Responses and adaptations of collembolan communities (Hexapoda: Collembola) to flooding and hypoxic conditions

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Abstract – Standard ecological methods (pitfall traps, trunk eclectors and soil cores) were used to evaluate collembolan community responses to different flooding intensities. Three sites of a floodplain habitat near Mainz, Germany, with different flooding regimes were investigated. The structures of collembolan communities are markedly different depending on flooding intensity. Sites more affected by flooding are dominated by hygrophilic and hygrotolerant species, whereas the hardwood floodplain is dominated by mesophilic species. The survival strategies of the hygrophilic and hygrotolerant species include egg diapause and passive drifting. The physiological adaptations to hypoxic conditions of several collembolan species were analyzed using a microcalorimeter. The activities were tested under normoxic and hypoxic/anoxic conditions as well as during post-hypoxic recovery. Lactate was increased after hypoxic intervals in the species studied, suggesting that, in addition to a massive decrease in metabolic rate, a modest glycolytic activity may be involved in the tolerance to hypoxia.

Index terms: behavioral adaptation, ecological adaptation, egg diapause, inundation, morphological adaptation, physiological adaptation.

Introduction

Floodplains are among the most diverse and fluctuating terrestrial habitats and offer a wide variety of ecological niches for animals and plants. Sterzyńska (2003) characterized floodplains as hotspots of biodiversity. Amazonian inundation forests are notable as short-term refuges and long-term generators of species richness and taxon pulses, a result from the monomodal and predictable flood pulse and the stable climatic conditions over long evolutionary periods (Erwin & Adis, 1982; Junk, 2000; Adis & Junk, 2002). These unique conditions have enabled the development of morphological, phenological, physiological and behavioural adaptations to inundation and hypoxic conditions, especially in many invertebrate taxa.

The floodplains of Central Europe have a less predictable flood pulse but a more significant seasonal...
light and temperature pulse (summer/winter), which is insufficient for the development of intrinsic adaptation strategies (Weigmann & Wohlgemuth-von Reiche, 1999; Adis & Junk, 2002). Instead, most species combine high reproduction rates with remigration after flood events (Adis & Junk, 2002; Rothenbücher & Schaefer, 2006), and relatively few species show morphological, phenological and physiological adaptations to cope with flooding (Tamm, 1986; Zulka, 1994; Rothenbücher & Schaefer, 2005, 2006). Such adaptations are designated as “pre-adaptations”, primarily because of the short evolutionary period since the last Ice Age, but also due to the lack of a predictable inundation regime (Weigmann & Wohlgemuth-von Reiche, 1999).

Ghilarov (1978) regards soil invertebrates as good indicator groups since they reflect changes in soil conditions. Collembola, as a key group inhabiting all soil layers with large populations, play an important role in soil food webs, and according to Russell et al. (2002) show great flexibility to soil disturbances. Changes in collembolan communities along European riparian habitats have been described by Deharveng & Lek (1995), Sterzyńska & Ehrensberger (1999), Russell et al. (2004) and Russell & Griegel (2006). In this investigation we demonstrate the surprisingly high number of strategies of springtails to cope with flooding in a Middle European floodplain habitat.

**Materials and Methods**

The study site is a typical fragmented floodplain forest of the Upper Rhine region near Heidenfahrt, Rhine, Germany (Figure 1 A). It is divided into three microhabitats according to the flooding regime: the hardwood floodplain; the softwood floodplain; and the new softwood floodplain. The hardwood floodplain (*Querco-Ulmetum*) is a rare natural floodplain, but not a primary forest (for example, alder and maple have been planted). The soil structure comprises a spatial sequence of small hillocks and depressions. The herbaceous plant layer differs between these sites. The depressions are partially free of any plants, whereas the hillocks are covered with dense vegetation. Also, the groundwater level varies within this characteristic mosaic for riparian forests. The dominant plant species of the tree stratum are *Quercus robur, Acer campestre*, *Ulmus minor* and *Tilia cordata* (hillocks), while *Corylus avellana* and *Ribes rubrum* dominate the shrub layer. The herb layer is composed of *Scilla bifolia*, *Allium ursinum*, *Anemone nemorosa*, *Hedera helix* and *Anemone ranunculoides*. The soil is characterized as a typical fluvisol with high clay and sand content, and a flood impact (flood duration) of less than ten days per year. Since the dry summer of 2003 there have been only two partial floods and no total flood event (Figure 1 B). As a consequence there is a comparatively large humus layer, especially on the hillocks.

The softwood floodplain (*Salicetum albae*), a constructed river bank reinforcement system that accumulates large amounts of debris after flooding (flood duration superior to 40 days per year). The tree stratum is dominated by *Salix alba* and *Salix rubens*, and the shrub layer is composed of *Salix purpurea* and *Salix viminalis*. The herb layer temporarily consists mainly of *Urtica dioica*, due to the medium flood impact. The soil is characterized as a sandy fluvisol with clay and a small humus layer.

The new softwood floodplain (*Salicetum albae*) has developed since the extreme hot and dry summer of 2003. Due to this extreme event the water line of the river Rhine decreased markedly and the riverbank was displaced 30–35 m towards the middle of the river. Seedlings of *S. alba* were able to colonize the new sandbanks because the water line was comparatively low until spring 2005. These newly developed softwood floodplains are positioned on both sides of the riverbank reinforcement system (Figure 1). They consist only of hygrophilic and ruderal plant communities in the understory (*Limosella aquatica, Centaurium pulchellum* and *Juncus bufonius*) and of *S. alba* in the tree stratum, because of the strong flood intensity (flood duration superior to 100 days per year). The soil is a sandy river soil lacking a humus layer.

Trunk eclectors, pitfall traps and soil cores were used for the evaluation of spatial and temporal dynamics of the collembolan population. Trunk eclectors (*n* = 6) were only used in the hardwood floodplain. They give information about the atmobiotic species composition, but their primary purpose was to quantify vertical migrations during flood events. Pitfall traps (*n* = 12 for the hardwood floodplain and *n* = 6 for the two softwood floodplains) were randomly...
placed to assess the spatial distribution of epedaphic species. Sampling took place between March 2005 and March 2008 (with traps replaced every 14 days to provide phenological data for selected species). As softwood floodplains were sampled with pitfall traps only from October 2007 until March 2008, the

Figure 1. Overview and aerial view (D-Sat, Buhl Data Service GmbH and GeoContent GmbH; modified by subsequent labelling) of the study area in Germany with the position of the three different microhabitats: hardwood floodplain, softwood floodplain and newly developed softwood floodplain (A). Detail of the hardwood floodplain forest under control and flooding conditions (B). AB7, hardwood floodplain; AE2 and LB1, softwood floodplains; LA0, position of the newly developed softwood floodplain; FO2, position of the riverbank after drought; HE4 and HE5, dike.
different floodplain sites were compared only for this sampling period. Soil cores (diameter = 4.8 cm, depth = 10 cm) were used for modelling temporal dynamics and the spatial distribution of eu- and hemiedaphic species. On each sampling date, 40 soil cores were extracted for 18 days; 20 were taken from each hardwood floodplain and 10 soil cores were taken from each softwood floodplain. Microarthropods were extracted for 18 days (25–60°C) with a modified Kempson apparatus (Kempson et al., 1963). The fixing agent was picric acid (2–3%) and ethanol (70%) was used for storage and further processing of the samples.

Orchesella villosa (epedaphic), Sinella coeca and Sinella curviseta (hemiedaphic) as well as Folsomia candida (euedaphic) were selected for physiological experiments on hypoxia and anoxia, because of their abundance and ease of culturing. A Calvet MS 80 twin calorimeter (Setaram, France) was operated at 21.9°C and proved sufficiently sensitive to measure the rate of heat dissipation of the springtails. The calorimeter was equipped with two cells (100 mL volume each): one to hold the experimental animals in a glass vial while the other served as reference cell, so that all changes in heat flow not caused by the experimental animals were automatically eliminated (Wegener & Moratzky, 1995). A flow of synthetic air (20% O₂, 80% N₂, Messer Griesheim, Frankfurt) through both cells was maintained at a constant rate (500±20 mL h⁻¹) to produce normoxia. Hypoxic/anoxic conditions were obtained by changing the gas flow to pure nitrogen at the same flow rate. In order to prevent water loss by evaporation from the animals, both artificial air and nitrogen were moistened (by passing through water in gas-washing bottles kept at 21.9°C) before being entered into the calorimeter. The calorimeter was calibrated by means of Joule cells and a 54 µV mW⁻¹ calibration factor (sensitivity). The baseline signal of the calorimeter with empty cells was followed between experiments and the heat flow data were corrected for shifts in the baseline, if necessary. The calorimeter signals were recorded every minute and the data were analyzed by the Setsoft 2000 software (Setaram, France).

Because experimental animals were kept in glass vials, strict anoxia might not have been reached in the microcalorimeter. Therefore a purpose-made small glass container was used to produce strict anoxic conditions (100% pure N₂) and to observe the animals during the experiments. This was indicated because some collembolan species have been reported to survive very low oxygen partial pressures (Joosse, 1966; Paul et al., 1997; Zinkler et al., 1999). Only species with a long survival time under severe hypoxic conditions (microcalorimeter) were tested in the glass container. Additionally, the lactate content of the animals was photometrically measured (Gruschczyk & Kamp, 1990) to evaluate metabolism during anoxia. In order to exclude the effect of gut bacteria, the springtails were fed a diet of agar containing a mixture of three different antibiotics (ampicillin, 100 mg L⁻¹; kanamycin, 50 mg L⁻¹; and tetracyclin, 30 mg L⁻¹) for six days.

All data were analyzed using the Statistica 6.1 software (Statsoft Inc., USA). For the comparison of the different microhabitats, descriptive statistics such as density, species composition, similarity index (Wainstein) and cluster analysis (Ward method, euclidian distances) were applied. For the statistical analysis of the soil cores, a nonparametric Mann-Whitney U-test was performed, because of the aggregation effects of springtails in the soil. Data of metabolite measurements were normally distributed (Kolmogorov-Smirnov test). They were tested for differences between means by the analysis of variance (ANOVA). Results were considered significant if p<0.05, and the levels of higher significance (p<0.01) are given in the text. Data are presented as arithmetic means±standard deviations.

Results and Discussion

Only two species (O. villosa and Lepidocyrtus lignorum) showed increasing densities in the trunk eclectors during the partial flood of April 2006. Among these, only O. villosa performed an active vertical migration during the flood period. Marx et al. (2008) detected vertical migration of L. lignorum without flood disturbance. These are preliminary findings that need confirmation. The similarity between the epedaphic species compositions of the hardwood and both softwood sites was only 7.63% (Wainstein similarity). This reflects the appearance and dominance (>50%) of some epineustic and hygrophilic species like Sinithurides sp., Podura aquatica and Isotomurus sp. in the two softwood floodplains (Table 1). These species are morphologically...
adapted (Palissa, 2000) for living on the surface of the water or on river banks. *Protaphorura campata* and *P. armata* were found only in both softwood floodplains and in higher numbers in the depressions of the hardwood floodplain after the partial flood (Tables 1 and 2). These results suggest a passive drifting of *Protaphorura* sp. within debris. Griegel (2000) extracted different soil arthropods from debris samples of the Oder river in Germany and found many individuals of the *Protaphorura* genus. Furthermore, specimens of *P. campata* had a survival time of more than 50 days on the water surface in a laboratory experiment (Griegel, 2000). The possibility of prolonged passive drifting of springtails was also proposed by Coulson et al. (2002) and Moore (2003).

In the hardwood floodplain, a more ubiquitous and mesophilic species composition dominated. Because no total floods occurred, it seems that these species replaced the specialized hygrophilic and epineustic species. Russell et al. (2004) and Russell & Griegel (2006) detected a distinct succession of ecologically isovalent collembolan groups according to the flood intensity in a similar habitat in the Upper Rhine valley. They found strong hygrophilic species such as *Sminthurides* ssp., *Isotomurus palustris* or *P. aquatica* limited to frequently inundated areas, whereas flood-intolerant and mesophilic species were generally found in higher, less frequently flooded sites or elsewhere only many weeks or months after inundation (Russell et al., 2004).

The hemi- and euedaphic species also showed a distinct succession according to flood intensity (Table 2). In both softwood floodplains, in addition to the typical epineustic genus *Sminthurides* sp., the species *Isotomiella minor*, *Mesaphorura hygrophilica* and *Anurida uniformis* also predominate. The possible (pre-) adaptation of *I. minor* and *M. hygrophilica* against inundation is egg dormancy (Rusek, 1984; Gauer, 1997). After the flood the juveniles hatch very quickly, recolonize the available resources with little competition, and multiply to large numbers. The hemi- and euedaphic collembolan community structure of the hardwood floodplain resembles that of the epedaphic species. Here, mesophilic and ubiquitous

Table 1. Species composition, number of individuals and dominance of the collembolan population in the pitfall traps (10/2007–5/2008).

| Species                  | No. of individuals | Dominance (%) |
|--------------------------|--------------------|---------------|
|                         | Hardwood floodplain (n = 12) |               |
| *Lepidocyrtus lignorum*  | 187                | 34,308        |
| *Orchesella villosa*     | 794                | 14,855        |
| *Lepidocyrtus curvicolis*| 570                | 10,611        |
| *Ceratophysella denticulata* | 368             | 6,850         |
| *Sminthurinus aureus*    | 287                | 5,343         |
| *Pogonognathelius flavescens* | 279             | 5,194         |
| *Dicrytoma ornatia*      | 215                | 4,002         |
| *Entomobrya macrorum*    | 139                | 2,587         |
| *Isotoma viridis*        | 123                | 2,290         |
| *Alacma fusca*           | 98                 | 1,824         |
| *Xenyllodes armatus*     | 83                 | 1,545         |
| *Orchesella cincta*      | 82                 | 1,526         |
| *Pseudachorutes subcrassus* | 77               | 1,433         |
| *Lepidocyrtus lamahinus* | 66                 | 1,229         |
| *Tomocerus vulgaris*     | 58                 | 1,080         |
|                         | Softwood floodplains (n = 6) |               |
| *Sminthurides aquaticus* (1) | 138             | 21,133        |
| *Lepidocyrtus lignorum*  | 108                | 16,539        |
| *Sminthurides malgremi* (1) | 92              | 14,089        |
| *Isotomurus palustris* (1) | 83                | 12,711        |
| *Sminthurinus aureus*    | 81                 | 12,406        |
| *Protaphorura sp.*       | 57                 | 8,729         |
| *Lepidocyrtus lanahinus* | 14                 | 2,144         |
| *Entomobrya nivalis*     | 13                 | 1,991         |
| *Podura aquatic* (1)     | 9                  | 1,378         |
| *Isotomurus maculatus* (2) | 9                | 1,578         |
| *Lepidocyrtus cyanus*    | 8                  | 1,225         |
| *Orchesella flavescens*  | 8                  | 1,225         |
| *Vertagopus arboraeus*   | 7                  | 1,072         |

(1)Epineustic and hygrophilic species.

Table 2. Comparison of total collembolan individual numbers of randomly selected soil cores (n = 20) under control conditions, and following the partial flood of April 2006. Only the most dominant collembolan species are presented.

| Species                  | Hardwood floodplain hillocks | Hardwood floodplain depressions | Hardwood floodplain depressions - flood | Softwood floodplain | New developed softwood floodplain |
|--------------------------|------------------------------|---------------------------------|-----------------------------------------|---------------------|----------------------------------|
| *Folsomia fimetaria*     | 135                          | 80                             | 3                                       | 0                   | 0                               |
| *Folsomia quadrioculata* | 90                            | 80                             | 3                                       | 0                   | 0                               |
| *Lepidocyrtus lignorum*  | 187                          | 9                              | 0                                       | 1                   | 0                               |
| *Pseudosinella alba*     | 159                          | 19                             | 0                                       | 0                   | 0                               |
| *Heteromurus nitidus*    | 92                            | 13                             | 0                                       | 0                   | 0                               |
| *Mesaphorura krausbaueri* | 27                          | 7                              | 8                                       | 0                   | 0                               |
| *Isotomiella minor*      | 11                            | 17                             | 187                                     | 334                 | 208                             |
| *Mesaphorura hygrophilica* | 0                            | 0                              | 0                                       | 48                  | 0                               |
| *Anurida uniformis*      | 1                            | 0                              | 0                                       | 24                  | 80                              |
| *Sminthurides sp.*       | 0                             | 0                              | 2                                       | 23                  | 136                             |
| *Protaphorura sp.*       | 0                             | 6                              | 22                                      | 33                  | 13                              |
species like *Folsomia quadrioculata, L. lignorum, Pseudosinella alba* and *Heteromurus nitidus* are also dominant. After the partial flood of the depressions, the numbers of individuals of these species decreased markedly (p<0.01, U-test). Only *I. minor* showed a significant increase (p<0.05, U-test), attributable to the egg dormancy adaptation. The survival strategy of the mesophilic species is opportunistic. After a flood they migrate from the higher not flooded sites, to which they might have been transported, to the depressions and replace the hygrophilic species.

Comparisons of the hemiedaphic and euedaphic species composition of the hardwood floodplain and the two softwood floodplains show these noticeable differences (Figure 2). However, the species composition in the depressions after the partial flood is more similar to the species composition of the softwood floodplains. This impact of the partial flood suggests small-scale species shifts within the collembolan community.

Metabolic activity of various collembolan species during normoxia and hypoxia were followed by means of a microcalorimeter (Figure 3). Hypoxia caused a reduced heat production, indicating reduced metabolic rates as a common reaction of all species. However, the species markedly differed in their tolerance to hypoxia, a phenomenon also observed in winged insects (Wegener, 1993). All individuals of the epedaphic species *O. villosa* died after two hours of severe hypoxia. This was demonstrated by a total loss of the jump response after exposure to (pure) nitrogen. *O. villosa* survived anoxic conditions in the glass container for only about one hour. In contrast, survival under hypoxic and anoxic conditions of the hemi- and euedaphic species was greatly prolonged. Both *Sinella* species survived these conditions for 24 hours and *F. candida* for even 48 hours. Heat dissipation during posthypoxic recovery exceeded the normoxic rate in *Sinella*, whereas both rates were almost the same in *Folsomia*. The latter feature seems to be associated with high tolerance to hypoxia in

![Figure 2](image_url)

**Figure 2.** Cluster analysis (Ward-method, euclidian distances) of the hemiedaphic and euedaphic species composition of soil cores (n = 10) from different microhabitats (only species with more than 1% dominance are included). HF, hardwood floodplain; SF, softwood floodplain; ndSF, newly developed softwood floodplain; h, hillocks; d, depressions; c, control; f, flood.
winged insects, which show also a marked metabolic depression if oxygen is lacking (Wegener, 1993; Wegener & Moratzky, 1995).

Lactate content of the hypoxia-tolerant collembolan species increased modestly, yet significantly (p<0.05) during anoxia (Figure 4). Hodkinson & Bird (2004) have reported similar results for arctic microarthropods. A possible contribution of gut bacteria to the lactate content is unlikely, since the animals were fed with a mixture of antibiotics. Zinkler & Rüssbeck (1986) also found increased lactate content in F. candida after hypoxia. Glycolysis with modest production of lactate could facilitate posthypoxic recovery, as discussed by Wegener (1993). Floods in Middle Europe are usually caused by single events that bring about fast increasing water levels. A high tolerance of hypoxia/anoxia is a special advantage in euedaphic species, because these animals are not able to migrate fast.

Figure 3. Microcalorimetric response curves of various collembolan species representing different life forms: Orchesella villoosa, epedaphic; Sinella coeca and Sinella curviseta, hemiedaphic and Folsomia candida, euedaphic. The heat production (black line) shows a significant decrease after nitrogen exposure (bottom black bar).

Figure 4. Lactate content of Sinella coeca, Sinella curviseta (A) and of Folsomia candida (B) not treated with antibiotics (no AB) and after six days on antibiotics (+ AB). Lactate was significantly increased after hypoxia, but antibiotics had no effect on lactate content. Data are given as mean±SD (No AB, n = 4; + AB, control and N₂ + air, n = 5; N₂, n = 3). *Significant at 5% of probability.
enough to the soil surface, whereas epedaphic species often drift on the water surface due to the anti-wetting and hydrophobic properties of their cuticle (Figure 5). Further physiological studies are necessary to assess whether more efficient metabolic pathways than lactate production for surviving hypoxic and anoxic conditions (for example those producing acetate, malate or propionate as end products) may occur in eu- and hemiedaphic collembolan species.

Conclusions

1. Springtails from Middle European floodplain forests show a variety of (pre-) adaptations to cope with floods.
2. The diversity of survival strategies in this soil arthropod group suggests that similar adaptations may be present in other animals, i.e. be more widespread in Middle European invertebrates than it had been previously assumed.

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