



## Recovery of alluvial meadows after an extreme summer flood: a case study

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### Abstract

Recovery of alluvial meadows after one of the highest floods in history (1997) was studied for six years in the floodplain of the Morava River, in the southeastern part of the Czech Republic, central Europe. Above-ground vegetation did not survive the flood, but 23 species, i.e. 20% of all species (117) recorded during the study, regenerated from underground organs shortly after the flood. Other species established later from the seed bank. Various ruderal species were typical for the first 4 years, but, gradually, typical meadow species largely prevailed. The total number of species increased during the first 4 years, then decreased slightly as some ruderals disappeared from the recovering meadows. Recovery of the meadows seemed to be nearly completed after 6 years, especially in lower elevations, indicating rather good adaptation of the studied alluvial meadows to flooding. Both direct vegetative regeneration of resident species and secondary succession contributed to vegetation development.

**Key words:** Flooding, Secondary succession, Species number, Vegetation change, Vegetative regeneration.

### 1. Introduction

Natural and semi-natural vegetation in any floodplain with a retained natural flow regime is well adapted to flooding (Ellenberg 1996; Baird, Wilby 1999; Lytle, Poff 2004). In such floodplains, biota, flow regime and geomorphology are mutually linked, forming an integrated, highly dynamic system, which can be seen as resilient in a short time-scale and resistant over a longer perspective (Neiman, Décamps 1990). The adaptations can be morphological, biochemical or through various life-history traits (Blom, Voeselek 1996; Hroudová

*et al.* 2004). Some life-history adaptations are most effective under the predictable, i.e. regular, flooding regime, while others are more important under unpredictable floods (Lytle, Poff 2004). However, humans have largely changed the natural character of both the flow regimes and floodplains of most European rivers (Boon *et al.* 2000), so the present, largely transformed plant communities may not be completely adapted to excessive flooding in comparison with natural ones. Moreover, really extreme flooding may act as a strong selective factor in any occasion (Blom 1999; Vervuren *et al.* 2003; Lytle, Poff 2004).

In July 1997, the eastern part of the Czech Republic experienced a sudden and long-lasting extreme flood in the middle of the vegetation season. The floodplain under consideration was flooded for three weeks, and in depressions for more than one month. As a result all above-ground biomass died. Immediately after the emerging of the floodplain surface, regeneration and secondary succession was observed. This study had the following aims: (a) to follow changes in species composition in three particular sites differing in elevation; and (b) to identify species that were able to survive flooding and regenerate immediately.

## 2. Materials and methods

### Study site

The study area was in the flat floodplain of the lower stretch of the Morava River near the town of Veselí nad Moravou in the southeastern part of the Czech Republic (ca. 48°58'N, 15°22'E, altitude c.170 m). The river flows in a partly natural river bed, normally c. 3 m below the floodplain surface. Dikes were built at a distance of approximately 20m from the river in the first half of 20th century, so the rest of the floodplain had not been flooded for a long time. The floodplain is 4 km wide on average.

The climate is transitional between oceanic and continental, with average annual temperature of 9.5°C and annual precipitation of 585 mm (Quitt 1971). The floodplain is formed by Tertiary and Pleistocene sand and gravel sediments, which are covered by late Holocene alluvial silt of up to several meters thick (Opravil 1983).

The recent vegetation cover consists mostly of secondary alluvial meadows, which are regularly cut twice a year. Meadows in the depressions are dominated by *Alopecurus pratensis*. They are rather species poor and can be classified as *Alopecurion pratensis* - wet variant. Most of the floodplain is covered by species rich *Alopecurus* meadows classified as transitional between *Alopecurion pratensis* and continental *Cnidion venosi* alliances. Mesic meadows of the alliance *Arrhenatherion* are typical for the elevated parts of the floodplain (Balátová-Tuláčková 1966).

### Methods used

The floodplain was visited in August 1997, immediately after flooding, and in October 1997, when sites were selected for the establishment of permanent plots. On both dates, species regenerating vegetatively and species germinating from the seed bank were recorded. In spring 1998,

eleven permanent plots 5 × 5 m in size were fixed in three main habitats, i.e. depressions (4 replicate plots), elevations (3 plots) and intermediate sites (4 plots). Phytosociological relevés (percentage scale) were recorded in each plot every year in the second half of May, i.e. just before the first cut.

Jaccard's coefficient (Kent, Coker 1992) was used to express floristic similarity between samples. This measure was used by comparing values from the same plot sampled in two successive years, to reflect the rate of vegetation change (Bornkamm 1981).

Univariate data (i.e. species numbers and Jaccard's coefficients) were analyzed using repeated measures ANOVA in Statistica software (Anonymous 1998) and loess smoother in R1.8 software (R Development Core Team 2003). Vegetation (multivariate) data were analyzed using CANOCO for Windows 4.5 software (ter Braak, Šmilauer 2002). Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) were used to evaluate main trends in vegetation composition. Unimodal methods were used because the length of the gradient in DCA exceeded 3 SD units (Lepš, Šmilauer 2003). Cover values were log-transformed prior to the analyses; species occurring only in one relevé were omitted. In CCA, plot identity was used as a covariable and the significance of the model was tested using a Monte Carlo permutation test adjusted to the repeated measures structure (Lepš, Šmilauer 2003).

Nomenclature of plant species follows Rothmaler (1994).

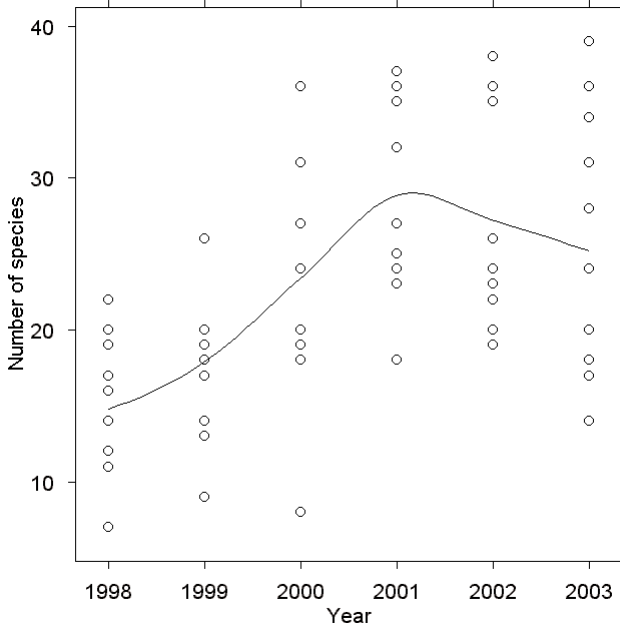
## 3. Results

### Regeneration in 1997

Only 23 species, i.e. 19.7 % of the total number of species recorded during the six year study (117), survived the long lasting flood. These species regenerated after flooding in most of the studied plots from underground organs (roots, rhizomes, etc.) (see Appendix). Some others had already regenerated from the seed bank in autumn 1997, namely *Plantago lanceolata*, which dominated some plots. In total, 43 species were found during autumn 1997 and the cover of vegetation reached c. 40 percent on average, except for the deepest depressions, which were still almost bare.

### Changes in species number

The effect of time and differences between particular vegetation types were tested by repeated measures ANOVA regarding the number of species. Both the effect of time, i.e. differences in



**Fig. 1.** Number of species per plot. The trend in species number change was visualized by loess smoother (degree=2, span=2/3).

average number of species in particular years, and the effect of vegetation type, i.e. differences in average number of species in all plots of the particular type, were highly significant ( $F=8.83$  and  $26.15$ , respectively;  $p=10^{-6}$  for both tests). Among the vegetation types, depressions had the lowest number of species on average, and elevations the highest. The time and vegetation type interaction was also significant ( $F=2.26$ ,  $p=0.03$ ). Thus, the number of species changed differently in particular vegetation types, but the quite low significance indicates that the differences were much smaller in comparison with the main effects. The only marked difference was a one-year delay in the increase of species number in depressions.

Changes in species number for all plots are summarized in Fig. 1. The number of species per plot increased from the beginning of recovery to the fourth year after flooding (2001), when it reached its highest value. Then a certain decrease was evident as some ruderals disappeared.

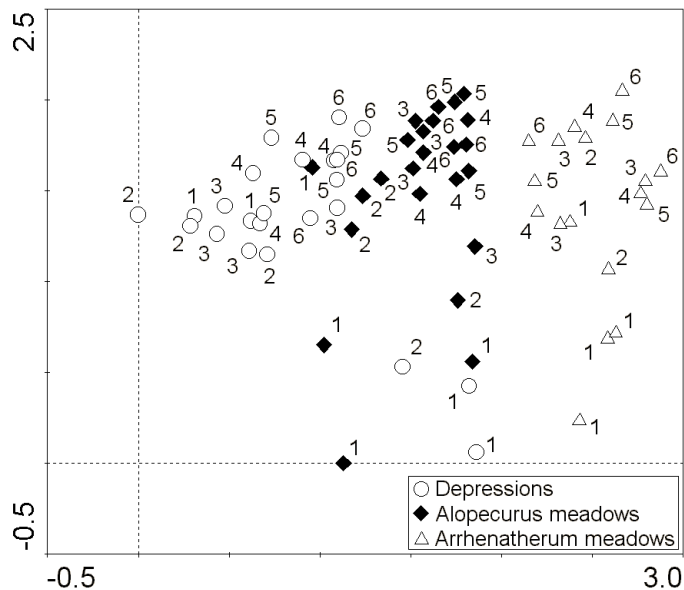
**Community composition**

The first DCA ordination axis explained 12.7 percent of the variance and can be interpreted as reflecting a

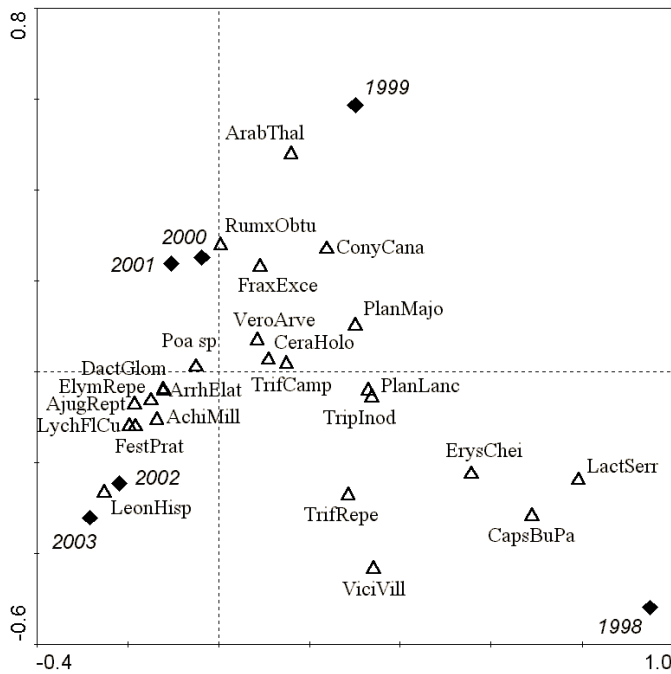
moisture (elevation) gradient (Fig. 2). The three particular vegetation types (habitats) clearly separated along this axis. The second ordination axis explained 6.9 percent of the variance and reflected the gradient of increasing time since flooding. It is evident that vegetation was changing more rapidly during the first two or three years after flooding than later.

The analysis of similarity between samples (Jaccard's coefficient) revealed a significant effect of time (ANOVA,  $p = 4.10 \cdot 10^{-5}$ ), but differences between vegetation types and the interaction were not significant. Multiple comparisons (Tukey test) showed that only the values from 1998 and 1999 differed significantly from the others. This indicates that species composition of the studied communities changed notably between these two years, but mainly quantitative changes in participation of species occurred later on.

Results of the direct ordination method (CCA), demonstrating the relationship between community composition and time, are presented in Fig. 3. As indicated by previous analyses, the rate of recovery of the studied communities differed between years (faster development in the first years, slower later). Therefore, time was coded as a set of nominal variables (years) instead of a single continuous (quantitative) variable. No other variables were used. Because plot identity was used as a covariable, the results represent a trend common



**Fig. 2.** DCA ordination diagram of study plots. The first and second ordination axes are displayed. The year of sampling is indicated by numbers from 1 (1998) to 6 (2003).



**Fig. 3.** CCA ordination diagram with particular years as independent variables and plot identity as covariables. The first and second ordination axes were considered. The species that fit the model best are shown. Species name abbreviations consist of the first four letters of the respective generic and specific names (see the Appendix).

to all plots (vegetation types). All canonical axes together explained 16% of the variance in species data and the model was non-significant at the 5% level. However, the insignificant result is probably caused by the low number of replications and some interpretable trends can be identified in the diagram. The first ordination axis, which explained 8.5 percent of variance, is correlated mostly with the year 1998. The second axis, which explained 2.9 percent of variance, is correlated mostly with the year 1999. Each other axis explained less than 2 percent of the variance. It shows again that the main differences were between the years 1998 and 1999 and the others. Ruderal and weedy species were relatively abundant in the first years after flooding, whereas they were replaced by meadow species in the later years (Fig. 3).

#### 4. Discussion

Vegetation occurring in the lower parts of a floodplain is generally better adapted to flooding than vegetation in the higher parts. This is because a higher frequency of floods is the factor by which adapted species are selected (Blom 1999). That also held for the case studied here. Recovery of *Alopecurus pratensis* meadows, which occur in the low and intermediate eleva-

tions, was faster than that of *Arrhenatherum elatius* meadows in the elevated parts of the floodplain.

A different recovery rate of dominant species seems to be crucial in producing differences between particular vegetation types in their reaction to flooding. *Alopecurus pratensis* started to regenerate immediately after flooding from underground organs and, after two seasons, its regeneration was more or less completed. The cover of this species reached 60-70% (in wet depressions up to 90%) and remained stable afterwards. On the contrary, regeneration of *Arrhenatherum elatius* was considerably slower. During the first two years after flooding, its cover reached only 1-3% and after 6 years it was about 40%. These results correspond with those of Blom, Voesenek (1996: 291, Fig. 1) and general ecological observations of Balátová-Tulácková (1966) from a downstream part of the same floodplain. Unfortunately, exact vegetation records from the studied area prior to the flood are not available; we only visually observed the area in earlier years and noticed only the dominant species.

Typical species of alluvial meadows regenerated immediately after the flood from underground organs (Ellenberg *et al.* 1991; Chytrý, Tichý 2003) (see Appendix). Shortly after the flood, many ruderal and some meadow species established from the seed bank, e.g. *Capsella bursa-pastoris*, *Matricaria maritima* ssp. *inodora*, *Plantago major*, *Plantago lanceolata*. It was impossible to distinguish between seeds that survived the flood in the site and those that were transported by the flood water. Some species with light anemochorous seeds probably colonized the sites after the flood, such as the ruderal species *Conyza canadensis* and the meadow species *Leontodon hispidus*. Many ruderal species colonized gaps before the meadow species re-formed a compact cover. Ruderal species were less frequent in depressions, where mostly resident species regenerated.

Water has been repeatedly reported as an efficient vector for dispersal of invasive alien species (Pyšek *et al.* 2002). However, their participation was negligible in our case.

The decrease in total species number in the last two years of observation was caused by the decline of ruderal species from the recovered grassland. Fast competitive exclusion, especially of annual ruderals, is typical of many secondary successions (Walker, del Moral 2003; Vervuren *et al.* 2003). A similar decrease in the number of

species after four years was observed during an experimental restoration of alluvial meadows in another Central European river, the Lužnice (Straškrabová, Prach 1998).

The observed process of recovery consisted of (i) a direct vegetative regeneration of resident species and (ii) secondary succession *per se* when new species established. The proportion of directly regenerated species among all species recorded during the study was ca. 20%, which can be used as a very approximate indication of the relative importance of these two processes in the recovery of the studied meadows. Despite the rather drastic impact of the extreme flood on the vegetation (no above-ground organs survived except those of *Polygonum amphibium*, which formed natant forms), the recovery of the studied alluvial meadows was rather fast, especially in the lower and intermediate parts of the floodplain. After 6 years, the regeneration seemed to be more or less complete, especially in the *Alopecurus pratensis* dominated meadows. Some changes in species composition can be expected in the future, due to the establishment of some other species. However, it is difficult to make any exact prediction, because of the lack of data prior to the flood and the lack of a reference state.

The studied alluvial meadows appeared to be rather well adapted to floods, including one of the highest in the history of the area. Our results on vegetation regeneration of alluvial meadows after flooding corresponded to general expectations (Blom, Voeseck 1996; Blom 1999; Lytle, Poff 2004). However, this particular problem has only rarely been studied directly. We are aware of only one other study investigating recovery of alluvial meadows after flooding, which was performed in the floodplain of the Rhine River (Vervuren *et al.* 2003). Our results are in general accordance with those obtained by that study.

The results of this study support potential rehabilitation of river systems (de Waal *et al.* 1998). The restoration of a regular flooding regime, where a river was disconnected from its floodplain, should not have a negative effect on biota adapted to floodplain conditions. Restoration of a natural flooding regime in non-inhabited parts of the floodplain can be recommended as a part of integral flood-defense measures.

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**Appendix**

The presence of species in the studied sites in the period between 1997 (0) and 2003 (6). Those species which regenerated obviously from underground organs shortly after flooding (August-October 1997) are printed **in bold**.

- Acer campestre* 4  
*Agropyron repens* 0123456  
*Achillea millefolium* agg. 0123456  
*Ajuga reptans* 3456  
*Allium scorodoprasum* 0123456  
*Alopecurus aequalis* 1  
***Alopecurus pratensis*** 0123456  
*Arabidopsis thaliana* 24  
*Arctium* sp. 0345  
*Arrhenatherum elatius* 123456  
*Aster* sp. 4  
*Astragalus glycyphyllos* 5  
*Bromus hordeaceus* 123456  
*Campanula patula* 123456  
*Campanula rapunculoides* 3  
*Capsella bursa-pastoris* 014  
***Cardamine pratensis*** 0123456  
*Carduus acanthoides* 245  
*Carduus personata* 1  
***Carex acutiformis*** 046  
*Carex hirta* 0123456  
*Carex praecox* 1  
***Carex vulpina*** 023456  
*Centaurea jacea* 23456  
*Cerastium holosteoides* 0123456  
*Chenopodium album* 0  
*Chenopodium polyspermum* 01  
*Cirsium arvense* 0123456  
*Cirsium canum* 123456  
*Cirsium vulgare* 0123456  
***Colchicum autumnale*** 0123456  
*Convolvulus arvensis* 23456  
*Conyza canadensis* 124  
*Crataegus* sp. 46  
*Crepis biennis* 36  
***Dactylis glomerata*** 0123456  
*Daucus carota* 123456  
*Deschampsia cespitosa* 23456  
*Epilobium* sp. 013  
***Equisetum arvense*** 0123456  
*Erigeron annuus* 123456  
*Erophila verna* 4  
*Erysimum cheiranthoides* 0125  
*Euphorbia esula* 3456  
*Festuca pratensis* 3456  
*Festuca rubra* 2456  
*Fraxinus excelsior* juv. 0123456  
***Galium album*** 0123456  
*Galium aparine* 3  
***Galium boreale*** 013456  
*Galium wirtgenii* 3456  
***Geranium pratense*** 023456  
*Geum urbanum* 25  
*Glechoma hederacea* 23456  
*Holcus lanatus* 356  
*Humulus lupulus* 46  
*Hypericum perforatum* 5  
*Lactuca serriola* 12  
*Lamium purpureum* 3  
*Lathyrus pratensis* 23456  
*Lathyrus tuberosus* 4  
*Leontodon hispidus* 56  
*Leucanthemum ircutianum* 0123456  
*Linaria vulgaris* 23456  
*Lotus corniculatus* 3456  
*Lychnis flos-cuculi* 3456  
*Lysimachia vulgaris* 456  
***Lythrum salicaria*** 024  
*Matricaria maritima* ssp. *inodora* 0123456  
*Myosotis arvensis* 123456  
***Pastinaca sativa*** 0123456  
***Phalaris arundinacea*** 023456  
*Plantago lanceolata* 0123456  
*Plantago major* 012356  
*Poa pratensis* 123456  
***Polygonum amphibium*** 01234  
***Potentilla anserina*** 023456  
***Potentilla reptans*** 0123456  
*Prunella vulgaris* 3456  
*Pseudolysimachium longifolium* 6  
*Quercus robur* 5  
*Ranunculus acris* 13456  
*Ranunculus auricomus* 123456  
***Ranunculus repens*** 0123456  
***Rorippa palustris*** 01234  
*Rosa* sp. 34  
*Rubus* sp. 23456  
*Rumex acetosa* 23456  
***Rumex crispus*** 0123456  
*Rumex obtusifolius* 2345  
***Sanguisorba officinalis*** 012346  
*Serratula tinctoria* 46  
*Setaria viridis* 0  
*Silaum silaus* 46  
*Silene pratensis* 56  
*Solidago canadensis* 5  
*Sonchus oleraceus* 0  
*Stellaria graminea* 3  
*Symphytum officinale* 0123456  
*Tanacetum vulgare* 23456  
*Taraxacum* sp. 0123456  
*Trifolium campestre* 0123456  
*Trifolium dubium* 1236  
*Trifolium hybridum* 123456  
*Trifolium pratense* 23456  
*Trifolium repens* 1456  
*Urtica dioica* 01  
*Valerianella locusta* 5  
*Verbascum blattaria* 45  
*Veronica arvensis* 123456  
*Veronica serpyllifolia* 012456  
*Vicia angustifolia* 123456  
*Vicia cracca* 2345  
*Vicia hirsuta* 123456  
*Vicia villosa* 16  
*Viola hirta* 23456  
*Viola pumila* 23456.