Chapter 7
Soil Fauna

M. Schaefer and J. Schauermann

7.1 Introduction

The beech forests studied provide three different environments for the soil fauna and are located in a gradient from base-rich to acid soils. The forest “Göttinger Wald” is characterized by mull soil; soil conditions in the forest “Kleiner Gudenberg” (near the town of Zierenberg; hence denoted as forest “Zierenberg”) are moder-like; and in the “Solling” forest moder soils prevail. In this chapter, the relationship between the fauna and the soil milieu is analysed, with the perspective to explain relational patterns with factors of a causal nature.

The beech forests are described in detail in several chapters of this volume (Meesenburg and Brumme; Panferov et al.; Meesenburg et al.; Schmidt). We highlight some habitat characteristics directly related to the soil fauna.

At the *Göttinger Wald* site, the soil is shallow and belongs to the soil series which has developed on the limestone, forming “terra fusca-rendzina” (about 50% of the area), rendzina (about 26%), terra fusca (about 14%) and some form of brown earths. The organic layer contains mainly leaf material (550 g dry mass m^{-2}) and the annual canopy leaf litter fall is 309 g dry mass m^{-2} (mean value for 1981–1991; Schmidt, unpublished results). The soil pH ranges from 6.8 to 4.3 with a mean value of about 5.8. The soil is base-rich with high cation exchange capacity. Further details are given by Schaefer (1990, 1991a) and Schaefer and Schauermann (1990).

The beech forest *Zierenberg* consists of three sites along the slope of a hill forming a gradient from basalt to limestone: it extends from the upper part of the hill (basalt site) via an intermediate site (transition zone) to the lower part of the hill (limestone site). The average mass of leaf litter is 1,900 g at the basalt site, 1,400 g at the intermediate site and 1,600 g dry mass m^{-2} at the limestone site. Annual beech leaf litter input (in 1989) was 509 g for the basalt, 445 g for the intermediate and 375 g dry mass m^{-2} for the limestone site (Hartwig et al. 1991). The input of litter of stinging nettles (*Urtica dioica*) is 70–90 g dry mass m^{-2} at the intermediate site (Scheu 1997). Soil pH of the basalt site is about 4–5, the values for the intermediate and limestone site are 5.7 and 6.7, respectively. Cation exchange

R. Brumme and P.K. Khanna (eds.), *Functioning and Management of European Beech Ecosystems*, Ecological Studies 208,
DOI: 10.1007/b82392_8,

capacity is intermediate between that of the forests Göttinger Wald and Solling. Further details are presented in Eichhorn (1991) and Alphei (1995).

At the *Solling* site, the soil belongs to the series on carbonate-free silicate rocks: it is an acid brown earth with a moder humus form. The mass of organic layer on the soil increased from 2,960 g m^{-2} in 1966 to 4,460 g dry mass m^{-2} in 1979, while annual canopy leaf litter fall had a mean value of 290 g dry mass m^{-2} for the period from 1967 to 1976. Values of pH range from about 3 to 4. The soil is base-poor and cation exchange capacity is low. Further details are given in Ellenberg et al. (1986).

7.2 Fauna

The fauna of the two forests, Göttinger Wald and Solling, was sampled with different methods (soil and litter samples, photo-eclectors, pitfall traps) and different intensities over long periods, namely from 1980 to 1995 for Göttinger Wald and from 1967 to 1995 for Solling. For many (not all) animal groups, species numbers of the two forests can be compared because the intensity of sampling was similar. A synopsis of species numbers, population density and biomass is presented in Table 7.1, which is based on a synthesis of the data for the fauna of the two forests presented by Schaefer and Schauermann (1990). Additionally, more recent results are given for Nematoda (Solling) (Alphei 1995), Cryptostigmata, Gamasina and Uropodina (Göttinger Wald) (Schulz 1991a, b), Gamasina (Solling) (Buryn, unpublished results) and Diptera (Göttinger Wald) (Hövemeyer 1992). Some minor groups are omitted. For the Solling forest, several important and species-rich taxa were not studied.

The fauna of the Zierenberg forest was studied from 1990 to 1997 and is not completely known for the whole range of the soil fauna. The data for selected taxa of the soil fauna are presented for the gradient from basalt to limestone (Table 7.2). Data were obtained for Protozoa (Wellner, Coenen, Bonkowski, unpublished results), Nematoda (Alphei 1995), Enchytraeidae (Schlaghamerský 1998), Cryptostigmata (Heiligenstadt, unpublished results, Schulz 1991a), Collembola (Koch 1993), Gastropoda (Nieselt 1991), Lumbricidae (Bonkowski 1991), Isopoda (Nieselt 1991), Diplopoda (Nieselt 1991), Coleoptera (Nolte 1993), and Diptera (Markwardt 1993).

7.3 Macro-Gradient from Base-Rich to Acid Beech Forests

The series mull > mull-like moder > moder constitutes a macro-gradient with decreasing pH, decrease of the ratio C_{mic} to C_{org} and of the ratio bacteria to fungi, decreasing importance of the macrofauna, increasing significance of the meso-fauna and decreasing zoomass (cf. Fig. 12.7 in chapter 12). In the following sections, we compare the biota in the macrohabitats at Göttinger Wald, Zierenberg and Solling in more detail.

The mull-structured forest Göttinger Wald is characterised by high faunal biomass with earthworms as the dominant macrofauna group. This saprophagous

Table 7.1 Synopsis of species richness (*S*), mean annual population density (*N*, ind m^{-2}) and mean annual biomass (*B*, mg dry mass m^{-2}) in the beech forests Göttinger Wald (with mull soil) and Solling (with moder soil). Modified from Schaefer and Schauermann (1990). Additional data from Schulz (1991a, b), Hövemeyer (1992), Alphei (1995) and further unpublished sources

Animal group	Göttinger Wald			Solling		
	S	N	B	S	N	B
Microfauna						
Flagellata	?	2.7×10^9	54	?	?	?
Amoebina	?	3.5×10^9	1,133	?	?	?
Testacea	65	84×10^6	343	51	57×10^6	256
Turbellaria	3	859	8	3	1,882	4
Nematoda	110	732,000	146	90	3×10^6	65
Rotatoria	13	4,893	5	?	?	?
Tardigrada	4	4,207	4	?	41	9
Harpacticoida	?	3,873	2	1	3,300	0.6
Saprophagous and microphytophagous mesofauna						
Enchytraeidae	36	22,300	600	15	108,000	1,640
Cryptostigmata	75	22,445	241	72	101,810	195
Uropodina	11	1,971	19	4	1,525	?
Symphyla	2	57	?	1	?	?
Diplura	?	161	?	>1	277	?
Protura	?	2,481	?	>1	278	?
Collembola	48	37,835	153	50	63,000	246
Zoophagous mesofauna						
Gamasina	80	3,151	50	53	10,800	397
Saprophagous macrofauna						
Gastropoda	30	120	430	4	0	0
Lumbricidae	11	205	10,700	4	19	168
Isopoda	6	286	93	0	0	0
Diplopoda	6	55	618	1	0	0
Elateridae	11	37[a]	104[a]	4	332[a]	706[a]
Diptera	299	2,843[a]	161[a]	?	7,415[a]	628[a]
Zoophagous macrofauna						
Araneida	102	140	47	93	462	173
Pseudoscorpionida	3	35	16	2	89	10
Opilionida	8	19	11	4	20	6
Chilopoda	10	187	265	7	74	155
Carabidae	24	5	144	26	7	93
Staphylinidae	85	103	76	117	314	180

? = not studied; 0 = not present; [a]Larvae

guild is responsible for a high degree of bioturbation. In the moder-structured forest Solling, microphytophagous mesofaunal taxa (oribatid mites, collembolans) are prevalent. Generally, species diversity is lower in the Solling forest. A notable exception are staphylinid beetles. Total animal species number is 1,918 in the forest Göttinger Wald, among them 704 hymenopteran and 299 dipteran species (Schaefer 1996); the forest Solling contains 734 species (with the Hymenoptera and Diptera not studied), well below the corresponding 915 species of the mull-structured forest

Table 7.2 Synopsis of species richness (*S*), mean annual population density (*N*, ind m^{-2}) and mean annual biomass (*B*, mg dry mass m^{-2}) in the beech forest Kleiner Gudenberg (Zierenberg) for three sites along the slope of the hill: upper part of the hill (basalt site), intermediate site (transition zone), lower part of the hill (limestone site). From different sources

Animal group	Basalt site			Intermediate site			Limestone site			Total
	S	N	B	S	N	B	S	N	B	S
Microfauna										
Flagellata					5×10^6					
Amoebina			ca.800		5×10^6	ca.900		ca.400		
Ciliata	>53			>15			>29		>70	
Nematoda	71	1.8×10^6	High	85	1.87×10^6	medium	79	1.32×10^6	low	129
Saprophagous and microphytophagous mesofauna										
Enchytraeidae	18	23,000	900	19	22,000	1,000	11	13,500	500	23
Cryptostigmata	53	High	High	35	Medium	Medium	42	Low	Low	60
Uropodina	4	Low	Low	7	Medium	Medium	6	High	High	7
Collembola	38	44,800	140	45	44,200	167	38	30,400	123	49
Zoophagous mesofauna										
Gamasina	23	High	High	25	Medium	Medium	22	low	low	25
Saprophagous macrofauna										
Gastropoda	23	487	395[a]	28	881	809[a]	31	926	689[a]	33
Lumbricidae	8	114	15,000[b]	9	218	24,000[b]	9	67	23,000[b]	11
Isopoda	5	1,104	232	6	746	170	5	725	269	6
Diplopoda	6	272	646	8	200	365	8	355	639	8
Diptera		2,339[c]	288[c]		2,707[c]	384[c]		2,602[c]	493[c]	
Zoophagous macrofauna										
Carabidae	16		832[c]	17		1,823[c]	16		1,344[c]	21
Staphylinidae	34		147[c,d]	42		187[c,d]	29		122[c,d]	49

[a]Slugs not included. [b]Fresh wt. [c]Emerging adults per year (photo-eclectors). [d]Excluding Aleocharinae

Göttinger Wald. The fauna of the Zierenberg site appears to be intermediate between that of Göttinger Wald and Solling concerning species number, dominance of macro- and mesofauna and zoomass.

In a more detailed analysis, some general trends become apparent from the synopsis of the more important animal groups in the three forests (cf. Tables 7.1 and 7.2). Total soil zoomass amounts to about 15 g dry mass m^{-2} in the mull soil of the forest Göttinger Wald and about 5 g dry mass m^{-2} in the moder soil of Solling (with a value for Zierenberg in between). This difference is mainly due to the predominance of earthworms and, to a lesser degree, of saprophagous macro-arthropods in the mull forest. The following faunal groups exhibit – partly striking – differences in the gradient Göttinger Wald → Zierenberg → Solling: Protozoa, Nematoda, Gastropoda, Enchytraeidae, Lumbricidae, Cryptostigmata, Isopoda, Diplopoda, Collembola, Diptera and some predatory macroarthropod groups (Araneida, Chilopoda and Staphylinidae). In the mull soil, many Protozoa (naked Amoebae, flagellates and ciliates), the nematodes, gastropods, lumbricids, isopods, diplopods and chilopods are favoured. The testaceans (Protozoa), enchytraeids, oribatid mites, collembolans, dipterans, araneids and staphylinids occur with higher population density and/or biomass in the moder soil. Thus, mainly microphytophagous mesofauna groups dominate in the moder environment. Zoophagous macroarthropods occur in comparable numbers in the three forest types. In the following paragraphs, some more detailed analyses of dominant species, abundance and biomass relations of edaphic key groups are given: microflora, Nematoda, Cryptostigmata, Collembola, earthworms and gastropods, and saprophagous macro-arthropods (data mainly from Schaefer and Schauermann (1990), Schaefer (1991a)).

Microflora. In the series from mull to moder with a gradient of increasing acidity, the specific respiration of the microflora qCO_2 [unit CO_2–C released per unit microbial biomass, (μg CO_2–C × mg^{-1} C_{mic} × h^{-1})] increases because more carbon is needed for the energy metabolism of the microorganisms (Fig. 7.1) (cf. Anderson, this volume). Less carbon is fixed in microbial biomass (decreasing ratio C_{mic} to C_{org}) in the moder soil. The species number of ectomycorrhizal fungi is twice as high on the base-rich site as compared to the acid site (Scheu, unpublished results).

Microfauna: Nematoda. Among the non-protozoan microfaunal groups, the Nematoda are clearly the most abundant (Alphei 1995). Species numbers are similar on the three sites; however, species composition is different. In the base-rich site, bacterial feeders are dominant whereas fungal or root feeders are prevalent in the forest on acid soil (Alphei 1998). Biomass was dominated by root hair feeders and the mycetophagous *Tylolaimophorus* in moder soil, whereas pantophagous taxa, mainly *Aporcelaimellus*, dominated in mull soil.

Saprophagous and microphytophagous mesofauna: Cryptostigmata, Collembola. Oribatid abundance is significantly higher in the moder than in the mull soil. However, biomass does not distinctly surpass values for the mull soil (mean body mass of mites in the Solling forest 0.002 mg, in the Göttinger Wald forest 0.007 mg dry mass). In Göttinger Wald, the oribatids *Steganacarus magnus*, *S. striculus* and *Nothrus palustris* dominate in biomass. In Solling *Platynothrus*

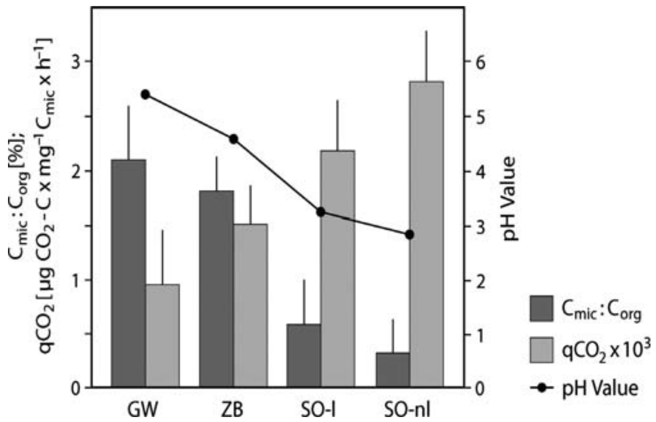

Fig. 7.1 Specific respiration qCO_2 and ratio C_{mic} to C_{org} in three different beech forests forming a gradient from base-rich to base-poor soil conditions. *GW* Göttinger Wald, *ZB* Kleiner Gudenberg (Zierenberg), *SO–l* Solling, limed, *SO-nl* Solling unlimed. Measurements in spring 1995 (means plus SD). (Scheu, unpublished results). Please note the Erratum at the end of the book

peltifer, *Nothrus silvestris*, *Nanhermannia coronata* and *Chamobates voigtsi* constituted over 50% of adult zoomass (Heiligenstadt 1988). In Göttinger Wald, mean annual population density and biomass of Collembola are about half of the corresponding values in the Solling soil. Thus, mean body mass is almost the same in both habitats (0.004 mg dry mass). In Göttinger Wald, several collembolan species dominate (measured in biomass): *Tomocerus flavescens*, *Lepidocyrtus lignorum, Folsomia quadrioculata*, *Isotomiella minor*, *Hypogastrura denticulata*. In Solling *Folsomia quadrioculata*, *Mesaphorura* sp., *I. minor*, and *Isotoma notabilis*, are the most abundant species. The oribatid and collembolan fauna of the Zierenberg site is more akin to that of Göttinger Wald (Koch 1993; Schulz 1991b).

Saprophagous macrofauna: Lumbricidae, Gastropoda. The Göttinger Wald mull soil is characterised by high zoomass of Lumbricidae (dominant in terms of biomass are *Lumbricus terrestris*, *Aporrectodea caliginosa*, *Octolasion* spp.) and of Gastropoda (dominants are *Perforatella incarnata*, *Arianta arbustorum*, *Aegopinella nitidula*, *Arion rufus*). In the Solling forest, only a few slug species, with negligible population density, and no snail species occur. In the moder soil, the earthworms are represented by the epigeic *Dendrobaena octaedra* and other species near tree stumps (e.g. *Lumbricus rubellus*); the mean body size of lumbricids is 8.8 mg dry mass which compares with 52.2 mg dry mass of the Göttinger Wald population. In the Zierenberg forest, endogeic species dominate with 15–24 g fresh mass m^{-2} (Bonkowski 1991). In this forest, Gastropods reach high values of density and biomass (Nieselt 1991).

Saprophagous macroarthropods. Diplopoda (dominant are *Glomeris marginata*, *G. conspersa*, and Isopoda (dominant is *Trichoniscus pusillus*) are typical faunal elements of the mull-structured forests of Göttinger Wald and Zierenberg (Schaefer 1991a; Nieselt 1991). Larvae of elaterid beetles are typical moder-soil inhabitants, consisting almost solely of *Athous subfuscus* in the Solling forest. The community in the Göttinger Wald forest is more diverse, with *A. subfuscus*, *A. vittatus* and *A. haemorrhoidalis* as the dominant species. In the Solling forest, population density and biomass of dipteran larvae are considerably higher than in the mull soil of Göttinger Wald. Mean average individual mass of the larvae in Göttinger Wald is 0.057 mg dry mass, while it is 0.085 mg dry mass in Solling. Dominant families in the Göttinger Wald (in terms of biomass) are Sciaridae, Empididae, Rhagionidae, Lestremiidae, Limoniidae and Tipulidae. In the Solling forest, Sciaridae and Sciophilidae have distinctly higher zoomass values than other dipteran groups. The dipteran community in the Zierenberg forest is rather similar to that of Göttinger Wald (Markwardt 1993).

Some presumptions about the reasons for different habitat preferences of the fauna are possible (Schaefer 1991a, b, c). Protozoa and Nematoda probably utilise the rich bacterial populations in mull soils. The reason for the suppression of shell-bearing gastropods in moder soils appears to be the low Ca availability; this element is required for the formation of the shell. Enchytraeids need high moisture, which is secured more in moder soils than in mull soils. Density and biomass of Enchytraeidae are inversely related to density and biomass of earthworms and are perhaps directly influenced by earthworm occurrence. The susceptibility of individuals to low pH values (Edwards and Bohlen 1996) may be one reason for the absence of most earthworm species in acid soils; another reason may be the restricted substrate feeding in the A and B horizons of moder soils. Oribatid mites and collembolans might be favoured in moder soils by the high quality of available fungal food. Fungi would provide enough Ca which is accumulated by these microfloral populations. Many collembolan species are preferably fungal feeders and may be favoured by high population densities of microfungi (Hopkin 1997). The reason for the absence of isopods and diplopods in acidic moder soils may be the low Ca availability; this element being an important constituent of the skeleton. Generally, the absence of herbs will have a detrimental effect on some groups of the saprophagous macrofauna (see Chap. 12). The voluminous organic layers in the moder ground floor may favour the establishment of predatory macrofauna populations, such as spiders, chilopods, carabids and staphylinids. According to Wallwork (1970), zoophagous arthropods (such as centipedes, spiders, pseudoscorpions, opilionids and predatory beetles) are generally better represented in moder profiles than in mull, probably in parallel to the high numbers of microarthropods as potential prey.

7.4 Meso-Gradient from Basalt to Limestone at the Zierenberg Site

Some of the animal groups are distributed in a characteristic pattern along the hill gradient of the Zierenberg site (cf. Table 7.2). There is a tendency for high faunal diversity in the intermediate site; however, species numbers were rather similar in all three sites covering the gradient. Nematodes and the mesofauna reach high numbers in the basalt site. Groups of the macrofauna (saprophagous and zoophagous) attain high densities in the intermediate site and are less pronounced in the limestone site. The distribution pattern of nematodes and earthworms is discussed below in more detail.

Nematoda. The limestone site is characterised by lower nematode numbers and biomass (Alphei 1995). In this case, lower soil moisture appears to be a decisive factor. Herbivorous populations are well developed in the intermediate and basalt sites because of the high availability of aboveground and belowground herb litter. The root ectoparasites *Paratylenchus*, *Helicotylenchus* and *Rotylenchus* had their highest density at the intermediate site with abundant *Urtica* litter. It appears that *Helicotylenchus* is favoured by this nitrogen-rich plant material.

Lumbricidae. The earthworms had their highest density and biomass at the intermediate site (Bonkowski 1991). Obviously, they are favoured by abundant high-quality herb litter material (mainly stinging nettle) and by the balanced moisture regime of this site. Some endogeic lumbricids prefer soil rich in Protozoa and the rhizosphere of herbs and/or grasses. Adverse factors in the basalt site might be frost in winter, and in the limestone site, low soil water content in summer. However, the low numbers of *L. terrestris* at the Zierenberg site are difficult to explain (Bonkowski 1991; Schaefer et al. 1993).

Obviously, the presence of stinging nettle in the intermediate site as a rich high-quality resource favours the saprophagous fauna and offers high structural diversity for carabid and staphylinid beetles. High availability of basic cations in the limestone site is a key factor for the development of the macrofauna. More acid conditions are responsible for the dominance of the mesofauna in the basalt site. Here, bioturbation is less pronounced, which explains the fact that the fauna does not occur deeper in the soil than at the limestone site.

7.5 Conclusions

Some distinct patterns emerge for the distribution of the animal taxa in the macro- and meso-gradient from mull to moder. The change of abiotic soil conditions and of the availability of specific food resources from base-rich to acid soils leads to faunal and microfloral change. The patterns are diverse and may concern the composition of the fauna on higher taxonomic levels and on species levels, population densities, faunal and microfloral biomass, life-forms and trophic types and mean body size.

Some of the trends are interpretable, as was demonstrated for the macro-gradient and the meso-gradient. As factors responsible for the observed patterns, the following emerge: soil pH, cation exchange capacity, depth and structure of the litter layer, bioturbation by earthworms, composition and biomass of the microflora and quality of litter resources (herb, canopy litter). However, often causal relationships are cryptic. The spatial sequence of woodland sites with different pH conditions can be regarded as a false time-series for human impact via acid rain (see Chap. 12).

Acknowledgements We thank David H. Wise (Chicago, Illinois) for reading and commenting on the manuscript.

References

Alphei J (1995) Die freilebenden Nematoden von Buchenwäldern mit unterschiedlicher Humusform: Struktur der Gemeinschaften und Funktion in der Rhizosphäre der Krautvegetation. Berichte des Forschungszentrums Waldökosysteme Göttingen (A) 125:1–165

Alphei J (1998) Differences in soil nematode community structure of beech forests: comparison between a mull and moder soil. Appl Soil Ecol 9:9–15

Bonkowski M (1991) Untersuchungen zum Verteilungsmuster der Regenwürmer (Lumbricidae) in einem Buchenwald auf Basalt und Kalk. Diplomarbeit, Göttingen

Edwards CA, Bohlen PJ (1996) Biology and ecology of earthworms. Chapman and Hall, London

Eichhorn J (ed) (1991) Fallstudie Zierenberg: Stress in einem Buchenwaldökosystem in der Phase einer Stickstoffübersättigung. Forschungsberichte der Hessischen Forstlichen Versuchsanstalt 13, Münden

Ellenberg H, Mayer R, Schauermann J (eds) (1986) Ökosystemforschung: Ergebnisse des Sollingprojektes. Ulmer, Stuttgart

Hartwig J, Heiligenstadt B, Judas M, Karst H, Schauermann J (1991) Abiotische Parameter der tierökologischen Untersuchungsflächen im Basalt-Kalk-Gradienten des Kleinen Gudenbergs (Zierenberg, Nordhessen). Forschungsberichte der Hessischen Forstlichen Versuchsanstalt 13:45–52

Heiligenstadt B (1988) Zur Ökologie von Hornmilben (Acari: Oribatida) in einem Moder-Buchenwald: Phänologie und räumliches Verteilungsmuster. Diplomarbeit, Göttingen

Hövemeyer K (1992) Die Dipterengemeinschaft eines Kalkbuchenwaldes: eine siebenjährige Untersuchung. Zoologische Jahrbücher, Abteilung Systematik 119:225–260

Hopkin SP (1997) Biology of the springtails. Oxford University Press, Oxford

Koch M (1993) Zur Ökologie der Springschwänze (Insecta: Collembola) eines Buchenwaldes in einem Gradienten von Basalt zu Kalk. Diplomarbeit, Göttingen

Markwardt D (1993) Zur Ökologie der Zweiflügler (Insecta: Diptera) eines Buchenwaldes in einem Gradienten Basalt–Kalk. Diplomarbeit, Göttingen

Nieselt A (1991) Untersuchungen zum Verteilungsmuster saprophager Makroarthropoden (Isopoda, Diplopoda) und Gastropoden in einem Buchenwald auf Basalt und Kalk. Diplomarbeit, Göttingen

Nolte S (1993) Das Verteilungsmuster der Käfer (Coleoptera) eines Buchenwaldes: Die Bedeutung von Brennesselbeständen in einem Gradienten von Basalt zu Kalk. Diplomarbeit, Göttingen

Schaefer M (1990) The soil fauna of a beech forest on limestone: trophic structure and energy budget. Oecologia 82:128–136

Schaefer M (1991a) Animals in European temperate deciduous forests. In: Röhrig E, Ulrich B (eds) Temperate deciduous forests (Ecosystems of the World). Elsevier, Amsterdam, pp 503–525

Schaefer M (1991b) Ecosystem processes: secondary production and decomposition. In: Röhrig E, Ulrich B (eds) Temperate deciduous forests (Ecosystems of the World). Elsevier, Amsterdam, pp 175–218

Schaefer M (1991c) The animal community: diversity and resources. In: Röhrig E, Ulrich B (eds) Temperate deciduous forests (Ecosystems of the World). Elsevier, Amsterdam, pp 51–120

Schaefer M (1996) Die Artenzahl von Waldinsekten: Muster und mögliche Ursachen der Diversität. Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie 10:387–395

Schaefer M, Schauermann J (1990) The soil fauna of beech forests: comparison between a mull and moder forest. Pedobiologia 34:299–314

Schaefer M, Bonkowski M, Judas M, Schauermann, J (1993) Die Habitatbindung von Bodentieren: das Problem einer Kausalanalyse am Beispiel des Verteilungsmusters der Regenwurmfauna eines Buchenwaldes in einem Gradienten von Basalt zu Kalk. Mitteilungen der Deutschen Bodenkundlichen Gesellschaft 69:67–74

Scheu S (1997) Effect of litter (beech and stinging nettle) and earthworms (*Octolasion lacteum*) on carbon and nutrient cycling in beech forests on a basalt-limestone gradient: a laboratory experiment. Biol Fertil Soils 24:384–393

Schlaghamerský J (1998) The enchytraeids of a beech forest on a basalt-limestone gradient. In: Pižl V, Tajovský K (eds.). Soil zoological problems in Central Europe. Academy of Sciences of the Czech Republic, České Budějovice, pp 179–189

Schulz E (1991a) Die Milbenfauna (Acari: Mesostigmata und Cryptostigmata) in Lebensräumen auf Kalkgestein: Populationsökologie, Sukzession und Beziehungen zum Lebensraum. Berichte des Forschungszentrums Waldökosysteme Göttingen (A) 79:1–245

Schulz E (1991b) Die Milbenfauna (Acari: Gamasina, Uropodina, Oribatei) in verschiedenen Buchenwäldern. Berichte des Forschungszentrums Waldökosysteme Göttingen (B) 22:373–376

Wallwork JA (1970) Ecology of soil animals. London, McGraw-Hill