4. General cover of the area at the end of the monitored period (%)



(a) Number of species in a transect
(b) Average cover in a transect (%)

Fig. 5. Development of vegetation in particular transects. A1, A2, … D1 – names of transects

of particular places were clearly evident. On average 18% of the surface was covered with greens, the values in transects being divided quite equally at the interval of 1.7–44.2%. After three years of development it was already as much as 20.0–92.7%. The increase in 2000 and 2001 proceeded with a different intensity at particular sites (Figs. 4 and 5). The differences are caused by the combination of site conditions and climatic and moisture conditions of the given growing season. In the case of transect D1 the decrease of the annual additions occurs simply because of the diminishing free space.

The proportion of particular species occupying the surface was changing too (Fig. 6). In the first year of monitoring the values of the cover of single species were low, general cover of the species in most cases not reaching even 1%. The most dominant was *Juncus effusus* (2.0%), being alike *Scirpus sylvaticus* (1.3%) able to create relatively continuous overgrowths in wet depressions in a short time, *Persicaria lapathifolia* (1.45%) expanded the most quickly along the water. In advancement they receded, being suppressed by other species. *Phalaris arundinacea* became dominant, being followed by *Calamagrostis epigejos*, still more and more significant were willows – *Salix purpurea, S. alba, S. fragilis*.

Species diversity

The amount of species in a concrete locality corresponds with the variety of site conditions. In 1999 in the mapped

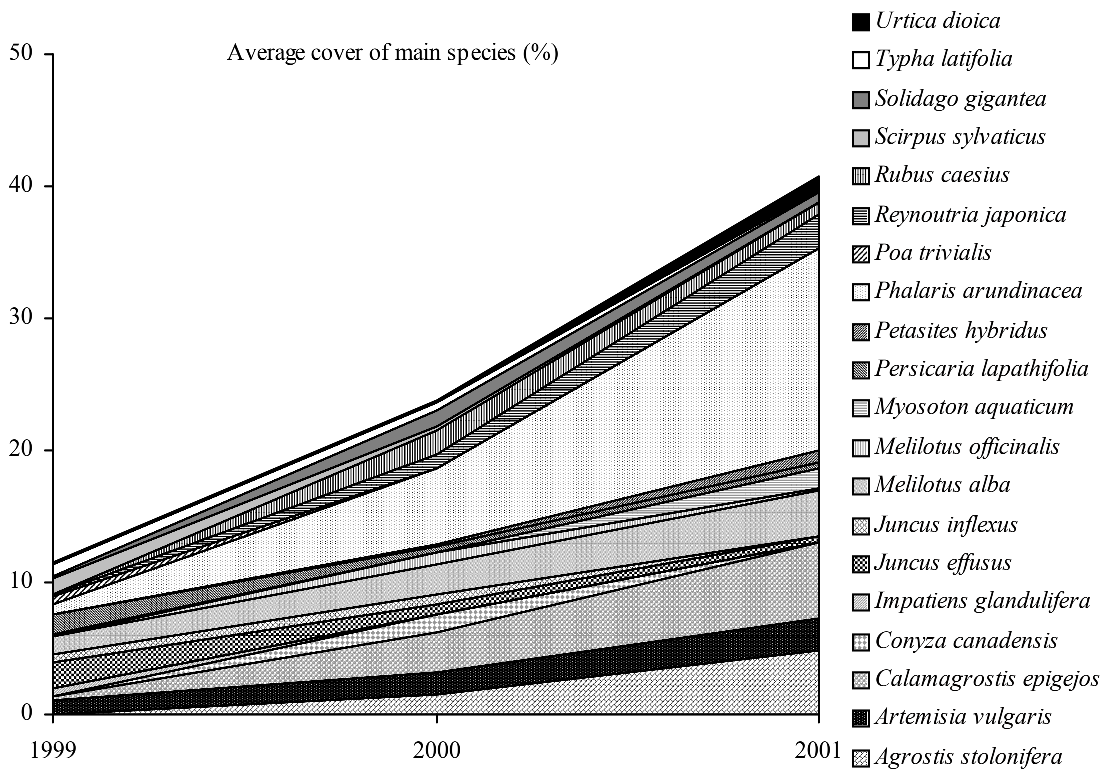


Fig. 6. Development of main species

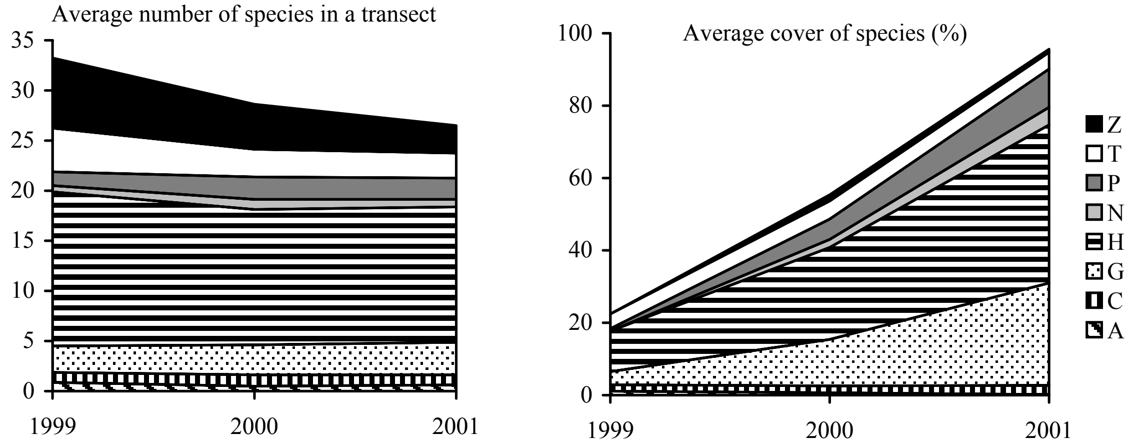


Fig. 7. Development of vegetation according to the life form. A – hydrophytes, C – chamephytes, G – geophytes, H – hemicryptophytes, N – nanophanerophytes, P – phanerophytes, T – terophytes, Z – woody chamephytes. Note: The species creating more life forms are included in each of them

areas 229 species were found, two years later only 177. The average number for a single transect dropped from 84.75 to 69.63 (Fig. 5). Closing of the originally open societies seems to be an obvious cause. The reasons for a distinct decrease followed by an increase in the species diversity in some transects need to be sought probably primarily in climatic conditions of the given growing season, to a smaller extent possibly also in alternations in supplies of diasporas due to upstream events, the way of management on neighbouring lands, etc. The presumption that it could be the case of constantly growing dominance of competitively strong species to the prejudice of the others, alternatively a recovery of the association after a disturbance, was not confirmed.

At the beginning of the development of pebble alluvium societies the species composition can be affected among others by the diasporas supplied by the flood itself. It can be illustrated by the species *Lycopersicon esculentum* and *Brassica napus* common in 1999, which were only rarely found in the next floodless years, which meant a lack of new seed inputs. Nevertheless, we must emphasize that the conditions reigning in the bed during really extreme flow rates enable propagation rather exceptionally. An absolute majority of species settles there only subsequently, dispersing from the surroundings (cf. JANOUŠKOVÁ 2001).

Life form

Despite the expectation not terophytes but hemicryptophytes were the most frequent ones in all transects from the very beginning (15% on average at that time). The number of species of other life forms was significantly lower. In the course of time the proportion did not change fundamentally, nevertheless, according to the presumptions the number of terophytic species decreased and the number of phanerophytes increased.

The proportion of plants of particular forms in the general cover remained quite constant as well. Hemicryptophytes were dominant from the beginning, followed by geophytes, phanerophytes asserted themselves increasingly (Fig. 7).

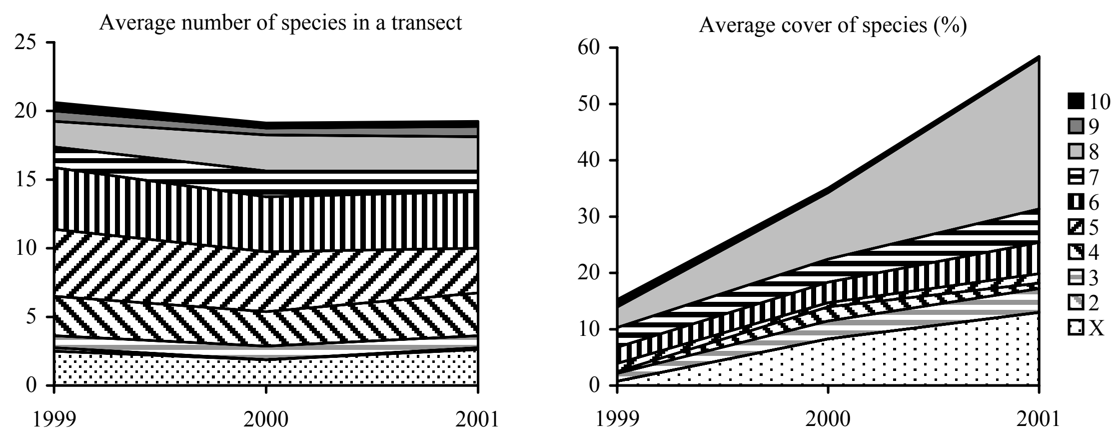


Fig. 8. Development of vegetation according to the moisture requirements. X – indifferent, 2 – on dry or even extremely dry soils, 3 – between 4 and 5, 5 – on fresh, i.e. "normal" soils, 6 – between 5 and 7, 7 – on wet never drying soils, 8 – between 7 and 9, 9 – on wet soils, often poorly aerated, 10 – on regularly overflowed soils. Note: Only species of known requirements are included

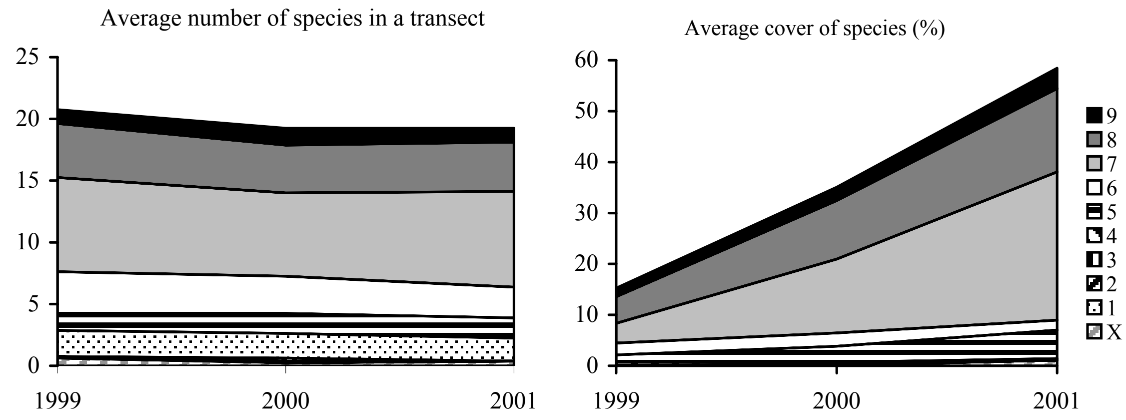


Fig. 9. Development of vegetation according to light requirements. X – indifferent, 2 – strong sciophytes, 3 – sciophytes, 4 – between 4 and 5, 5 – hemisciophytes (more than 10, but mostly less than 100% of full daylight), 6 – between 5 and 7, 7 – hemiheliophytes, 8 – between 7 and 9, 9 – heliophytes (rarely less than 50% of full daylight). Note: Only species of known requirements are included

Moisture requirements

The observed biotope of pebble beds includes a wide scale of moisture conditions. Most of the determined species prefer fresh, i.e. "normal – medium wet" soils. Towards the extremes of both the surplus and deficit of moisture the number of species falls. Development trends in the monitored period are distinct only in the already mentioned most numerous category, where the permanent fall was in progress. As for the cover, the situation in the representation of single categories is analogous, the species of the "mean" being dominant from the beginning. It must be remarked that only the cover of the species of moist or hydric sites (above all thanks to *Phalaris arundinacea*) and indifferent species (especially *Calamagrostis epigejos*) increased during the monitored period. The other ecological groups kept their original values from the year 1999 despite the increasing general cover in the area (Fig. 8).

Light requirements

The open space of the young pebble alluvium was fully insolated, with the exception of margins bordered by high-grown woody species. With the development of vegetation the differentiation of light conditions at particular sites was in progress too and in closed willow stands even shade-loving plants could occur. However, in the followed transects no expansion of sciophytes was registered. The constancy as well as the cover remained just about constant during the time of surveys. The recorded shade-loving species *Oxalis acetosella, Lysimachia nemorum, Galeobdolon luteum, Brachypodium sylvaticum* were found scattered at different sites, not preferring the relatively closed stands of woody plants. However, in further development some originally supposed growing of the representation of sciophytes can be expected. Near and full helophytes (rarely under 50% of full daylight) were the most constant then, being represented by *Urtica dioica, Artemisia vulgaris, Tanacetum vulgare, Barbarea vulgaris, Leucanthemum vulgare, Mentha longifolia, Myosoton aquaticum, Tripleurospermum inodorum*, etc. The species of this category were permanently the most dominant ones and their dominance was becoming increasingly noticeable during the monitoring (Fig. 9). *Phalaris arundinacea* and *Calamagrostis epigejos* had thereon the leading share but the proportion of *Agrostis stolonifera, Salix purpurea, Artemisia vulgaris, Reynoutria japonica* etc. was growing as well.

Mineral nitrogen requirements

The results of observations showed a lasting predominance of the species mainly of nitrogen-rich soils. During the time of monitoring their general cover also grew noticeably (from 3.1 to 26.0%) becoming unambiguously dominant. The main proportion of the general cover fell on *Phalaris arundinacea* (15.5%) followed by *Salix alba* (4.5%) and *Reynoutria japonica* (2.5%). An increasing cover, although by far not so expressive, could also be seen in other species of high or mean requirements for nitrogen in the soil. The constancy of species declined gradually with their decreasing nitrophily. The species bound to nitrogen-deficient soils occur only very rarely, with a minimal cover (Fig. 10).

Soil reaction requirements

In the repeatedly washed material of pebble deposits the pH values are practically purely dependent on river water. Structure of vegetation corresponds with the supposed neutral soil reaction. Passing over the most constant group of indifferent species that accounted for approximately one third of all the found species (*Cirsium arvense, Artemisia vulgaris, Barbarea vulgaris, Leucanthemum vulgare, Ranunculus repens, Taraxacum officinale, Agrostis stolonifera, Calamagrostis epigejos*, etc.) the plants preferring pH 7 were the most common. An example can be *Tripleurospermum inodorum, Melilotus albus, Urtica dioica, Arrhenatherum elatius.* Noticeably

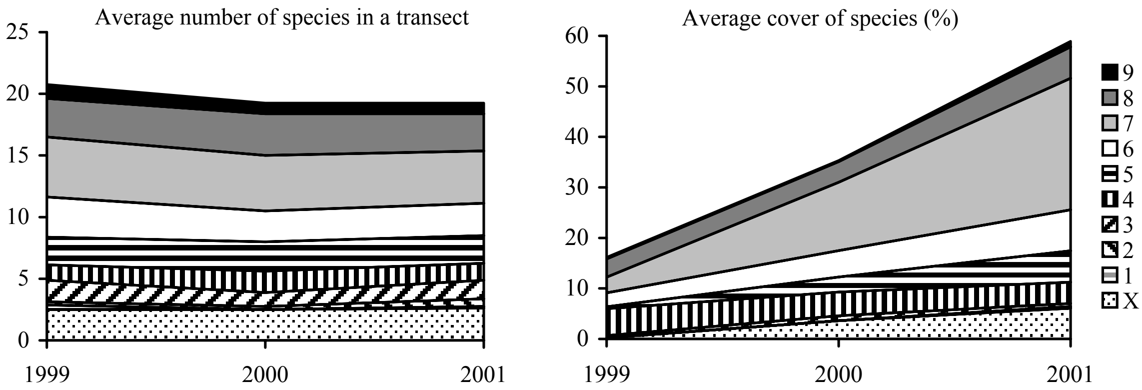


Fig. 10. Development of vegetation according to soil nitrogen requirements. X – indifferent, 1 – only on soils low in mineral nitrogen, 2 – between 1 and 3, 3 – mostly on soils low in mineral nitrogen, 4 – between 3 and 5, 5 – mostly on medium rich soils, 6 – between 5 and 7, 7 – mostly on soils rich in mineral nitrogen, 8 – nitrogen indicator. Note: Only species of known requirements are included

less frequent were neighbouring categories (pH 6 and 8) and only minimal was the presence of species preferring either acid or base-rich soils. As far as the cover is concerned, the influence of increasing dominance of *Phalaris arundinacea* was evident there too, thus the vegetation of neutral sites dominated. However, besides the indifferent species the proportion of plants preferring basic sites also increased (Fig. 11).

Woody species

Woody species on the pebble alluvium could be found for the first time a year after the floods. As for willows, i.e. the most frequent ones, buried branches and trunks were partly sprouting. The propagation by seeds could be seen more often, with *Salix alba* and *S. purpurea* forming the continuous cover of well prospering seedlings at places well supplied with water. Drier locations farther from the stream were colonised by the woody species only with difficulties due to the moisture deficit and even the condition of the present young specimens reflected the extreme conditions. The situation changed with development of root system and the plants flourished well in the following years. However, with respect to the conditions of propagation no closed stands were formed. Besides willows a number of other woody species was found, 45 in total (Table 1).

At the end of monitoring the presence of woody plants was registered at an absolute majority of places in the form of seedlings at least to a minimum extent. The exceptions were a young pebble sediment at the edge of the bed A and a sandstone outcrop on the bed D (Fig. 12). Five years after the floods willows, first of all *Salix alba*, reached routinely the growth over 5 meters. The very tallest specimen was *Alnus glutinosa* in a wet part of the bed D, being approximately 7 meters tall in 2002. In general, the high-grown woody species occurred in groups namely at sites well supplied with water. The above-mentioned depressions in the lower parts of the beds and locations along the inner edge of the upper wide bed are concerned in particular.

Myricaria germanica

Myricaria germanica is a critically endangered species, a shrub of the young sandy and gravelly alluvium of

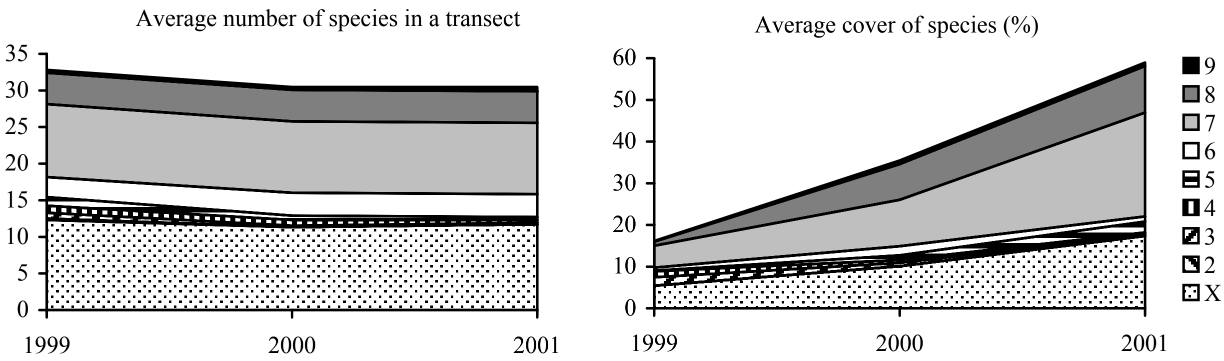


Fig. 11. Development of vegetation according to soil reaction requirements. X – indifferent, 1 – on very acid soils only, 2 – between 1 and 3, 3 – mostly on acid soils, 4 – between 3 and 5, 5 – mostly on low acid soils, 6 – between 5 and 7, 7 – mostly on neutral soils, but also on acid and alkaline ones, 8 – between 7 and 9, 9 – only on neutral or alkaline soils. Note: Only species of known requirements are included

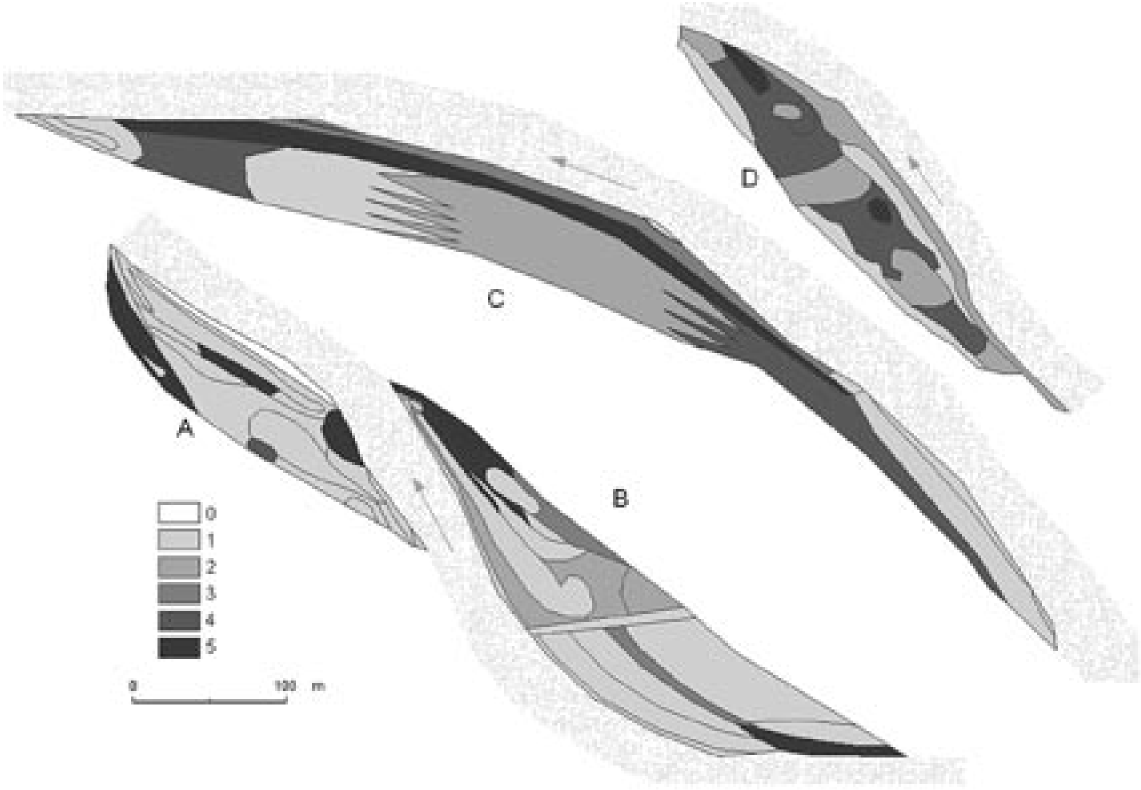


Fig. 12. Woody vegetation in the area at the end of monitoring. 1 – woody species sporadically, seedlings only, 2 – rarely even older specimens, 3 – cover up to 40%, 4 – cover of 40–80%, 5 – cover of 80–100%

mountain and foothills streams. It has no strict requirements for the soil moisture but it is highly heliophilous and without the regular renewal of early succession stadiums in competition with other plants it disappears with time. At present the only known occurrence is on Morávka banks between Nošovice and Dobrá and at several places along the stream Lomná between Dolní and Horní Lomná (HEJNÝ, SLAVÍK 1990; ŠINDLAR et al. 1996). Sporadical findings at secondary sites in quarries, pebble-pits and dumps were reported (CHYTIL pers. commun.).

In the observed area in the neighbourhood of the B3 transect on pebble alluvium several meters aside the permanent water level, an approximately 2 m tall specimen

Table 1. Recorded woody species and their maximum growth

Alnus glutinosa	III	*Corylus avellana*	V1	*Rhus typhina*	V1
Alnus incana	IV	*Crataegus monogyna*	V1	*Ribes alpinum*	V1
Robinia pseudo-acacia	IV	*Eleagnus angustifolius*	V1	*Ribes nigrum*	V1
Salix alba	IV	*Euonymus europaeus*	V1	*Rosa canina*	V1
Salix fragilis	IV	*Fraxinus excelsior*	V1	*Rubus caesius*	V1
Salix purpurea	IV	*Grossularia uva-crispa*	V1	*Rubus idaeus*	V1
Salix triandra	IV	*Ligustrum vulgare*	V1	*Salix aurita*	V1
Salix viminalis	IV	*Myricaria germanica*	V1	*Salix caprea*	V1
Salix × rubens	IV	*Padus racemosa*	V1	*Sambucus nigra*	V1
Salix × rubra	IV	*Picea abies*	V1	*Swida sanguinea*	V1
Acer campestre	V1	*Populus alba*	V1	*Tilia cordata*	V1
Acer pseudoplatanus	V1	*Populus tremula*	V1	*Ulmus glabra*	V1
Betula pendula	V1	*Populus × canadensis*	V1	*Ulmus minor*	V1
Carpinus betulus	V1	*Populus niger*	V1	*Acer negundo*	V2
Cerasus avium	V1	*Quercus robur*	V1	*Malus sp.*	V2

Classes of vertical differentiation (Randuška et al. 1986) was found in the summer 2001. The original assumption that an example of wind propagation from a larger distance is concerned was contested in the end. Several reasons were taken into account: (1) No finding of *M. germanica* had been reported so low down the stream ever before, despite the fact that natural populations had formerly existed in upper parts of the basin and there was no lack of suitable habitats in the locations of the monitored area at that time. (2) The circumstances of the observation are obscure in a way. According to its growth the plant had to arise just after the flood in 1997 or in the following year (ÚRADNÍČEK 2002). It is not likely that the growing specimen would have been overlooked in the neighbourhood of the observed transect during two years of monitoring. (3) Although the specimen produces an amount of seeds annually, absolutely no seedlings were found at similar suitable sites in the surroundings. The environmental conditions seem to be favourable only seemingly, at least for the ecesis of *Myricaria*.

Expansive neophytes

A fast dispersal of expansive neophytes was one of the supposed processes at the newly established sites. The only two of such successful species in this country asserting themselves more in the monitored area were *Reynoutria japonica* and *Solidago gigantea*. Common but by far not so abundant were *Aster novi-belgii, Helianthus tuberosus, Impatiens glandulifera* and *Lupinus polyphyllus.*

Reynoutria japonica

In the native area of south-eastern Asia *R. japonica* occurs from lowlands to subalpine locations. In lowlands it occupies eroded riversides, in mountains it is a plant of early succession stadiums exploiting sites with a regime of regular disturbances (WADE et al. 1994). In the topmost locations it can be found on inhospitable lava plains where it is one of the key species of the initial succession stadiums thanks to the ability of nitrogen accumulation (BÍMOVÁ et al. 2003).

The conditions of newly established sites of the Bečva's pebble alluvium largely agree with those in the land of its origin, as well as with the general ecological strategy of the species. However, the course of colonisation in the observed area is highly differentiated. After the floods on the Bečva River continuous stands originated at flooded locations of the riparian slopes or possibly of the margins of the neighbouring woods, i.e. at normal moist sites with mature soil. The pebble beds were colonised more slowly and in a scattered way. At the beginning (even the third year after the flood) isolated specimen occurred largely. Variedly stately polycormons were created in the following years only. On the whole *R. japonica* covered approximately 2.5% of the alluvium surface in the fifth year. Generally, the progress of the plant is not by far as rapid as for example in analogous conditions of the pebble alluvium on Morávka near Raškovice (ANONYMUS 2003). Neither related *R. sachalinensis*, nor *R.* × *bohemica* were registered there.

Solidago gigantea

Solidago gigantea comes originally from the North America. It colonises sandy soils in river floodplains from the planar to the top part of the submontane stage. It generates a huge number (as many as 20 thousand pieces per specimen) of seeds propagated by wind and animals, fragile rhizomes are spread by streams too. Just the middle part of the Bečva is an example of an area with extensive growths (PYŠEK, TICHÝ 2001).

Only sporadic findings of mostly isolated specimens were made on the pebble beds. More frequently they could be seen at sites with a higher content of fine earth in the substrate. The centre of occurrence with continuous stands was situated outside the wide bed, above all on insolated locations with a coat of flood deposits. *S. canadensis*, although generally more frequent in this country, was not noticed there.

DISCUSSION

In the early succession stadiums, i.e. in open societies, the physiological amplitude of a plant is decisive for its prosperity. Data on species occurrence and dynamics in the area alone can illustrate its width. The information capability of the results of applied Ellenberg's classification evaluating the ecological requirements of plants is rather informative at first, when regularity in the occurrence of species is often hard to find. With the progressing development the situation changes rapidly and the importance of the particular plant specialisations for the final structure of stands becomes still more perceptible. It holds even despite other significant factors such as the propagation ability of species, the structure of immigrating diasporas, the casualness of climatic factors, etc. Among the above followed characteristics all moisture and light requirements of a plant together with its life form seem to be determining for its prosperity. From the beginning hemiheliophytes prevail, species of moist or hydric soils, life form hemicryptophytes (SLAVÍKOVÁ 1986).

During the monitoring the dominance of *Phalaris arundinacea* rose noticeably, covering 15.5% of the area on average in the end. Although its physiological optimum is fine sandy or even clayey substrates, it colonised the barren pebbles successfully in case they were supplied with enough water. In a similar way like KOPECKÝ (1961) reported, the relatively rapid alternation of substrate quality proceeded subsequently namely due to the stripping of fine-grained particles from the water flow during inundation and enrichment of the soil with its own detritus. The increase in water erosion intensity in the adjacent parts of the bed owing to deflection of the streamline by stands of *Phalaris*, however, was not noticed there. An explanation can be found in the extreme fluctuation of flow rates on the Bečva River with an intensive motion of pebbles when the effect of the grass growth is minimal regarding the scale of the bed forming process.

As for woody species, first of all willows logically asserted themselves on the alluvium. They colonise the locations along the watersides best supplied with water in the first place. Perceptible is the colonisation of a locality by particular generations, when on larger areas even-aged stands of different age with expressive dominance of a single species occur. Such a structure comes into existence very likely due to a certain combination of climatic, hydrological and phenological factors. By a particular water level in the time of seeding the seeds can reach only some places and subsequently they must not be washed out or on the contrary get dry. Concrete conditions of the growing season thus affect the extent of colonisation in a particular year. After the occupation of an area further colonisation is limited there, thereby the growth keeps its monotonous age structure to a great extent. JENÍK (1955) illustrated the effect of the water rate year's going for the structure of riparian growths in a similar way.

Neophytes propagate only in a limited scale. *Reynoutria japonica* asserts itself more significantly, nevertheless, with a progressive tendency. Hard to explain is the absence of this plant on the observed bed lying at the highest location up the stream. No specimen was noticed there, although close up the stream it creates lush riparian stands.

The transformation of the river bed resulted in an expressive change of site conditions. Undoubtedly a shift from the original STG *Ulmi-fraxineta carpini* to wetter sites of STG *Saliceta fragilis inf.* occurred there.

With progressing succession the differentiation of growths is well perceptible. The originally slight site differences increase with the development of vegetation and its back incidence. A mosaic structure with frequently sharp bounded segments (patches) comes into existence. On the other hand, with the ongoing progress prosperous plants act still more significantly on their surroundings, farther propagate vegetatively and gradually the process of homogenisation begins. Therefore, further development will depend on the frequency of disturbances. According to the dynamics of floodplain environment the variedly intensive repeated resetting of development by flood water rates to lower stadiums, forming the fluvial succession sere (BUČEK, LACINA 1994), can be expected in the wide river bed.

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Received for publication December 30, 2003
Accepted after corrections April 9, 2004

Raná stadia sukcese lužního lesa v povodňových korytech řek na příkladu Bečvy

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ABSTRAKT: V letech 1999–2001 byla sledována mladá stadia sukcesního vývoje měkkého luhu v širokém korytě Spojené Bečvy vzniklém za povodně v r. 1997. Byly sledovány měnící se podmínky prostředí, opakovaně byla podrobně mapována vegetace štěrkových náplavů. V závislosti na stanovištních podmínkách byly popsány typy biotopů. Údaje o vegetaci byly vyhodnoceny podle životní formy a ekologických nároků zjištěných druhů. Výsledky ukazují na rostoucí diferenciaci původně relativně homogenního prostředí vlivem fluviálních procesů a rozvíjející se vegetace. Obecně úspěšné jsou především hemikryptofyty a hemiheliofyty, stále silněji dominuje *Phalaris arundinacea*. Z dřevin se od počátku uplatňují zejména vrby, na sušších stanovištích rostou izolovaně a s menší vitalitou zástupci dalších rodů. Zjištěný exemplář *Myricaria germanica* byl pravděpodobně vysazen uměle. Z neofytů se ve větší míře, ale velmi nerovnoměrně šíří jen *Reynoutria japonica*. Celkově u nás dosud málo dokumentovaný vývoj podobných společenstev odpovídá STG *Saliceta fragilis inf.*

Klíčová slova: sukcese; povodně; štěrkové lavice; *Myricaria*; *Salix*

Při katastrofální povodni v roce 1997 došlo místy na řece Bečvě v úseku mezi Valašským Meziříčím a Hranicemi na Moravě k zásadnímu přemodelování koryta. V kilometrových úsecích zde místo napřímeného toku s lichoběžníkovým profilem koryta vzniklo často více než 100 m široké řečiště se zákruty a pestrou mozaikou biotopů. Díky poloze mimo zastavěná či jinak intenzivně využívaná území nebylo po povodních nutné přistoupit k novému opevňování či přímo k navracení koryta do původního stavu. Do současné doby tak na lokalitě nerušeně probíhají další procesy říční modelace a vegetace se spontánně vyvíjí. V podmínkách středoevropské kulturní krajiny je to jev ojedinělý. Článek shrnuje výsledky sledování změn v biotopu koryta a jejich průběhu v počátečních letech.

Vývoj byl sledován v letech 1999–2001. Napříč širokým korytem Bečvy byly vytyčeny a geodeticky zaměřeny transekty a formou série fytocenologických snímků opakovaně mapována vegetace. Na základě výsledků sledování byly popsány hlavní procesy říční modelace, definovány typy stanovišť a vyhodnocena úspěšnost hlavních rostlinných druhů a ekologických skupin (Ellenberg et al. 1992).

Ve sledovaném úseku probíhají intenzivní korytotvorné procesy, zejména břehová eroze. V nejexponovanějších úsecích činil pohyb břehové čáry v průměru i několik metrů ročně. Tvar profilu se jinak výrazně neměnil, chod štěrků ale měl značný dopad na rozvoj vegetace v pravidelně zaplavovaných polohách. Podle výsledků sledování má právě zaplavování – jeho frekvence a charakter – hlavní vliv na diferenciaci poříčních společenstev. Z ostatních faktorů je na převážně štěrkovitém substrátu širokého říčního koryta limitující především dostupnost vláhy. Kombinacím uvedených faktorů odpovídají základní typy zdejších terestrických stanovišť.

Nástup vegetace na povodní obnažených plochách probíhal v závislosti na stanovištních podmínkách diferencovaně co do druhového složení i rychlosti. Průměrná pokryvnost se v transektech na konci sledovaného období pohybovala mezi 20,0 a 92,7 %. Druhová rozmanitost poklesla z 229 druhů v roce 1999 na 177 v roce 2001. Důvodem je patrně uzavírání se původně otevřených společenstev. Nejúspěšnějším druhem se postupně stala *Phalaris arundinacea* následována v sušších polohách *Calamagrostis epigejos*, stále výrazněji se ale uplatňovaly vrby – *Salix purpurea*, *S. alba* a *S. fragilis*. Obecně nebyly proti očekávání ani zpočátku nejčastější terofyty, ale po celou dobu sledování poměrně výrazně převládaly hemikryptofyty. Pokud se týká nároků na vláhu, zdaleka nejvíce byly zastoupeny druhy normálně až středně vlhkých půd, jinak druhy téměř nebo plně heliofytní. Trvale a stále silněji dominantní byly druhy nitrofilní, což odpovídá trofnosti fluviálních sedimentů obecně.

Z dřevin byly hojné především vrby, které ve vlhkých polohách tvořily až 5 m vysoké zapojené porosty, místy bohatě s příměsí *Alnus glutinosa, A. incana, Salix viminalis, S. triandra* aj. Na sušších stanovištích se rozptýleně a většinou s menší vitalitou vyskytovaly další druhy – především *Robinia pseudacacia, Populus nigra* a *Fraxinus excelsior*. Vůbec nejvyšším exemplářem dřeviny byla *Alnus glutinosa*. Pozoruhodný je zjištěný výskyt *Myricaria germanica,* který, ač velmi vitální a bohatě plodící, je přítomen v jediném exempláři. Nelze proto vyloučit, že byl na lokalitu vysazen uměle.

Proti očekávání nedošlo na nově vzniklých stanovištích štěrkových lavic k expanzi invazivních neofytů. Z možných druhů se výrazněji uplatňuje jen *Reynoutria japonica,* která velmi nerovnoměrně pokrývá celkem asi 2,5 % sledované plochy. V navazujícím okraji lužního lesa je však velmi hojná a i v širokém korytě lze očekávat její další rozvoj.

S postupující sukcesí je dobře patrná diferenciace porostů v závislosti na původně nevelkých rozdílech stanovištních podmínek, které jsou zpětným působením vegetace prohlubovány. Na druhou stranu s postupným rozvojem nejúspěšnějších druhů se zvyšuje schopnost kolonizovat nové plochy navzdory nepříznivým stanovištním podmínkám či druhové konkurenci a probíhá tak i proces určité homogenizace. Další vývoj bude záležet na frekvenci a charakteru disturbancí, očekávat lze formování dynamické fluviální sukcesní série (BUČEK, LACINA 1994). Současný vývoj odpovídá STG *Saliceta fragilis inf.*

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