Acta Soc. Zool. Bohem. **74**: 75–83, 2010
ISSN 1211-376X

Effect of flood and drought on epedaphic communities of springtails (Collembola) in floodplain forests in south-western Germany

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Received 10 August 2009; *accepted 26 November 2010*
Published 20 December 2010

Abstract. Between 2000 and 2005 the epedaphic collembolan community on different islands and in different riverbank habitats of the nature protection area "Inselrhein near Mainz", Germany, were investigated. Altogether 53,915 individuals belonging to 11 families and 43 species were caught using pitfall traps. In contrast to the periodic flooding in spring 2001 and 2002 the extremely dry and hot summer of 2003 caused an immediate decrease in the number of species and average numbers of individuals. The mesophilic and more xerotolerant species, like *Pogonognathellus flavescens* (Tullberg, 1871), *Orchesella cincta* (Linnaeus, 1758) and *Orchesella villosa* (Geoffroy, 1762), showed a rapid recovery. These species are better adapted to drought conditions and in the absence of the other species rapidly increased in abundance. The species composition of the communities on the islands and riverbanks were clearly different before the extreme drought in 2003. After this event the communities were very similar. Compared to the effects of periodic spring floods the extreme summer drought in 2003 had a greater and longer lasting effect on the whole collembolan community.

Key words. Soil zoology, ecology, long-term drought, periodic flooding, recovery time, Collembola, Germany, Palaearctic Region.

INTRODUCTION

Floodplains are amongst the most diverse terrestrial habitats as the changing moisture conditions result in a wide variety of ecological niches. The nature protection area "Inselrhein near Mainz" includes some islands and riverbanks with fragmented softwood and hardwood floodplain forests and is categorized as an environmental zone that is very vulnerable to climate change. This region, where the highest temperatures are currently recorded in Germany, is expected to show the strongest warming in the future (Schröter et al. 2005). It is also predicted that there will be an increase in the incidence of extreme droughts and aperiodic flooding in Middle Europe during the vegetation period in summer (Christensen & Christensen 2002, Schär et al. 2004, Gerstengarbe & Werner 2005, Jentsch et al. 2009). It is likely that a increase in periods of severe drought could result in a loss of the natural character of the remaining floodplain forest sites in this region. Therefore, the effects of the extreme hot and dry summer of 2003 upon the epedaphic collembolan community in different floodplain forests in the area of reserve were measured. June and August of summer 2003 were characterised by long-lasting high-pressure weather conditions. Consequently there were a greater number of hours of sunshine and greatly reduced amount of rainfall that year. In Germany this summer was the sunniest since 1951 and fifth driest since 1901.

Collembola are a key group, because they have a very flexible reaction to disturbances (Russell et al. 2002). Some details of how Collembola respond to inundation in European riparian habitats

Presented at the 10th Central European Workshop on Soil Zoology, České Budějovice, Czech Republic, 21–24 April 2009.

are reported by Rusek (1984), Deharveng & Lek (1995), Čarnogurský (1998), Sterzyńska & Ehrnsberger (1999), Russell et al. (2004) and Russell & Griegel (2006). In addition, some studies record the influence of altered precipitation and drought on collembolan communities (Alvarez et al. 1999, Pflug & Wolters 2001, Lindberg & Bengtsson 2005), but little is known about the effects of a severe drought on the collembolan community in floodplain forests.

MATERIAL AND METHODS

The study area "Inselrhein near Mainz" is part of the Northern Upper Rhine rift and a nature protection area, number 6013-401 (EU directive NATURA 2000). The climate in this region is described as warm and relatively dry (average temperature 10 °C; average precipitation about 500 mm). Altogether 11 study sites (5 islands and 6 riverbanks) were sampled in order to evaluate the effects of floods or droughts (Fig. 1). Most of them have not been managed for at least 40 years and are subjected to flooding when the river Rhine occasionally floods from late autumn to spring. The sites are covered with softwood (*Salicetum albae* and *Salicetum albae* cornetosum with *Populus* × *canadensis*) and hardwood (*Querco Ulmetum* and *Carici Tilietum*) floodplain forests (Table 1). In the vegetation period from May to October, between 2000 and 2005 pitfall traps were used (Ø funnel: 8 cm; Ø inner hole: 3 cm) to catch different invertebrate groups. The killing agent was formalin (2–4%) in 2000 and 2001 and ethanol (80%) in the following four years. Pitfall traps were replaced every two weeks and arthropods present in the traps were sorted in the laboratory under a stereo-microscope at up to 40× magnification. Collembola were determined to species using a phase-contrast microscope (Leica Microscope DML) at up to 1000× magnification. Because of the different numbers of traps and sample periods (due to floods and droughts

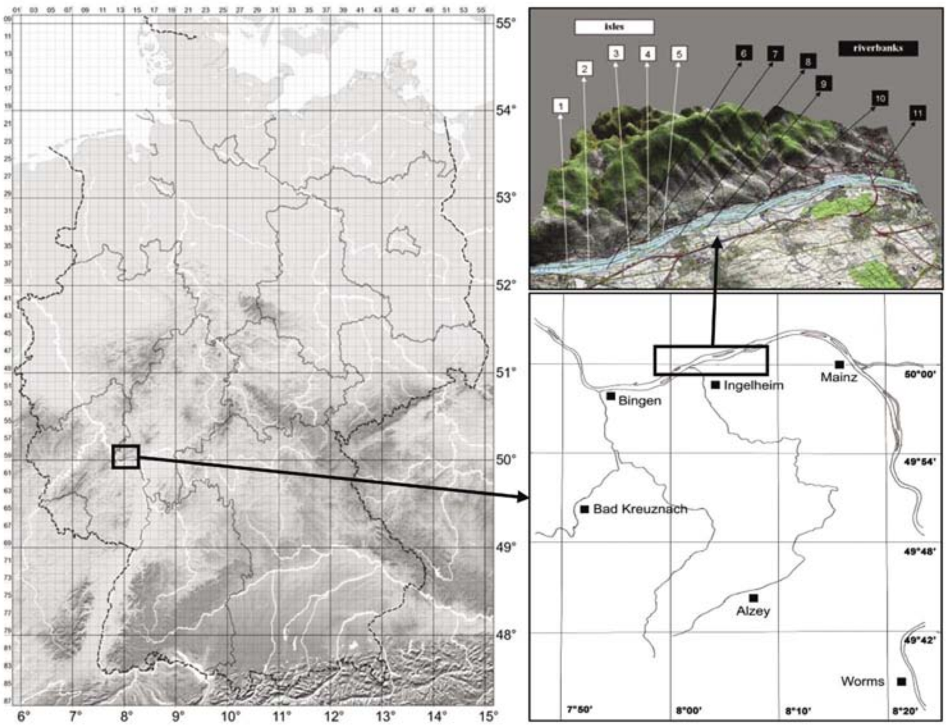

Fig. 1. Position of the different study sites in the nature protection area "Inselrhein near Mainz" in south-western Germany. 1 – Rüdesheimer Aue, 2 – Ilmenaue, 3 – Fulder Aue West, 4 – Fulder Aue Ost, 5 – Winkeler Aue, 6 – Gaulsheim, 7 – Geisenheim, 8 – Ingelheim Ufer, 9 – Ingelheim Große Heide, 10 – Erbach, 11 – Mombach.

Table 1. Sampling period in days and number of pitfall traps used each year (vegetation period). Shorter sampling periods are due to flood* and drought** events. Abbreviations: softwood floodplain (sf), hardwood floodplain (hf)

sites	abbr.	sampling period (days) / number of pitfall traps					
		2000	2001	2002	2003	2004	2005
isles							
Fulder Aue West	FuW / sf	114*/ 5	169 / 3	169 / 4	85** / 3	135 / 3	169 / 3
Fulder Aue Ost	FuO / hf	114*/ 5	169 / 3	169 / 4	85** / 3	135 / 3	169 / 3
Winkeler Aue	WA / sf	114*/ 5	169 / 3	169 / 4	85** / 3	135 / 3	169 / 3
Ilmenaue	Ilm / sf	–	–	169 / 4	–	–	–
Rüdesheimer Aue	Rüd / sf	–	–	169 / 4	–	–	–
riverbanks							
Ingelheim Ufer	Ing / sf	113* / 5	126* / 3	167 / 4	85** / 3	141 / 3	167 / 3
Ingelheim Große Heide	GH / sf	–	126* / 3	165 / 4	85** / 3	141 / 3	167 / 3
Gaulsheim	Gau / sf	–	–	165 / 4	85** / 3	141 / 3	167 / 3
Mombach	Mom / sf	–	–	128* / 4	85** / 3	141 / 3	167 / 3
Geisenheim	Gei / hf	–	–	169 / 4	–	–	–
Erbach	Erb / hf	–	–	169 / 4	–	–	–

during the vegetation period, Table 1) the average number of individuals per trap per day was calculated. Furthermore a cluster analysis (after Ward (log transformed); Euclidian distances) of the collembolan communities was used to show differences between islands and riverbanks over the period 2002 to 2005.

RESULTS

Over the whole sampling period 53,915 individuals belonging to 11 families and 43 species were caught (Table 2). The spring floods in the years 2001 and 2002 resulted in a decrease in individual numbers and slight increase in the total number of species (Fig. 2). In winter 2002/2003 the last complete flooding of this region occurred. During the extreme summer 2003 and in the following two years the water level of the river Rhine decreased significantly (Fig. 3).

This extreme and long-term drought had a strong effect on the collembolan community. Total number of species and numbers of individuals decreased remarkable at all study sites compared with preceding years. There was an especially marked decreare in the numbers of individuals of the hygrotolerant *Isotomurus palustris* (Müller, 1776), *Isotomurus plumosus* Bagnall, 1940 and nearly all symphypleonid species. In 2004 and 2005 the collembolan community recovered slowly but did not reach the values recorded in the years 2000 to 2002. However, some species like *Orchesella cincta*, *Orchesella villosa* and *Pogonognathellus flavescens* made a fast recovery at nearly all the sites studied. The numbers of *Isotomurus palustris* also increased, but only at the riverbank site near Ingelheim (Ing).

Figure 4 indicates there were different clusters of island and riverbank sites from 2002 to 2005. During the vegetation period in 2002 a clear differentiation between islands and riverbank sites is obvious, whereas in the following 3 years the communities are more similar.

DISCUSSION

The decrease in the numbers of individuals in 2001 and 2002 was caused by periodic spring floods. Because flooding is regarded as a normal event at floodplain forest sites, it is assumed that the soil fauna at these sites is well adapted to these conditions. Collembolan communities react to changes in habitat conditions more by an adjustment of dominance than in the appearance or

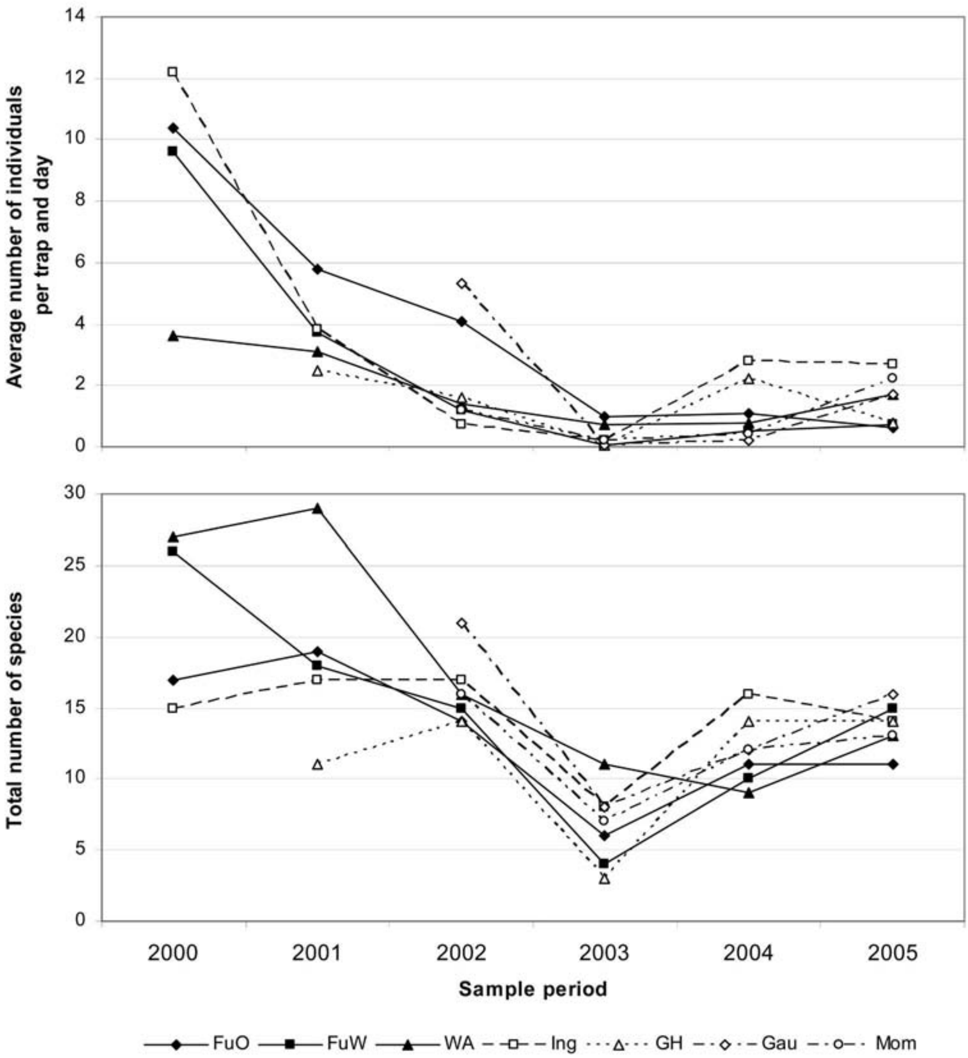

Fig. 2. Average number of individuals of Collembola (caught per trap per day) and total number of species at the different sites over the whole sampling period (Abbreviations see Table 1). Only sites for which there were at least four years of results are included (Islands: black labels and solid lines; Riverbanks: white labels and dashed lines).

disappearance of species (Dunger 1968). This is confirmed by the relatively constant total number of species from 2000 to 2002. The collembolan communities at nearly all sites studied recovered rapidly. Especially the hygrotolerant *Isotomurus*, which were most abundant immediately after the flooding in May and June, followed by more mesophilic and ubiquitous species like *Orchesella villosa*, *Pogonognathellus flavescens* and *Tomocerus vulgaris* (Tullberg, 1871). The latter species occurred most frequently in the traps later in July and August. Thus, it is likely they probably

Table 2. Total numbers of individuals of Collembola caught at the different study sites during the whole sampling period (Abbreviations see Table 1)

species \ vegetation period	2000				2001					2002											2003							2004							2005						
	FuW	FuO	WA	Ing	FuW	FuO	WA	Ing	GH	FuW	FuO	WA	Ilm	Rüd	Ing	GH	Gau	Mom	Gei	Erb	FuW	FuO	WA	Ing	GH	Gau	Mom	FuW	FuO	WA	Ing	GH	Gau	Mom	FuW	FuO	WA	Ing	GH	Gau	Mom
Arthropleona																																									
Brachystomellidae																																									
Brachystomella parvula (Schaeffer, 1896)	22	–	14	–	–	1	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hypogastruridae																																									
Ceratophysella denticulata (Bagnall, 1941)	33	–	105	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Neanuridae																																									
Neanura muscorum (Templeton, 1835)	4	–	2	–	3	–	2	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	1	2	–	–	–	–	–	–
Odontellidae																																									
Xenyllodes armatus Axelson, 1903	11	–	12	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Odontella lamellifera (Axelson, 1903)	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Isotomidae																																									
Folsomia quadrioculata (Tullberg, 1871)	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Isotoma viridis Bourlet, 1839	748	38	285	1885	261	173	119	506	21	13	–	20	2	3	28	15	12	12	7	1	–	–	2	–	–	–	–	22	1	1	449	59	–	–	13	–	27	439	2	30	23
Isotomurus antennalis Bagnall, 1940	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–	–
Isotomurus maculatus (Schaeffer, 1896)	115	–	115	–	–	67	126	–	–	2	–	6	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–	1	–	–	–	–	–	–	19	–	–	–	–
Isotomurus palustris (Muller, 1776)	1522	93	449	1688	924	999	251	244	293	289	597	532	151	35	149	689	1925	238	840	14	–	–	13	7	–	–	7	8	1	–	269	32	15	21	28	1	86	305	4	34	68
Isotomurus plumosus Bagnall, 1940	449	26	80	602	275	394	137	275	2	34	–	26	19	2	6	5	119	133	95	11	–	–	–	–	–	–	–	3	–	–	34	–	–	6	–	–	–	–	–	–	4
Isotomurus unifasciatus (Borner, 1901)	10	–	–	11	6	6	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Vertagopus arboreus (Linnaeus, 1758)	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Entomobryidae																																									
Entomobrya muscorum (Nicolet, 1842)	–	46	–	–	–	4	1	–	–	–	6	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	1	13	–	–	–	–	–
Entomobrya nivalis (Linnaeus, 1758)	230	110	360	27	13	38	42	–	–	4	7	53	20	22	2	–	28	4	61	1	–	2	7	–	–	3	3	1	10	16	10	–	3	9	–	–	4	2	–	1	5
Lepidocyrtus lignorum (Fabricius, 1793)	–	–	1	–	–	2	–	2	–	–	2	–	–	–	–	–	16	–	2	6	–	–	–	6	–	–	–	–	–	–	1	8	7	–	1	–	–	1	2	7	–
Lepidocyrtus curvicollis Bourlet, 1839	–	1	–	–	–	–	1	–	–	5	–	–	249	8	1	–	–	–	–	11	–	–	–	1	–	–	–	–	–	–	2	1	7	–	1	2	–	–	1	3	–
Lepidocyrtus lanuginosus (Gmelin, 1788)	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Lepidocyrtus cyaneus Tullberg, 1871	167	24	62	714	11	8	101	77	5	1	1	1	–	1	74	1	11	–	15	–	–	–	–	2	–	1	–	–	4	1	20	109	5	–	3	1	1	–	27	1	1
Lepidocyrtus violaceus (Geoffroy, 1762)	42	–	32	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lepidocyrtus paradoxus Uzel, 1890	4	7	1	129	–	2	2	17	95	–	–	1	1	–	45	89	–	–	–	1	–	–	–	1	1	–	–	–	1	–	2	17	–	–	–	–	–	24	9	–	1
Heteromurus nitidus (Templeton, 1835)	–	38	–	–	–	12	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–
Orchesella cincta (Linnaeus, 1758)	907	1598	366	199	82	197	174	24	–	21	244	141	219	326	8	3	28	–	17	47	6	93	98	4	–	1	6	58	97	108	45	61	10	13	29	69	95	81	6	183	85
Orchesella flavescens (Bourlet, 1839)	–	–	1	–	–	–	1	7	–	–	–	–	–	3	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Orchesella villosa (Geoffroy, 1762)	432	205	3	1391	3	148	–	146	450	16	766	16	1042	1235	100	197	22	–	3	175	–	105	19	33	7	3	–	11	258	162	142	566	12	2	31	111	443	158	66	359	16
Pseudosinella alba (Packard, 1873)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–
Willowsia platani (Nicolet, 1842)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Willowsia nigromaculata (Luibbock, 1873)	109	35	31	21	11	12	19	1	–	–	1	–	–	1	7	1	13	2	19	–	–	3	4	–	–	–	–	–	–	3	1	–	–	–	–	1	1	–	–	–	–
Tomoceridae																																									
Pogonognathellus flavescens (Tullberg, 1871)	–	60	–	59	1	105	2	17	1	9	94	–	16	–	5	5	1	1	1	82	4	32	3	1	–	1	3	5	14	–	150	21	–	6	38	8	2	132	241	2	66
Pogonognathellus longicornis (Muller, 1776)	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–
Tomocerus vulgaris (Tullberg, 1871)	716	612	104	11	211	345	141	1		221	937	88	482	110	4	2	24	157	6	113	5	21	4			1	26	90	48	23	1	2	4	111	150	45	162	77	1	121	776
Symphypleona																																									
Sminthurididae																																									
Sminthurides aquaticus (Bourlet, 1843)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sminthurides malmgreni (Tullberg, 1876)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Katiannidae																																									
Sminthurinus elegans (Fitch, 1863)	61	–	16	–	–	–	6	–	–	–	–	15	–	–	–	–	12	30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	2	–	–
Sminthurinus aureus (Lubbock, 1862)	1	–	6	–	1	–	3	–	1	2	–	1	–	–	–	6	1	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
Dicyrtomidae																																									
Dicyrtoma fusca (Lubbock, 1873)	220	38	8	147	–	–	8	57	47	85	6	5	7	–	7	15	351	14	–	39	–	–	2	–	–	–	1	–	–	–	26	23	4	1	31	–	–	75	16	49	52
Dicyrtomina minuta (O.Fabricius, 1783)	–	–	–	–	1	–	3	26	2	–	–	–	1	–	–	1	1	4	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	4
Dicyrtomina ornata (Nicolet, 1842)	2	38	6	–	12	53	1	27	–	30	7	3	–	–	3	–	256	22	–	14	–	–	–	–	–	1	1	–	–	–	8	–	4	1	2	–	1	1	–	14	–
Ptenothrix atra (Linnaeus, 1758)	14	–	4	1	1	–	1	11	25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ptenothrix ciliata Stach, 1957)	3	–	2	–	–	–	4	–	–	–	–	3	3	8	–	–	1	2	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	1	–
Allacma fusca (Linnaeus, 1758)	65	966	1	2	64	339	17	6	–	87	131	53	169	118	5	4	109	2	–	29	3	–	8	–	1	3	–	3	10	13	20	10	2	3	17	30	15	33	4	26	11
Bourletiellidae																																									
Deuterosminthurus bicinctus (Koch, 1840)	–	–	–	–	1	21	–	–	–	–	1	–	4	–	1	–	577	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Deuterosminthurus pallipes (Bourlet, 1842)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	21	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
total ind. number / site / year	5500	5935	2068	6887	1881	2926	1186	1444	942	819	2800	964	2385	1875	449	1033	3530	635	1066	548	18	256	166	55	9	14	47	204	450	328	1180	913	75	180	347	282	858	1331	382	835	1112
total ind. number / year	20390				8379					16104											565							3330							5147						
total ind. number	53915																																								

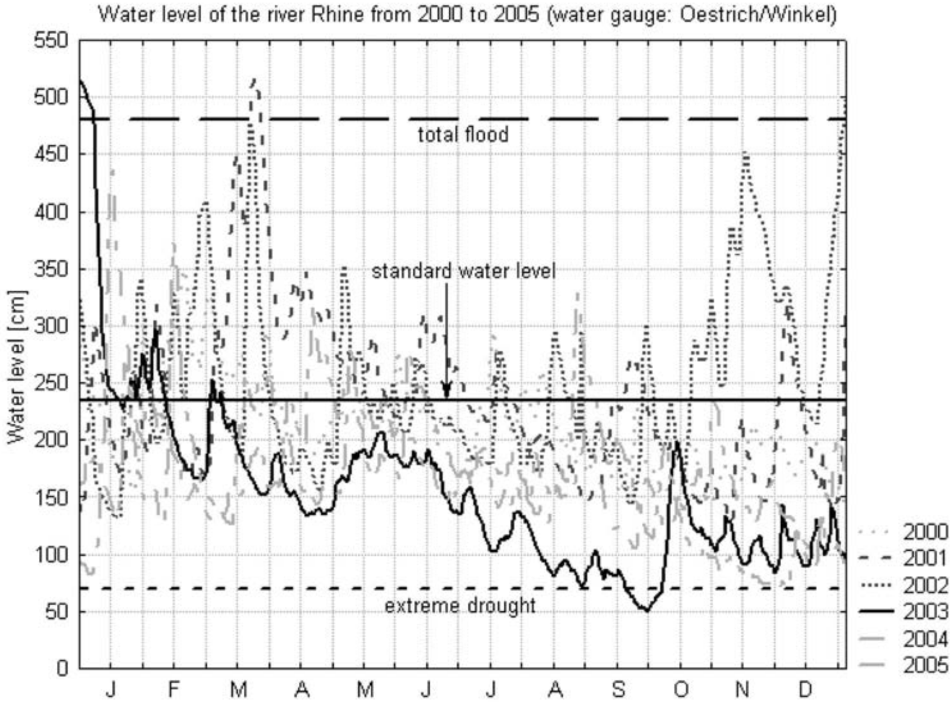

Fig. 3. Water level in the river Rhine (water gauge Oestrich/Winkel) from 2000 to 2005. Floods occurred in spring 2001, 2002 and winter 2002/2003. The extreme drought in 2003 resulted in a very low water level of nearly 50 cm (data are kindly provided by Wasser- und Schifffahrtsdirektion Südwest).

survive periodic spring floods in the egg stage. That dormant eggs are a pre-adaptation for suriving inundation has been demonstrated for several species of Collembola (Tamm 1984, 1986, Gauer 1997, Čarnogurský 1998, Russell et al. 2002, 2004, Marx 2008).

Compared to periodic floods the long-term drought of 2003 had a greater negative effect on the collembolan community. Both the numbers of individuals and species decreased markedly and the numbers had not reached pre drought levels when the study ended in 2005. Only some mesophilic and more xerotolerant species recovered faster. They are better adapted to survive drought conditions and exploited new resources in the absence of interspecific competition. Possible adaptations for reducing the rate of water loss are cuticle surface structures like ornamentation, scales and dense hairs (King et al. 1990), a dormant or quiescent state (Testerink 1983) or anhydrobiotic life stages (Massoud et al. 1968). The existence of seepage water at Ingelheim resulted in the fast recovery of *Isotomurus palustris*. Because of the low lying nature of this study site it is influenced by the groundwater table and mainly dominated by hygrotolerant species.

The extreme conditions in the summer of 2003 also had a strong effect on the community structure on the islands and riverbanks. In 2002 the collembolan communities on the islands were dominated by hygrotolerant species, particularly *Tomocerus vulgaris*. This species is widely distributed in forest litter in damp habitats. Otherwise, mesophilic species dominated at the riverbank sites. The communities on the islands and riverbanks in the year 2002 were different, whereas

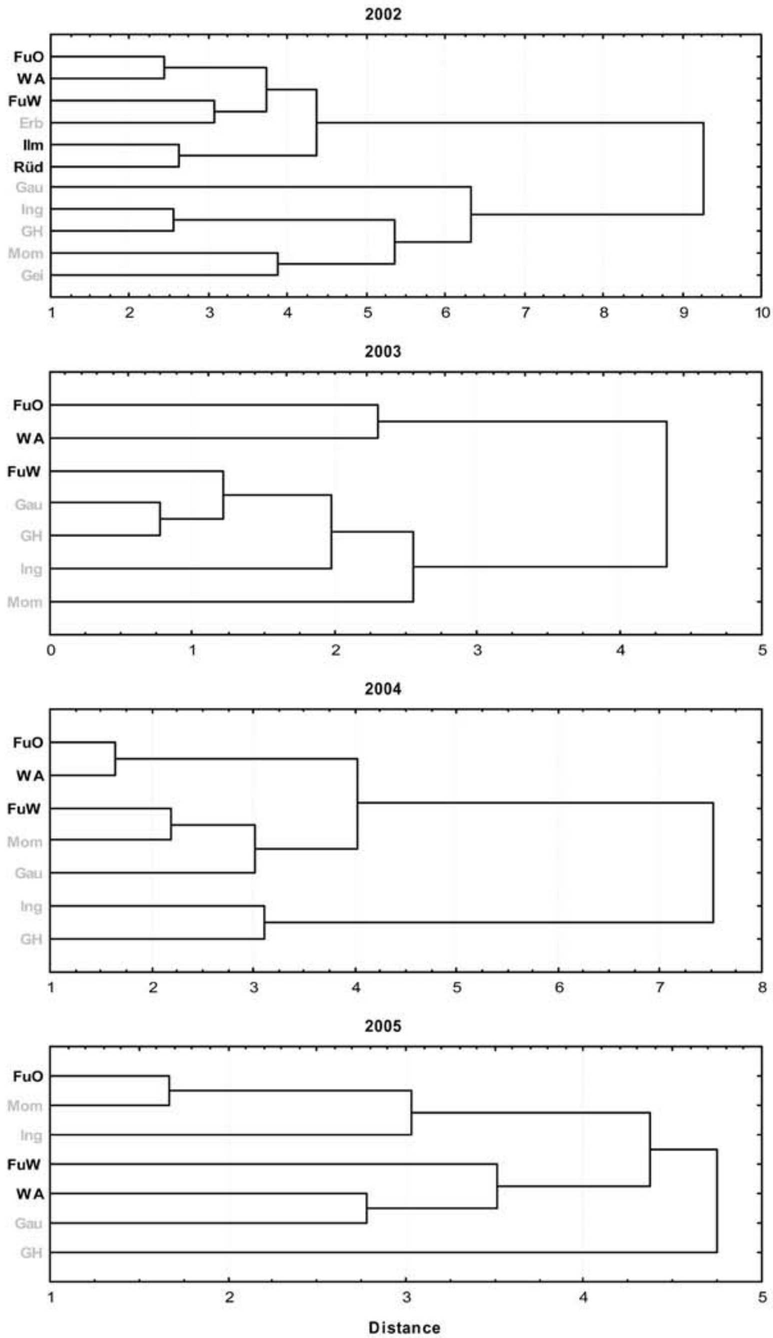

Fig. 4. Cluster analysis (Ward method; Euclidian distances) of the collembolan communities at the different study sites (Islands: in black; Riverbanks: in grey) from 2002 to 2005 (Abbreviations see Table 1).

after the drought in 2003 they are more similar. This was mainly caused by the absence of the hygrotolerant *Isotomurus* species in the spring and early summer months from 2003 to 2005 and the decrease in the numbers of individuals of *Tomocerus vulgaris* on the islands.

Compared to the effect of periodic spring floods the long-term drought in 2003 had a greater effect on the collembolan community in the floodplain forest studied. The collembolan community had not recovered even two years after this extreme event. An increase in the incidence of long-term heat-waves and aperiodic summer flooding in the future could result in a loss of many collembolan species and a dramatic decrease in their activity and abundance.

Acknowledgements

The study was financially supported by the Centre of Environmental Research and the Feldbausch foundation of the Johannes Guttenberg University of Mainz. The samples were kindly provided by the Department of Ecology (Prof. Dr. A. Seitz) of the Johannes Gutenberg-University of Mainz.

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