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

Michael Thomas Marx[(1)], Anna-Katharina Wild[(1)], Ulrich Knollmann[(2)], Günter Kamp[(2)], Gerhard Wegener[(2)] and Gerhard Eisenbeis[(1)]

[(1)]Johannes Gutenberg University of Mainz, Institute of Zoology, Soil Zoology and Ecology, Becherweg 13, 55099 Mainz, Germany. E-mail: marxm1@students.uni-mainz.de, annawild@students.uni-mainz.de, geisenbe@uni-mainz.de [(2)]Johannes Gutenberg University of Mainz, Institute of Zoology, Molecular Physiology, Becherweg 9-11, 55099 Mainz, Germany. E-mail: knollman@uni-mainz.de, kamp@uni-mainz.de, gwegener@uni-mainz.de

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.

Respostas e adaptações de comunidades de colêmbolos (Hexapoda: Collembola) a condições de inundação e hipoxia

Resumo – Foram utilizados os métodos ecológicos padrão (armadilhas "pitfall", armadilhas de tronco e amostras de solo) para avaliar as respostas de comunidade de colêmbolos a diferentes intensidades de inundação. Foram investigados três locais de um habitat de leitos de inundação perto de Mainz, Alemanha, com diferentes regimes de inundação. As estruturas das comunidades de colêmbolos foram nitidamente diferentes conforme a intensidade das inundações. Nos locais mais afetados por inundações, as espécies higrofílicas e higrotolerantes dominaram, ao passo que as espécies mesofílicas foram dominantes nos locais de leitos de inundação com angiospermas. As estratégias de sobrevivência das espécies higrofílicas e higrotolerantes incluem a diapausa dos ovos e o deslocamento passivo. Foi testada a adaptação fisiológica a condições hipóxicas de espécies selecionadas de colêmbolos através de análises por microcalorimetria. A atividade das espécies foi testada em condições normóxicas e hipóxicas/anóxicas e durante a recuperação pós-hipoxia. Verificou-se que o lactato aumentava após condições hipóxicas nas espécies avaliadas, o que sugere que, além de um decréscimo massivo na atividade metabólica, deve haver também certa atividade glicolítica associada à tolerância à hipoxia.

Termos para indexação: adaptação comportamental, adaptação ecológica, diapausa dos ovos, inundação, adaptação morfológica, adaptação fisiológica.

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 & Ehrnsberger (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

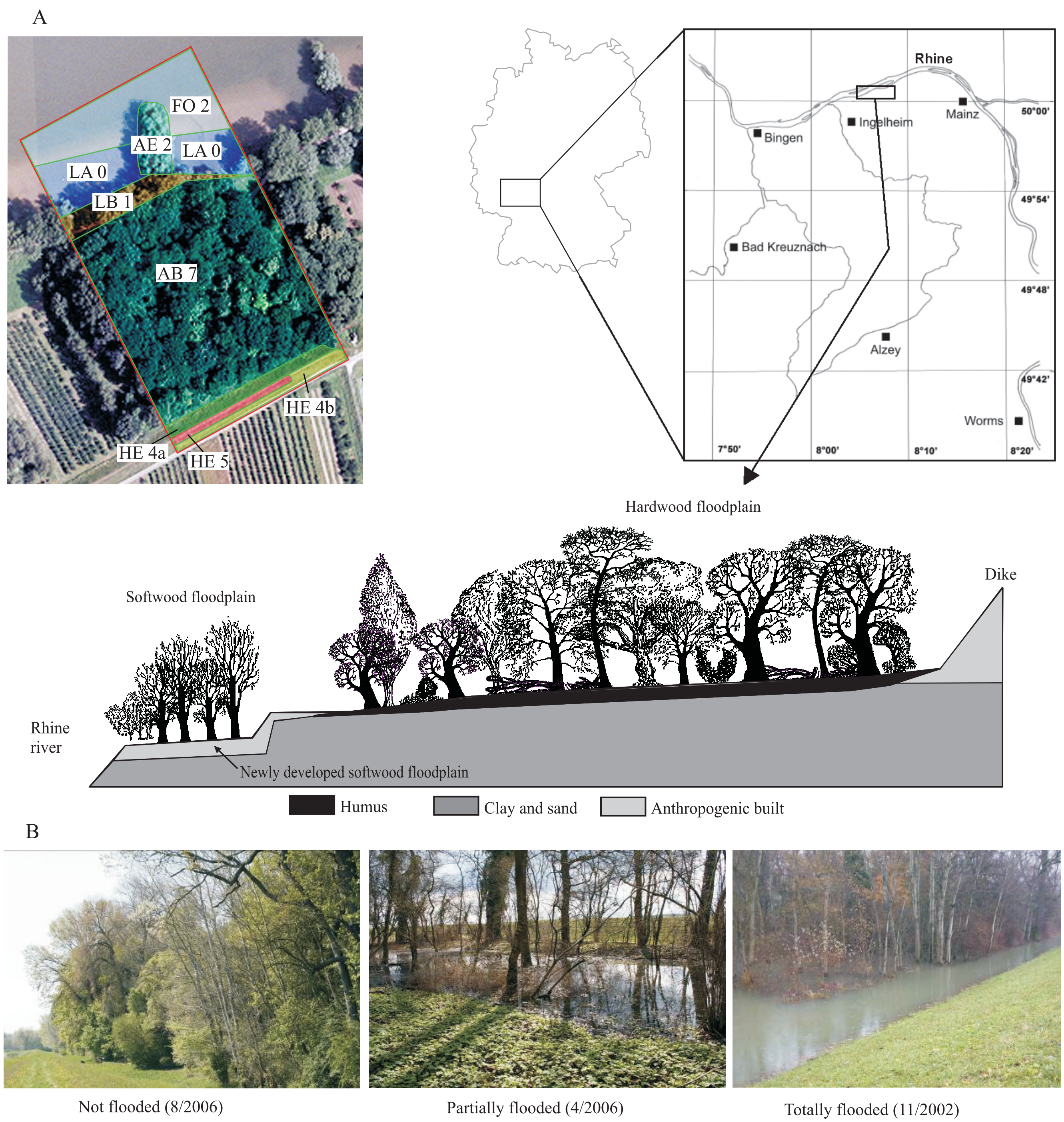

Figure 1. Overview and aerial view (D-Sat, Buhl Data Service GmbH and GeoContent GmbH; modified by subsequent labelling) of the study area in Germany with the position of the three different microhabitats: hardwood floodplain, softwood floodplain and newly developed softwood floodplain (A). Detail of 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 (from the hillocks and depressions, 20 each) were taken from the 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% O_2, 80% N_2, 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 N_2) 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 *Sminthurides* 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).

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	1,843	34,308
Orchesella villosa	798	14,855
Lepidocyrtus curvicollis	570	10,611
Ceratophysella denticulata	368	6,850
Sminthurinus aureus	287	5,343
Pogonognathellus flavescens	279	5,194
Dicyrtomina ornata	215	4,002
Entomobrya muscorum	139	2,587
Isotoma viridis	123	2,290
Allacma fusca	98	1,824
Xenyllodes armatus	83	1,545
Orchesella cincta	82	1,526
Pseudachorutes subcrassus	77	1,433
Lepidocyrtus lanuginosus	66	1,229
Tomocerus vulgaris	58	1,080
	Softwood floodplains (n = 6)	
Sminthurides aquaticus(1)	138	21,133
Lepidocyrtus lignorum	108	16,539
Sminthurides malmgreni(1)	92	14,089
Isotomurus palustris(1)	83	12,711
Sminthurinus aureus	81	12,404
Protaphorura sp.	57	8,729
Lepidocyrtus lanuginosus	14	2,144
Entomobrya nivalis	13	1,991
Podura aquatica(1)	9	1,378
Isotomurus maculatus(1)	9	1,378
Lepidocyrtus cyaneus	8	1,225
Orchesella flavescens	8	1,225
Vertagopus arboreus	7	1,072

(1)Epineustic and hygrophilic species.

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 hygrophila* and *Anurida uniformis* also predominate. The possible (pre-) adaptation of *I. minor* and *M. hygrophila* 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 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	188	0	0	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 hygrophila	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

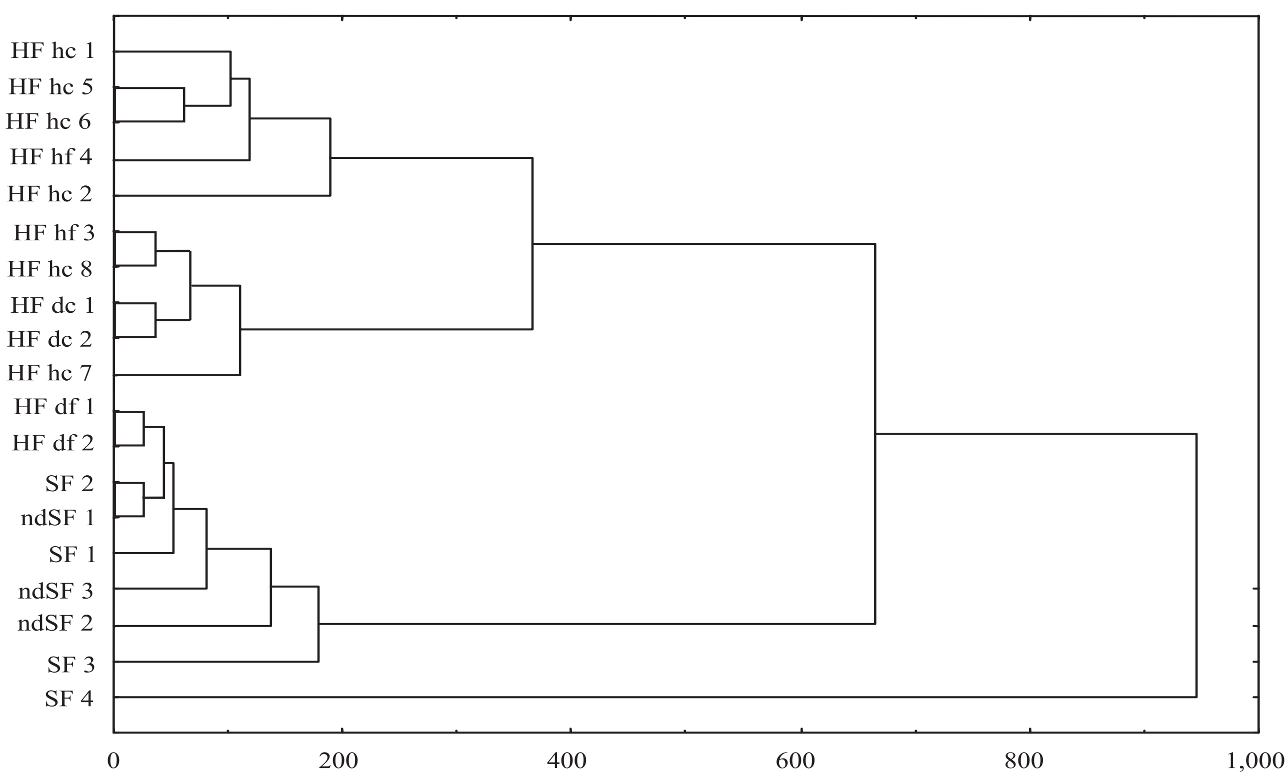

Figure 2. Cluster analysis (Ward-method, euclidian distances) of the hemi- and euedaphic species composition of soil cores (n = 10) from different microhabitats (only species with more than 1% dominance are included). HF, hardwood floodplain; SF, softwood floodplain; ndSF, newly developed softwood floodplain; 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

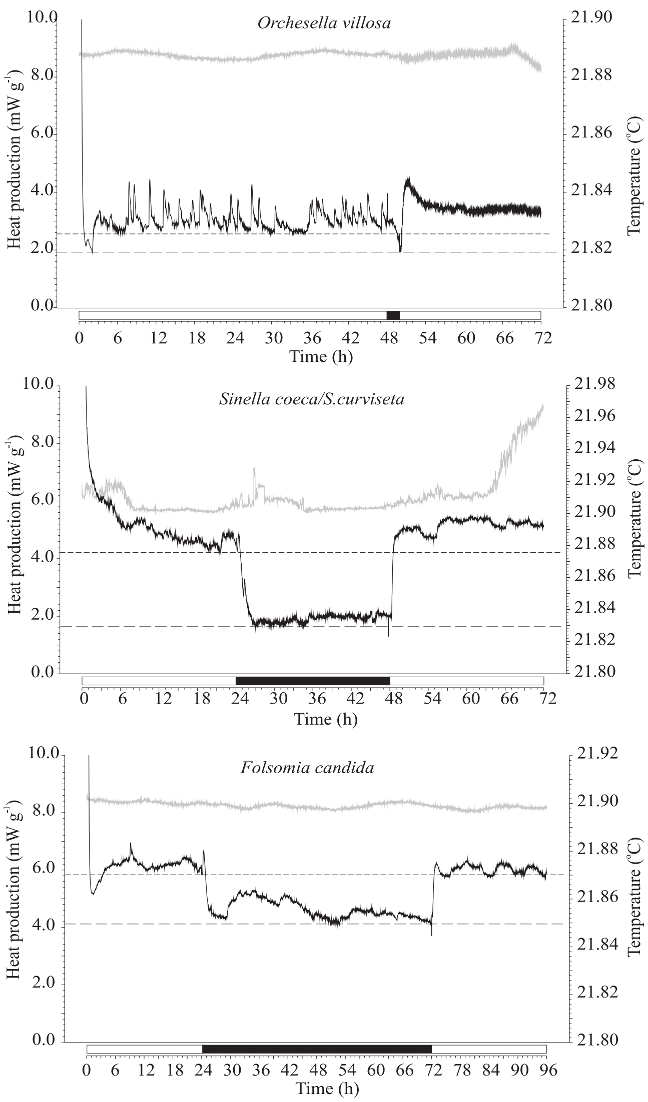

Figure 3. Microcalorimetric response curves of various collembolan species representing different life forms: *Orchesella villosa*, epedaphic; *Sinella coeca* and *Sinella curviseta*, hemiedaphic and *Folsomia candida*, euedaphic. The heat production (black line) shows a significant decrease after nitrogen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

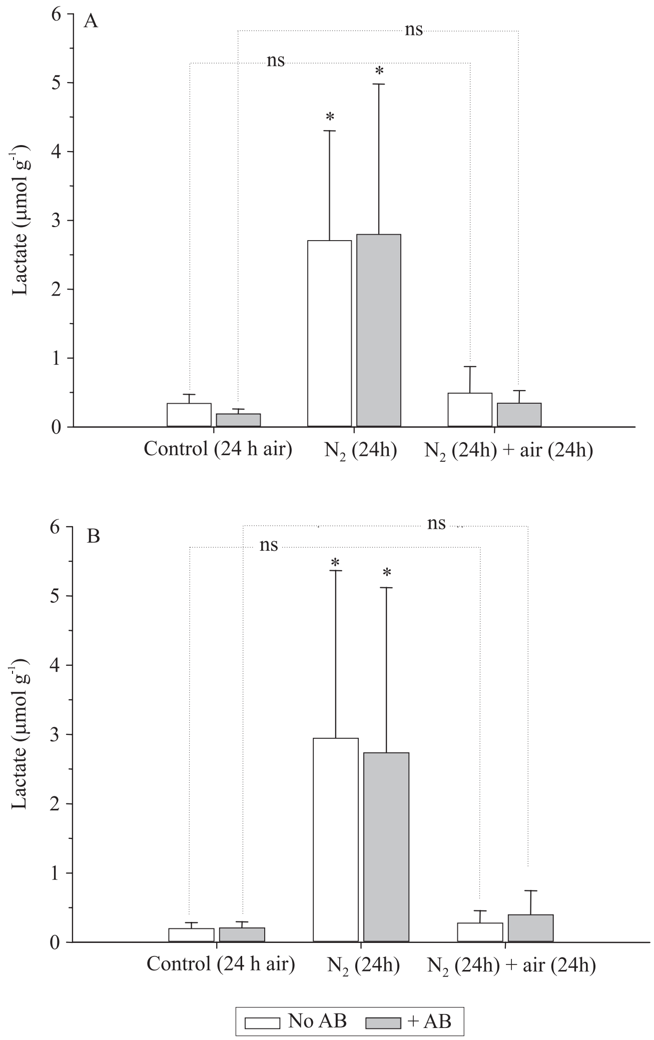

Figure 4. Lactate content of *Sinella coeca*, *Sinella curviseta* (A) and of *Folsomia candida* (B) not treated with antibiotics (no AB) and after six days on antibiotics (+ AB). Lactate was significantly increased after hypoxia, but antibiotics had no effect on lactate content. Data are given as mean±SD (No AB, n = 4; + AB, control and N_2 + air, n = 5; N_2, n = 3). *Significant at 5% of probability.

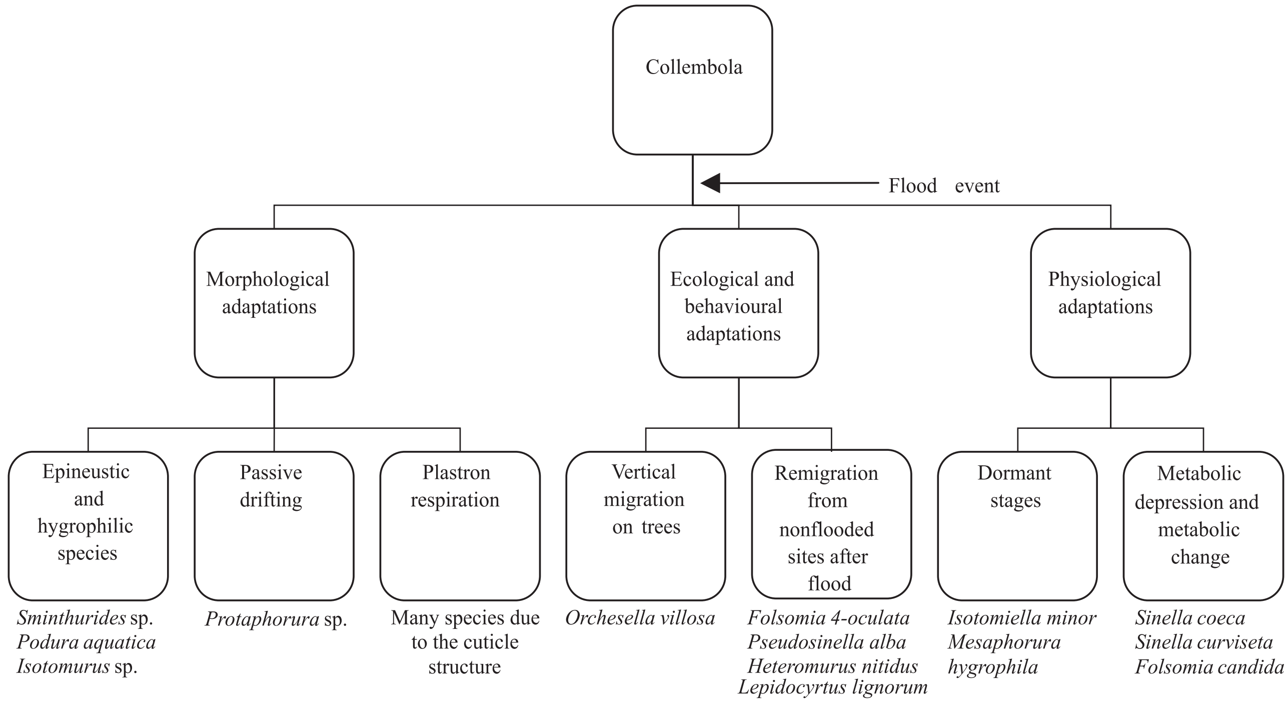

Figure 5. Scheme of (pre-) adaptations to flooding and hypoxia of various collembolan species of a Middle European floodplain.

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.

Acknowledgements

The authors are much obliged to David Bignell, for very valuable comments and linguistic revision of the manuscript. This study was financially supported by the Centre for Environmental Research and the Feldbausch foundation of the Johannes Gutenberg University of Mainz. Physiological studies were in part supported by the German Research Council (DFG).

References

ADIS, J.; JUNK, W.J. Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: a review. **Freshwater Biology**, v.47, p.711-731, 2002.

COULSON, S.J.; HODKINSON, I.D.; WEBB, N.R.; HARRISON, J.A. Survival of terrestrial soil-dwelling arthropods on and in seawater: implications for trans-oceanic dispersal. **Functional Ecology**, v.16, p.353-356, 2002.

DEHARVENG, L.; LEK, S. High diversity and community permeability: the riparian Collembola (Insecta) of a Pyrenean massif. **Hydrobiologia**, v.312, p.59-74, 1995.

ERWIN, T.L.; ADIS, J. Amazonian inundation forests: their role as short-term refuges and generators of species richness and taxon pulses. In: INTERNATIONAL SYMPOSIUM OF THE ASSOCIATION FOR TROPICAL BIOLOGY, 5., 1979, Caracas. **Proceedings**. New York: Columbia University Press, 1982. v.5, p.358-371.

GAUER, U. Collembola in Central Amazon inundation forests: strategies for surviving floods. **Pedobiologia**, v.41, p.69-73, 1997.

GHILAROV, M.S. Bodenwirbellose als Indikatoren des Bodenhaushaltes und von bodenbildenden Prozessen. **Pedobiologia**, v.18, p.300-309, 1978.

GRIEGEL, A. **Auswirkungen von Überflutungen auf die Zönosen der Collembolen und der Gamasiden (Insecta: Collembola, Acari: Gamasida) in der Flußaue des unteren Odertals**. 2000. 244p. Thesis (Ph.D.) - Freie Universität Berlin, Berlin.

GRUSCHCZYK, B.; KAMP, G. The shift from glycogenolysis to glycogen resynthesis after escape swimming: studies on the abdominal muscle of the shrimp, *Crangon crangon*. **Journal of Comparative Physiology B**: Biochemical, Systemic and Environmental Physiology, v.159, p.753-760, 1990.

HODKINSON, I.D.; BIRD, J.M. Anoxia tolerance in high Arctic terrestrial microarthropods. **Ecological Entomology**, v.29, p.506-509, 2004.

JOOSSE, E.N.G. Some observations on the biology of *Anurida maritima* (Guérin) (Collembola). **Zeitschrift für Morphologie und Ökologie der Tiere**, v.57, p.320-328, 1966.

JUNK, W.J. **The Central Amazon floodplain**: ecology of a pulsing system. Berlin: Springer, 2000. 525p.

KEMPSON, D.; LLOYD, M.; GHELARDI, R. A new extractor for woodland litter. **Pedobiologia**, v.3, p.1-21, 1963.

MARX, M.T.; WEIRICH, O.; EISENBEIS, G. Die Pseudoskorpionfauna (Arachnida: Pseudoscorpiones) eines Auwaldes bei Ingelheim am Rhein, unter besonderer Berücksichtigung der Auswirkungen des trocken-warmen Winters 2006/2007. **Arachnologische Mitteilungen**, v.35, p.21-28, 2008.

MOORE, P.D. Biogeography: springboards for springtails. **Nature**, v.418, p.381, 2002.

PALISSA, A. **Collembola**. Heidelberg: Spektrum Akademischer Verlag, 2000. 166p.

PAUL, R.J.; COLMORGEN, M.; HÜLLER, S.; TYROLLER, F.; ZINKLER, D. Circulation and respiration control in millimetre-sized animals (*Daphnia magna*, *Folsomia candida*) studied by optical methods. **Journal of Comparative Physiology B**: Biochemical, Systemic, and Environmental Physiology, v.167, p.399-408, 1997.

ROTHENBÜCHER, J.; SCHAEFER, M. Conservation of leafhoppers in floodplain grasslands: trade-off between diversity and naturalness in a Northern German National Park. **Journal of Insect Conservation**, v.9, p.335-349, 2005.

ROTHENBÜCHER, J.; SCHAEFER, M. Submersion tolerance in floodplain arthropod communities. **Basic and Applied Ecology**, v.7, p.398-408, 2006.

RUSEK, J. Zur Bodenfauna in drei Typen von Überschwemmungswiesen in Süd-Mähren. **Rozpravy Československé Akademie věd - Řada matematických a přírodních věd**, v.94, p.1-242, 1984.

RUSSELL, D.J.; GRIEGEL, A. Influence of variable inundation regimes on soil Collembola. **Pedobiologia**, v.50, p.165-175, 2006.

RUSSELL, D.J.; HAUTH, A.; FOX, O. Community dynamics of soil Collembola in floodplains of the Upper Rhine Valley. **Pedobiologia**, v.48, p.527-536, 2004.

RUSSELL, D.J.; SCHICK, H.; NÄHRIG, D. Reactions of soil Collembolan communities to inundation in floodplain ecosystems of the upper Rhine Valley. In: BROLL, G.; MERBACH, W.; PFEIFFER, E.M. (Ed.). **Wetlands in Central Europe**. Berlin: Springer-Verlag, 2002. p.35-70.

STERZYŃSKA, M. Protection, management and restoration of the wetland fauna of floodplain terraces in large lowland rivers in Poland. In: INTERNATIONAL CONFERENCE TOWARDS NATURAL FLOOD REDUCTION STRATEGIES, 2003, Warszawa. **Proceedings**. Warszawa: Museum and Institute of Zoology, 2003. p.1-5.

STERZYŃSKA, M.; EHRNSBERGER, R. Diversity and structure of collembola communities in wetlands. In: CENTRAL EUROPEAN WORKSHOP ON SOIL ZOOLOGY, 5., 1999, České Budějovice. **Soil zoology in Central Europe**: proceedings. České Budějovice: Academy of Sciences of the Czech Republic, 1999. p.325-334.

TAMM, J.C. Temperature-controlled under-water egg dormancy and postflood hatching in *Isotoma viridis* (Collembola) as forms of adaptation to annual long-term flooding. **Oecologia**, v.68, p.241-245, 1986.

WEGENER, G. Hypoxia and posthypoxic recovery in insects: physiological and metabolic aspects. In: HOCHACHKA, P.W.; LUTZ, P.L.; SICK, T.; ROSENTHAL, M.; THILLARD, G. van den (Ed.). **Surviving hypoxia**: mechanisms of control and adaptation. Boca Raton: CRC Press, 1993. p.417-437.

WEGENER, G.; MORATZKY, T. Hypoxia and anoxia in insects: microcalorimetric studies on two species (*Locusta migratoria* and *Manduca sexta*) showing different degrees of anoxia tolerance. **Thermochimica Acta**, v.251, p.209-218, 1995.

WEIGMANN, G.; WOHLGEMUTH-VON REICHE, D. Vergleichende Betrachtungen zu den Überlebensstrategien von Bodentieren im Überflutungsbereich von Tieflandauen. In: DOHLE, W.; BORNKAMM, R.; WEIGMANN, G. (Ed.). **Das untere Odertal**: Auswirkungen der periodischen Überschwemmungen auf Biozönosen und Arten. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung, 1999. p.229-240.

ZINKLER, D.; RÜSSBECK, R. Ecophysiological adaptations of Collembola to low oxygen concentrations. In: INTERNATIONAL SEMINAR ON APTERYGOTA, 2., 1986, Siena. **Proceedings**. Siena: University of Siena, 1986. p.123-127.

ZINKLER, D.; RÜSSBECK, R.; BIEFANG, M.; BAUMGÄRTL, H. Intertidal respiration of *Anurida maritima* (Collembola: Neanuridae). **European Journal of Entomology**, v.96, p.205-209, 1999.

ZULKA, K.P. Carabids in a Central European floodplain: species distribution and survival of inundations. In: DESENDER, K. (Ed.). **Carabid beetles**: ecology and evolution. Netherlands: Kluwer Academic, 1994. p.399-405.

Received on January 6, 2009 and accepted on June 14, 2009