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PROCEEDINGS OF THE XTH INTERNATIONAL COLLOQUIUM ON APTERYGOTA, ČESKÉ BUDĚJOVICE 2000: APTERYGOTA AT THE BEGINNING OF THE THIRD MILLENNIUM

Colonization behaviour of Collembola under different conditions of dispersal

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Summary

In soil dumps of the opencast mine site Berzdorf near Görlitz (Eastern Germany), different kinds of colonization behaviour of Collembola have been observed. In immigration test plots, exposed on a nearly vegetation free dump site between May 1997 and September 1998, 17 species of Collembola were proved to have been transported by air. The first immigrant was *Bourletiella pistillum*. After 4 months, stable populations were established by *Mesaphorura florae* and *Parisotoma notabilis*. The open area around the test plots was inhabited by 20 species of epedaphic Collembola. From these, only 6 species were found in the immigration test plots. The fauna was caught in drift-protected and normal pitfall traps. Nearly 80 % of the individuals profited from wind drifting. Of these, *Bourletiella pistillum* and *Isotoma viridis* were dominant. *Lepidocyrtus cyaneus*, *L. paradoxus*, *Orchesella cincta* and *O. villosa* were mainly caught in protected pitfall traps. Thus, their main means of dispersal might be through active locomotion.
Subterranean immigration to litter-filled minicontainers was tested in two 45-year-old afforested dump sites by successively checking the minicontainers in 6-week intervals from October 1997 to January 1999. Altogether, 26 species of Collembola invaded the minicontainers. Some species found in the humus layer only in recedent frequencies reached considerably higher dominances in the minicontainers 30 weeks after their installation: *Folsomia candida* even colonized minicontainers closed by gauze of 20-µm mesh size at high densities. *Mesaphorura tenuisensillata*, *Protaphorura meridiata*, and *Proisotoma minuta* occurred preferentially in minicontainers with larger mesh-sizes. Biological and methodical conclusions from the observations are discussed.

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Key words: Collembola, air plankton, colonization, wind drifting, litter minicontainer, mining

Introduction

Springtails are known to disperse in different ways. They are transported world-wide with soil particles and organic matter. They are found as „aerial plankton“ (Palmén 1944) and have been stated to settle newly emerged islands by wind and perhaps also by water transportation (Krakatau: Womersley 1932, Surtsey: Lindroth et al. 1973).
The colonization of primarily defaunate, freshly heaped dump areas of many square kilometres size is as instructive as that of islands, but easier to observe. Between 1996 and 1999 the settlement of springtails after aerial transport, their dispersal on the soil surface under the influence of wind, and their colonization of organic matter within the soil were investigated using the Berzdorf lignite open-cast district (Eastern Germany) as a test area.

Study sites and Methods

Study sites

Within the Berzdorf mine area, a 4-ha plot free from vegetation, previously prepared (but not used) for a waste-disposal site with a kaolin cover, was elected for immigration and dispersal tests. In the surroundings, 5-year-old afforestations with poplar and pine were present. Unfortunately, this plot was reverted into an afforestation area by the recultivation company in 1998. As a reference, the youngest heaped part of the Berzdorf mine area („Endstellung“, not far from the immigration plot, about two years old) was studied using soil samples and pitfall traps in 1996.
The colonization of minicontainers was investigated in a 45-year-old part of the Berzdorf mine area („Langteichhalde“, LTH) with deciduous (mine site A) and primarily pine (mine site L) afforestation (Dunger et al. 2001).

Methods

For the immigration tests, four plots of 1 m^2 each were filled with organism- and humus-free Pleistocene sandy loam from the geological overburden. One pair of plots was installed on the edge of a 5-year-old poplar plantation („UF 2“). The other pair was installed more openly exposed in the centre of the open site („UF 1“), 50 m from the first pair. The plots were fenced in with plastic planks to prevent immigration from the surrounding soil surface (Fig. 1). Two of the test plots were equipped with wind barriers to increase the sedimentation („UF 1 P“, „UF 2 P“), two without („UF 1K, „UF 2 K“). Five soil-core samples per test plot (each divided into 0–5 and 5–10 cm depths) were taken after 1, 2, 4, 8, 16, 32 and 64 days and subsequently every two months. From 14 May 1996 to 30 September 1997, the samples were extracted dynamically in the laboratory.
For tests of dispersal of epigeic springtails, five normal pitfall traps and five drift-protected traps (Dunger & Fiedler 1997; Fig. 2) were used at plots UF 1 and UF 2 each, thus resulting in 20 traps over 11 dates (220 trap contents) between 14 May 1996 and 2 June 1997.

Table 1. Springtails from immigration test plots at the Berzdorf mine site. Individual numbers from 10 soil samples (90.8 cm^2 total) at 0–10 cm depth.
Abbreviations: UF 1: test plot at the edge of a poplar plantation, UF 2: test plot 50 m more exposed in the centre, K+P: Test plots with and without wind barriers.
Species: 1 *Mesaphorura yosii* (Rusek, 1967), 2 *Pseudosinella decipiens* Denis, 1924, 3 *Bourletiella pistillum* Gisin, 1947, 4 *Protaphorura quadriocellata* Gisin, 1947,

	UF 1 K+P 0–10 cm																	
	species:	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*
days	date																	
1	*14/05/96*																	
2	*15/05/96*			4														
4	*17/05/96*		1	2														
8	*21/05/96*			1														
16	*29/05/96*			1														
32	*14/06/96*			6					1									
64	*16/07/96*																	
124	*05/09/96*													2				
184	*11/11/96*					1							2	8				
317	*17/03/97*												1	15				
377	*01/06/97*												2	5		1	5	3
437	*29/07/97*									4			151	106				
497	*30/09/97*									14			26	31				
total			**1**	**14**		**1**			**1**	**18**			**182**	**167**		**1**	**5**	**3**

The colonization of organic matter was investigated using the minicontainer test (Eisenbeis 1998). Ten minicontainer bars were inserted in 4-8 cm depth, each in crests and troughs at mine sites A and L from October 1997 to January 1999. At six-week intervals, one bar containing four minicontainers with 2000, 500 and 20 µm mesh size, resp., were taken from each stand (altogether four bars). The inhabitants were extracted using a thermoeclector, and the remaining organic material (poplar litter) weighed. Altogether, the test period covered 60 weeks.
Because of the preliminary character of the observations presented here, a detailed statistical analysis is omitted. The dominance values are calculated according to Engelmann (1978).

Results

Immigration test

The results of the immigration tests showed no significant differences between the test plots with or without wind barriers. Therefore, the figures of UF 1 K and P as well as UF 2 K and P, resp., were pooled in Table 1. During the first two months, single individuals of species drifted in, which did not colonize and were never found again (except *Pseudisotoma sensibilis*). The break at 16th July was not caused by a summer drought. Between September 1996 and September 1997, a continuous colonization of *Mesaphorura florae*

5 *Pseudisotoma sensibilis* (Tullberg, 1971), 6 *Cryptopygus thermophilus* Axelson, 1900, 7 *Folsomia candida* Willem, 1902, 8 *Stenaphorurella quadrispina* (Börner, 1901), 9 *Parisotoma notabilis* (Schäffer, 1896), 10 *Xenylla boerneri* Axelson, 1905, 11 *Ceratophysella* spec. juv., 12 *Mesaphorura florae* Simon et al., 1994, 13 *Mesaphorura* spec. juv., 14 *Mesaphorura macrochaeta* Rusek, 1976, 15 *Entomobrya multifasciata* (Tullberg, 1871), 16 *Isotoma viridis* Bourlet, 1839, 17 *Isotomurus palustris* (Müller, 1760)

UF 2 K+P 0–10 cm																
1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*
2	2															
		2														
	2		1	1												
		3			1	1										
		1														
		2														
								2				4				
				5				1	7	1						
								3				1				
								10								
								19				5	2			
								5								
2	**4**	**8**	**1**	**6**	**1**	**1**		**40**	**7**	**1**		**10**	**2**			

and, later, *Parisotoma notabilis* was observed in UF 1, of *P. notabilis* only in UF 2. As no other species of *Mesaphorura* was found in the respective sample, the juveniles of this genus can be ascribed at UF 1 to M. florae and to *M. macrochaeta* at UF 2. Nine species are proved at UF 1, 11 at UF 2, altogether 16 species.

As a reference, the collembolan settlement of the youngest normally heaped site („Endstellung"; about two years old) near the immigration test plots was investigated in 1996. Only three edaphic species were found: *M. florae* was eudominant, *P. notabilis* and Proisotoma minuta were recedent. The latter was never proved in the immigration test plots.

Dispersal of epigeic springtails

Epigeic springtails of the open kaolin-covered area around the immigration test plots were studied by normal pitfall trapping in combination with drift-protected traps. The results show four species that preferred the exposed area, whereas the majority of species indicated a more or less close relationship to the edge of the poplar plantation (Table 2). *Lepidocyrtus cyaneus* behaved intermediately, but showed a distinct preference for drift-protected pitfall traps.

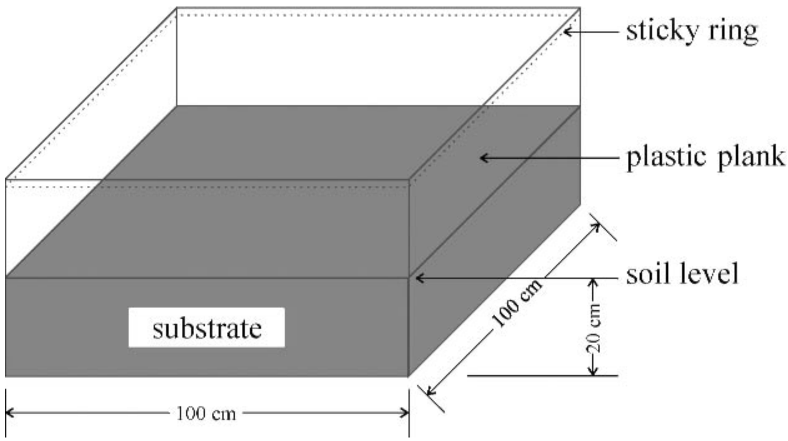

Fig. 1. Immigration test plot for detecting living, air-transported springtails in an initially humus- and organism-free substrate

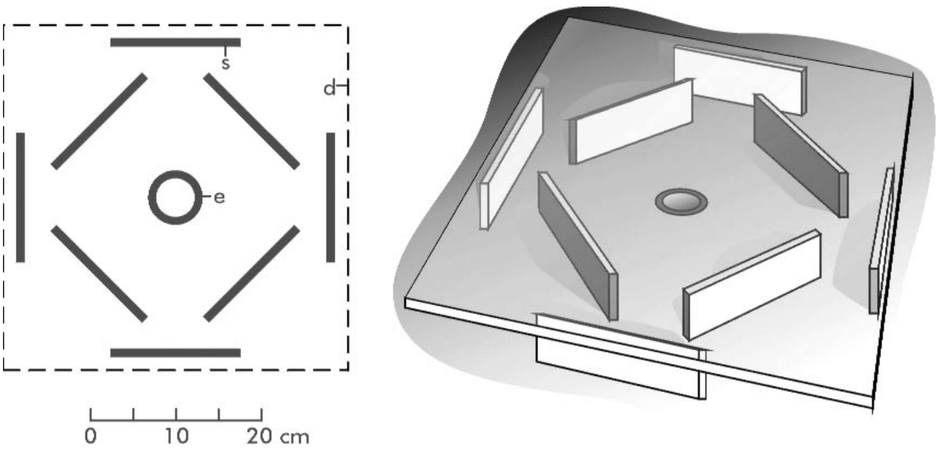

Fig. 2. Drift-protected pitfall trap according to Dunger & Engelmann (1978) with 2×4 plastic planks. The compact roof (20×20 cm) is presented transparently. e = trap, d = roof, s = plank

Parallel studies of the epigeic springtail fauna of the freshly heaped site „Endstellung" showed very typical results, such as the eudominance of *Entomobrya lanuginosa* and the presence of *Entomobrya myrmecophila*, *Lepidocyrtus lanuginosus*, *L. paradoxus*, *L. cyaneus* and *Orchesella cincta*. Instead of *Bourletiella pistillum*, only a few specimen of *B. hortensis* were caught.

Colonization of minicontainers

As part of litter-decomposition studies (see Methods), the colonization of minicontainers by soil microarthropods was investigated. As the humus layers of the deciduous mine site A and the initial pine mine site L have became so alike (due to site L beeing changed into a mixed wood over the last 30 years), the results of these two mine sites are partly pooled here. The same applies to the soil-surface profile, which contains crests and troughs (Dunger et al. 2001). Springtails were by far the most numer-

Table 2. Numbers of epigeic springtails trapped by normal („norm“) and drift-protected („prot“) pitfall traps at the vegetation-free, kaolin-covered immigration test site of the Berzdorf mine area between 14 May 1996 and 2 June 1997, divided into traps near UF 1 (free area) and near UF 2 (edge of a poplar plantation). Six subrecedent species have been omitted

	UF 1		UF 2		
	norm	**prot**	**norm**	**prot**	**dominance**
Bourletiella pistillum Gisin, 1946	7752	132	639	5	eudominant
Isotomurus palustris (Müller, 1760)	41	–	13	5	recedent
Entomobrya lanuginosa (Nicolet, 1841)	8	15	1	1	recedent
Schoettella ununguiculata (Tullberg, 1869)	14	–	2	–	recedent
Lepidocyrtus lanuginosus (Gmelin, 1788)	51	311	36	388	subdominant
Isotoma viridis Bourlet, 1839	1055	269	2137	326	dominant
Lepidocyrtus paradoxus Uzel, 1891	256	574	1026	939	dominant
Orchesella villosa (Geoffroy, 1764)	13	55	968	532	subdominant
Orchesella cincta (Linné, 1758)	61	20	901	552	subdominant
Sminthurides schoetti Axelson, 1903	27	1	860	–	subdominant
Entomobrya multifasciata (Tullberg, 1871)	3	8	64	10	recedent
Pseudosinella octopunctata Börner, 1901	–	–	29	7	recedent
Parisotoma notabilis (Schäffer, 1896)	2	1	9	27	recedent
Pseudosinella alba (Packard, 1873)	–	–	–	11	subrecedent

ous colonizers. They invaded in great numbers not earlier than after 30 weeks (Fig. 3). Minicontainers with 2000-µm mesh size showed the lowest density of springtails, but exhibited (as did those with 500-µm mesh size) a colonization peak between June and August 1998. Surprisingly, minicontainers with 20-µm mesh size yielded by far the highest numbers of springtails from June 1998 onwards.

Folsomia candida colonized the minicontainers at nearly all sites as the eudominant species (Table 3). In minicontainers from troughs of mine site L, mean numbers of *F. candida* were 1.6 (2000-µm mesh size), 5.9 (500 µm) and 27 (20 µm). In some cases (in autumn 1998), more than 100 specimen could be extracted from one minicontainer, colonizing only a remainder of about 150 mg dry mass of poplar litter. The species did not invade the 20-µm minicontainers until the 30th week. Most striking is the fact that *F. candida* was not found in the humus layer, except for three specimen from a total of 196 soil samples. Similar, but with a much lower density, was the distribution of *Mesaphorura tenuisensillata* and *Protaphorura meridiata* and, to some extent, of *Proisotoma minima*. The majority of species, however, behaved as expected: they showed high dominance in the humus layer and occurred at higher densities in the 2000-µm, but almost never in the 20-µm mesh size minicontainers (Table 3).

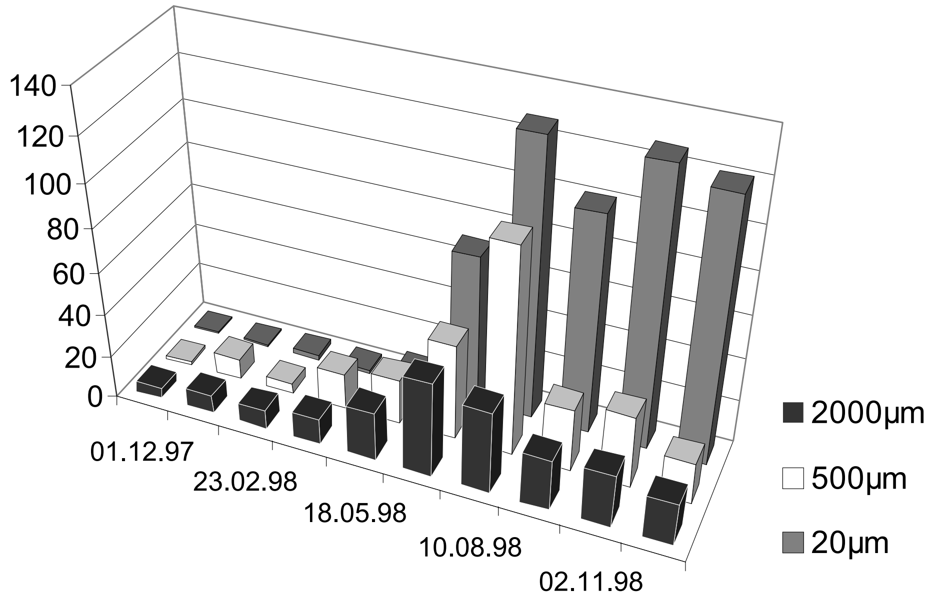

Fig. 3. Mean numbers of collembolan individuals in four minicontainers with 2000 µm, 500 µm and 20 µm mesh each, exposed in two afforested, 45-year-old mine sites. Determined at 10 dates between December 1997 and January 1999

Table 3. Comparison of the dominance structure of springtails in the humus layer and in minicontainers with 2000 µm, 500 µm and 20 µm mesh sizes. 0 = absent, 1 = sporadic, 2 = subrecedent, 3 = recedent, 4 = subdominant, 5 = dominant, 6 = eudominant

species	humus layer	Minicontainer		
		2000 µm	**500 µm**	**20 µm**
Mesaphorura tenuisensillata Rusek, 1974	0.0	3.5	2.0	0.7
Folsomia candida Willem, 1902	0.5	5.5	5.2	5.7
Protaphorura meridiata (Gisin, 1952)	0.5	1.0	0.7	1.2
Proisotoma minima (Absolon, 1901)	1.0	2.5	2.2	2.0
Heteromurus nitidus (Templeton, 1835)	1.0	2.2	2.2	0.0
Pseudosinella alba (Packard, 1873)	2.2	2.5	2.2	0.0
Megalothorax minimus Willem, 1900	3.7	4.7	5.0	2.0
Mesaphorura macrochaeta Rusek, 1976	4.7	2.2	3.2	1.5
Parisotoma notabilis (Schäffer, 1896)	5.0	4.2	3.5	0.5
Isotomiella minor (Schäffer, 1896)	5.0	2.2	2.2	0.5

Discussion

Aerial immigration and colonization

Since our studies were stopped by the activities of the mining company, we can only present preliminary results. In contrast to sampling dead or living arthropods in the air with sticky traps or other methods (Duelli et al. 1989), we studied the arrival of living springtails after aerial transport in initial by fauna-free substrate at the starting point of primary succession.

Little can be said about distance and direction of transport. The overall potential of invasive species can be roughly estimated by the list of springtails known from the surrounding Upper Lusatia and, more specifically, from previous records of Collembola at the Berzdorf mine district (Dunger 1968). Species prone to aerial transport can not be distinguished from others. Tree climbing, as found in Australia and Indonesia (Farrow & Greenslade 1992; Blackith & Disney 1988) is irrelevant in Europe since tree-inhabiting species are strongly specialized and can never be found on open land. Thus, the origin of air transported arthropods and the question of a possible selection of certain species remain open. The main conclusion from our results is that there is nearly no relationship between the species composition of the surrounding collembolan fauna and the airborne settlers.

With regard to the general process of immigration and colonization, all four plots showed the same results during the first month (Table 1). Eight species were imported mostly as single specimen. Except for the dominate *Bourletiella pistillum*, these are not known as pioneers and were neither able to establish stable populations nor had they been found again during the following months. There is no explanation for the gap during the second month, particularly as this summer was fairly cool and humid rather than hot and dry.

From the fourth month onwards, *Parisotoma notabilis* and *Mesaphorura florae* were continuously present and showed obvious propagation, especially the latter species. The position of the test plots had a clear influence: in UF 1 (in the bare area), the colonization of *Parisotoma notabilis* did not start before September 1997; in UF 2 (at the edge of the poplar plantation), their was no certain record of *Mesaphorura florae* at all. Apart from these colonizers, seven species were found only once within an entire year, thus beeing unable to colonize the plots. If the poplar plantation was the main source of immigrants, this could explain why *Parisotoma notabilis* arrived later and in smaller numbers in the plot further from poplar (UF 1) than in the closer plot (UF 2).

The immigration tests revealed only two species that colonized from the fourth month onwards and 14 species introduced by wind drift but not able to colonize. In the literature, there are thematically comparable studies on the settlement of volcanic ashes or flat house roofs, but non with an adequate technique (Darius & Drepper 1983; Klausnitzer 1988). Thus, the discussion focusses on the following questions:

– Are the colonizers typical pioneers (initial species sensu Dunger 1991)? This is true for *Mesaphorura florae* which was found as the dominant species in the youngest heaped substrate („Endstellung"). It was found for the first time in 1962 (as *„Tullbergia krausbaueri"* at „Außenhalde Berzdorf Nord") with a rapid propagation of up to 2000 individuals per m^2 (Dunger 1968). The other expected initial species, *Proisotoma minima*, well known from the first stages of freshly mined areas as well as from the first invasion at Surtsey (Lindroth et al. 1973), was not present in the test plots. On the other hand, *Parisotoma notabilis* was found as a dominant colonizer of the second stage of primary succession. It is linked with the first accumulation of organic matter (Dunger 1991).

– Have all colonizers been recorded ? Because it is unknown whether all immigrating species have been recorded, it cannot be stated whether further immigrating species occur. However, the question remains why there is no evidence of the most frequent initial species of the epedaphic springtails, *Entomobrya lanuginosa*. It was not found within the test plots, but it is known that *E. lanuginosa* can be recorded by soil cores. Therefore, this springtail is the only initial species that was expected, but not registered in the immigration tests.

– Which factors hamper unsuccessful invaders and enable colonizers? There is no evidence for unfavourable physical-chemical factors of the test plot substrate acting negatively against the development of springtail populations. Thus, the most important limiting factor may be food requirement. Many springtails are known to feed on pollen, algae or protozoans. This food is present from the first month onwards (Wanner et al. 1998). However, testate amoebae need five months to establish themselves (Wanner & Dunger 1999). Exactly from this time onwards, two species of springtails were observed colonizing in UF 1 and only one in UF 2. If the presence of decaying organic matter and – possibly linked with it – fungi is the most important cause of colonizing success, the test plots UF 1 and UF 2 have to be regarded separately from this point on. During early autumn, single poplar leaves were blown into the test plots of UF 2, whilst UF 1 received nothing. Our present conception tends towards the presumption that the first colonizers (in this case: *Mesaphorura florae*, UF 1) are able to survive without such food. More demanding colonizers (here: *Parisotoma notabilis*, UF 2) are quickly promoted by the presence of such food. Interactions between springtail species and other initial colonizers during the first stages of colonization were not noticed.

Recording epedaphic springtails in an area exposed to air current

Accompanying the immigration tests, the settlement of an open, kaolin-covered area surrounding the test plots was recorded. It must be assumed that epedaphic springtails are scattered to a high degree by wind and rain. Recording collembolans by soil sampling was not thought to be an adequate method. Instead, the Collembola were trapped by two types of pitfall traps, normal and drift protected. None of these reflect the true density because they are influenced by active or passive movement (Dunger & Engelmann 1978; Dunger & Fiedler 1997). Particularly drift-exposed species (*Bourletiella pistillum*, *Isotomurus palustris*, *Sminthurides schoetti*, *Isotoma viridis*) showed the highest numbers in normal pitfall traps, species with self-motile priority and a preference for sheltered areas (anachoresis) were found in high numbers in the drift-protected traps (*Lepidocyrtus cyaneus*, *L. paradoxus*, *Orchesella cincta*, *O. villosa*). Species with higher individual numbers in normal traps in the open UF 1 area were found in lesser numbers in the drift-protected traps. This suggests that their higher numbers in the unprotected area UF 1 is a result of higher wind dispersal compared with UF 2, which was hidden at the edge of a plantation.

The collembolan settlement on the vegetation-free, variably moist, kaolin-covered area is clearly distinct from that of the adjacent poplar plantation, as well as from the species inventory of vegetation-free young dump heaps. The latter is dominated by *Entomobrya lanuginosa* and – after two to four years – *Hypogastrura assimilis* and *Ceratophysella succinea*. These species were absent or very rare in UF 1 and 2. *Bourletiella pistillum* is replaced by *B. hortensis*. Nevertheless, nearly all of the trapped species are inhabitants of open land with a clear preference for pioneer sites. Only 6 of the 20 species were also found as infrequent invaders in the immigration test plots. There was no indication of an active immigration into the test plots from the surrounding area. Airborne transport over a very short distance appears plausible.

Endogeic invasion of poplar litter in minicontainers

The litter layer of the Berzdorf mine site LTH consisted of 20–40 % Populus sp. (hybrid) litter during the test period (Dunger et al. 2001). The same substrate was exposed in minicontainers at 4–8 cm soil depth. The first five species in Tab. 3 were more dominant in the minicontainers, which obviously exerted a „litterbag effect“ (Crossley & Hoglund 1962). This effect, although unknown in detail, is supposed to be caused by increased microbial decomposition. Chemical stimuli attract certain species of Collembola. As Fig. 3 shows, the microbial activity needed more than 30 weeks to become highly attractive to the „decomposer specialists“ and/or effective for their reproduction.

It is well known that *Folsomia candida*, though not very numerous in normal competitive communities, reaches high densities in decomposing organic substrates (Fromm 1998), especially under experimental conditions. It is a regular inhabitant of mine-dump soils (Dunger 1968; Zerling 1990). More surprising is the behaviour of *Mesaphorura tenuisensillata* and *Protaphorura meridiata*, species which up to now have not been described as having such a property.

The results need to be discussed under methodical aspects. Eisenbeis (1998) introduced the minicontainer method as a refined litter bag test for the study of decomposition rates with regard to the different participation of parts of the soil fauna (entire fauna, exclusion of macrofauna and participation of microfauna only). We used orig-

inal minicontainers from Eisenbeis and carefully checked the intact protection of the container opening by the gauze. According to the precaution rule of Törne (1997), the application of the minicontainer test with original litter from the site was acceptable. During the first 30 weeks, a typical course of decomposition can possibly be stated. The immigration of microarthropods during this period was low, similar to observations by Keplin (1999). A longer exposition of the minicontainers, unusual in comparable investigations, seems to lead to another state of decomposition, which creates „hot spots“. Just at this time, an intensive litter breakdown was observed in the 2000-µm containers, whilst decomposition showed a normal, slow progress in the other containers (Dunger & Wanner 1999). The collembolan numbers in containers with a larger mesh size decreased again in September – October. That was not the case in the 20-µm containers. Here, the density of *Folsomia candida* continued to be enhanced, as is thus far only known from compost (Chernova 1977).
It may argued that defaunation of the litter (drying at 60 °C for a few days, see Törne 1997) was not successful. If so, the parthenogenetic *Folsomia candida* should have reproduced many times during the first 30 weeks, as it normally takes 4–6 weeks at 15 – 20 °C from egg to egg (Dunger 1983; Snider 1973). Nothing like this could be observed. On the other hand, it is possible that freshly emerged juveniles can squeeze through the meshes, but cannot leave the container as adults. It cannot be excluded that females, attracted by chemicals, laid egg patches directly on the container gauze. However, such ideas appear speculative as long as only two series of minicontainers were investigated, even if longer than usual (60 weeks each).

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References

Blackith, R. E., Disney, R. H. L. (1988) Passive dispersal during moulting in tropical Collembola. Malayan Nature Journal 41, 529–531.

Chernova, N. M. (1977) Ekologičeskie sukcessii pri razloženii rastitel'nych ostatkov. Nauka, Moskva.

Crossley, D. A., Hoglund, M. P. (1962) A litter-bag method for the study of microarthropods inhabiting leaf litter. Ecology 43, 571–573.

Darius, F., Drepper, J. (1983) Ökologische Untersuchungen auf bewachsenen Kiesdächern in West-Berlin. Gartenamt 33, 309–315.

Duelli, P., Näf, W., Baroni-Urbani, C. (1989) Flughöhen verschiedener Ameisenarten in der Hochrheinebene. Mitteilungen der schweizerischen Entomologischen Gesellschaft 62, 29–35.

Dunger, W. (1968) Die Entwicklung der Bodenfauna auf rekultivierten Kippen und Halden des Braunkohlentagebaues. Ein Beitrag zur pedozoologischen Standortsdiagnose. Abhandlungen und Berichte des Naturkundemuseums Görlitz 43 (2), 1–256.

Dunger, W. (1983) Tiere im Boden. A. Ziemsen, Wittenberg Lutherstadt.
Dunger, W. (1991) Zur Primärsukzession humiphager Tiergruppen auf Bergbauflächen. Zoologische Jahrbücher, Systematik 118, 423–447.
Dunger, W., Engelmann, H.-D. (1978) Testversuche mit immissionsgeschützten Bodenfallen für Mikroarthropoden. Pedobiologia 18, 448–454.
Dunger, W., Fiedler, H.-J. (eds) (1997) Methoden der Bodenbiologie. 2. Aufl., Fischer, Jena.
Dunger, W., Wanner, M. (eds) (1999) Immigration und Sukzession ausgewählter Gruppen der Bodenfauna in terrestrischen Ökosystemen und Bergbaurandflächen. Schlußbericht des BMBF-Forschungsvorhabens BEO/ 51.0339668, Staatliches Museum für Naturkunde Görlitz.
Dunger, W., Wanner, M., Hauser, H., Hohberg, K., Schulz, H.-J., Schwalbe, T., Voigtländer, K., Zimdars, B., Zulka, P. (2001) Development of soil fauna at mine sites during 46 years after afforestation. Pedobiologia 45, 243–271.
Eisenbeis, G. (1998) Die Untersuchung der biologischen Aktivität von Böden. II. Der Minicontainer-Test. Praxis der Naturwissenschaften Biologie 47 (4), 22–29.
Engelmann, H.-D. (1978) Zur Dominanzklassifizierung von Bodenarthropoden. Pedobiologia 18, 378–380.
Farrow, R. A., Greenslade, P. (1992) A vertical migration of Collembola. Entomologist 111, 38–45.
Fromm, H. (1998) Räumliche und zeitliche Variabilität der Collembolenfauna und ihre Bedeutung für C- und N-Umsatz in einer Agrarlandschaft. Aachen, Shaker (FAM-Bericht 26).
Keplin, B. (1999) Abbau und Mikroarthropoden-Besiedlung von Kiefern-Wurzelstreu (*Pinus nigra* und *Pinus sylvestris*) im Minicontainer-Test auf rekultivierten Forststandorten. Braunschweiger Naturkundliche Schriften 5, 913–924.
Klausnitzer, B. (1988) Arthropodenfauna auf einem Kiesdach im Stadtzentrum von Leipzig. Entomologische Nachrichten und Berichte 32, 211–215.
Lindroth, C. H., Andersson, H., Bödvarsson, H., Richter, S. H. (1973) Surtsey, Iceland. The development of a new fauna, 1963–1970. Terrestrial invertebrates. Entomologica Scandinavica, Suppl. 5.
Palmén, E. (1944) Die anemohydrochore Ausbreitung der Insekten als zoogeographischer Faktor. Annales Zoologici Societas Zoologia - Botanica Fennica 10 (1), 1–162.
Snider, R. M. (1973) Laboratory observations on the biology of *Folsomia candida* (Willem) (Collembola: Isotomidae). Revue d'Ecologie et de Biologie du Sol 10, 103–124.
Törne, E. von (1997) Schätzung von Freßaktivitäten. In: Dunger, W., Fiedler, H.-J. (eds) Methoden der Bodenbiologie. Fischer, Jena, pp. 373–379.
Wanner, M., Dunger, W., Schulz, H.-J., Voigtländer, K. (1998) Primary immigration of soil organisms on coal mined areas in Eastern Germany. In: Pižl, V., Tajovsky, K. (eds) Soil Zoological Problems in Central Europe. Institute of Soil Biology České Budějovice, pp. 267–275.
Wanner, M., Dunger, W. (1999) Immigration und Sukzession von Protisten in terrestrischen Kippökosystemen und Bergbaurandflächen. Verhandlungen der Gesellschaft für Ökologie 29, 321–327.
Womersley, H. (1932) Collembola from Krakatau. Entomologist's Monthly Magazine 68, 88.
Zerling, L. (1990) Zur Sukzession von Kleinarthropoden, insbesondere Collembolen, im Bodenbildungsprozeß auf einer landwirtschaftlich genutzten Braunkohlenkippe bei Leipzig. Pedobiologia 34, 315–335.