

The influence of earthworms (Lumbricidae) on the nitrogen dynamics in the soil litter system of a deciduous forest

S. Scheu

II. Zoologisches Institut der Universität Göttingen, Abteilung Ökologie, Berliner Strasse 28, D-3400 Göttingen, Federal Republic of Germany

Summary. The influence of earthworms (*Aporrectodea caliginosa* (Savigny) and *Lumbricus castaneus* (Savigny)) on the rate of nitrogen net mineralization of the soil was studied in the laboratory and in the field. The additional mineralization of nitrogen caused by the burrowing activity of the substrat feeding earthworm *A. caliginosa* (N_L) was directly correlated to the biomass of the lumbricids independently of their number. A rise in temperature caused an exponential increase in N_L values. The Q_{10} value of this process (2.18) was found to be much higher than that of the nitrogen mineralization without earthworms ($Q_{10}=1.22$). At 15° C the N_L value caused by *A. caliginosa* was calculated to be about 250 $\mu\text{g N g}^{-1}$ fresh body wt d^{-1} . Using the experimentally determined exponential relationship between temperature and N_L values, the additional nitrogen mineralization caused by a population of *A. caliginosa* in a beechwood on limestone was calculated to be 4.23 $\text{kg ha}^{-1} \text{a}^{-1}$.

In contrast to *A. caliginosa* the litter dwelling species *L. castaneus* lost considerable amounts of biomass (56%) during the 4 week incubation period. Only $\frac{1}{3}$ of the nitrogen equivalent to the weight loss of the animals was recovered in the mineral nitrogen pool.

The addition of litter (old beech leaf litter, freshly fallen beech and ash leaf litter) had a pronounced effect on both nitrogen net mineralization and N_L values of the soil. Presence of old beech leaves caused an increase in both values, whereas the other litter types effected a decrease in nitrogen net mineralization. Fragmented ash litter was found to have the most distinct effect on N_L values (–69%) and nitrogen net mineralization (–74%).

Key words: Earthworms – Nitrogen dynamics – Nitrogen net mineralization – Beech wood – Field calculation

Mineralization of nitrogen is one of the key processes in terrestrial ecosystems. Soil invertebrates affect this primarily microbial process by modifying the soil microflora directly (grazing) or indirectly (modification of the microbial environment) (Anderson et al. 1983a; Coleman et al. 1983).

In terms of biomass lumbricids are the dominant animals in many terrestrial ecosystems. By their burrowing activity and intensive faeces production (Scheu 1987) they are of great importance for soil structure and microbial activity in the soil subsystem. These indirect effects on mi-

croflora-dominated processes are assumed to be more important for the mineralization of nitrogen than the excretion of the earthworms themselves. In previous studies however only data from laboratory experiments on nitrogen excretion of lumbricids were taken into account to calculate their effect on nitrogen mineralization in the field (Satchell 1967; El-Duweini et al. 1971; Lee 1983).

In this paper results are given of laboratory experiments on the influence of substrate feeding earthworms (especially *Aporrectodea caliginosa* (Savigny)) on the net mineralization of nitrogen (Runge 1970) at different temperatures. These data are used to obtain a realistic estimate of the effect of live lumbricids on the nitrogen mineralization process in a beechwood on limestone.

The site

The study site was located in a beechwood on limestone near Göttingen (Northern Germany), known as Göttinger Wald. Some more details about the wood are given by Scheu (1987), an outline of the research program can be found in Schaefer (in press).

Methods

The soil used in the experiments was taken from the upper 3 cm of the mineral soil horizons of the study site and passed through a 4 mm sieve. The leaf litter was sampled immediately after fall of leaves in October 1984. Fragmented litter was obtained by comminuting the leaves by hand and passing through a 2 mm sieve.

The studied earthworms (*Aporrectodea caliginosa* and *Lumbricus castaneus* (Savigny)) were sampled by hand at the study site and kept at 10° C in the laboratory.

The net mineralization of soil samples was studied after an incubation period of 4 weeks in polyethylen bags. They enable a sufficient exchange of oxygen and carbon dioxide, whereas they are almost unpermeable to water (Runge 1970). The experiments were performed in polystyrol boxes (8 × 8 × 6 cm) which were covered with 1 mm gauze at the six sides to enable undisturbed gas exchange.

The boxes were filled with freshly sampled soil equivalent to 70 g dry wt. The different species of leaf litter used (1 g dry wt per cage) were moistened with 3 ml of water.

Cages were set up containing 1, 2 and 4 individuals of *A. caliginosa* or 2 of *L. castaneus* (at 15° C) to study the effect of earthworms on the mineralization of nitrogen.

Another set of boxes containing one individual of *A. caliginosa* each were kept at 5, 10 and 15°C. These experiments were set up in the laboratory with 6 replicates. To determine the effect of different litter types on net mineralization of nitrogen three types of litter were added to a number of cages containing one individual of *A. caliginosa*: (1) old beech leaf litter (>1 year old, C/N ratio of 25.4), (2) freshly fallen beech leaf litter (C/N ratio of 43.3), (3) freshly fallen ash leaf litter (C/N ratio of 20.2). Each type of litter was offered as whole leaves and as fragmented material. These experiments were set up in June 1985 in the field (4 replicates). The cages were regularly distributed 0.5 m apart from each other, dug 6 cm into the soil and covered with litter. All lumbricids were weighed before and after the experiments.

To study the faeces of *A. caliginosa* the animals were kept in cages similar to those used by Evans (1947) (detailed description in Scheu 1987). The egesta produced during a period of 3 days at 15°C were sampled for the determination of mineral nitrogen content.

Mineral nitrogen was determined titrimetrically after extraction of the soil with $\text{KAl}(\text{SO}_4)_2$ and distillation in a Micro-Kjeldahl apparatus (Allen 1974). Carbon and nitrogen contents were determined by means of a gas chromatograph (Elemental Analyser, Fa. Carlo Erba, Mailand).

Results

Nitrogen mineralization and biomass of Aporrectodea caliginosa and Lumbricus castaneus

At the beginning of the experiments the soil contained 1.33 ppm $\text{NH}_4^+ - \text{N}$ and 15.32 ppm $\text{NO}_3^- - \text{N}$. After 4 weeks of incubation the ammonium content had remained almost constant (1.19 ppm N), whereas the amount of nitrogen had increased significantly to 24.56 ppm N. Mineralization of nitrogen resulted almost exclusively in the formation of nitrate as should be expected for a limestone soil.

The amount of ammonium in the soil was somewhat higher in the cages containing lumbricids, but in no case it exceeded 3% of the nitrate content. Therefore the further analysis will be restricted to nitrate.

There was a highly significant correlation between the additional amount of nitrate produced per day in cages with lumbricids and total earthworm biomass per cage ($r^2 = 0.86$, $P < 0.01$) (Fig. 1). Therefore the additional rate of nitrogen mineralization caused by the burrowing activity of *A. caliginosa* can be related to the total biomass of the earthworms (mean of the biomass before and after the experiments) irrespective of their number (N_L value).

In the cages with one *A. caliginosa* the animals gained weight by 5.51%, in the boxes with two specimen of lumbricids they lost weight by about 1.4%. However, these differences were not significant (*t*-test). In one cage the two earthworms increased their biomass by 13.6%; in this cage the additional nitrate content was distinctly higher (by 63%) than in the corresponding replicates. Presumably increasing biomass of the animals causes a further increase of nitrogen mineralization. In four replicates containing 4 specimens of *A. caliginosa* one or more animals were found to be in dormancy after the 4 week incubation period. Therefore only two replicates of this variant were taken into account.

In contrast to *A. caliginosa* the litter dwelling species

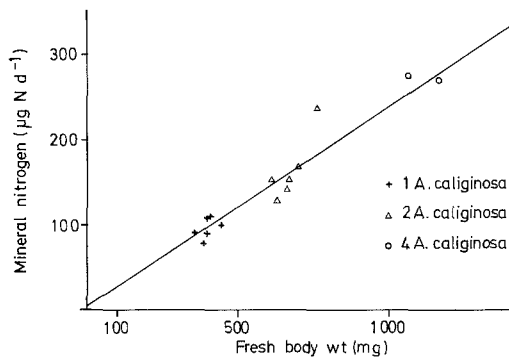


Fig. 1. Additional rate of nitrogen mineralization in soil caused by the burrowing activity of *Aporrectodea caliginosa* (1, 2 and 4 specimen per cage) in relation to the total biomass of the animals

L. castaneus lost on average 56% of its initial biomass. As the C/N ratio of the animals remained constant during the 4 week incubation period (4.5) this corresponds to a mean loss of nitrogen by the animals of 4.5 mg N per cage. The established increase in net mineralization caused by *L. castaneus* was only in the range of 1.6 mg N per cage. Therefore the loss of nitrogen by the earthworms was much greater than the additional increase in soil nitrate content caused by *L. castaneus*.

The N_L value for *L. castaneus* was calculated to be $351 \mu\text{g N g}^{-1} \text{ fresh wt d}^{-1}$ which is considerably higher than that for *A. caliginosa* ($243 \mu\text{g N g}^{-1} \text{ fresh wt d}^{-1}$). Presumably this reflects the loss of nitrogen by *L. castaneus*.

Temperature dependence of nitrogen mineralization

The data of the net mineralization obtained at 5, 10 and 15°C were used for a non linear regression analysis. The following equations were obtained:

(1) For the net mineralization rate in cages without *A. caliginosa*:

$$N_M = 70.8 e^{0.020 T}; r^2 = 0.951$$

$$N_M (\mu\text{g N } 100 \text{ g}^{-1} \text{ dry wt d}^{-1}), T (^\circ\text{C})$$

(2) For the increase in net mineralization rate caused by the burrowing activity of *A. caliginosa*:

$$N_L = 74.1 e^{0.078 T}; r^2 = 0.864$$

$$N_L (\mu\text{g N g}^{-1} \text{ fresh wt d}^{-1}), T (^\circ\text{C})$$

Both regressions are highly significant ($P < 0.001$).

Net mineralization of nitrogen increased with rising temperature only slightly ($Q_{10} = 1.22$), whereas the N_L values increased with a Q_{10} value of 2.18 (Fig. 2). Therefore the effect of temperature on the additional mineralization of nitrogen caused by the activity of *A. caliginosa* is distinctly stronger than the temperature effect on the net mineralization without lumbricids.

The content of mineral nitrogen in faeces of Aporrectodea caliginosa

Carbon and nitrogen content of the soil and faeces of *A. caliginosa* were not significantly different ($P < 0.01$, *t*-test; C/N ratio 14.6). This indicates that the animals ingested the soil homogeneously and did not select the more organic

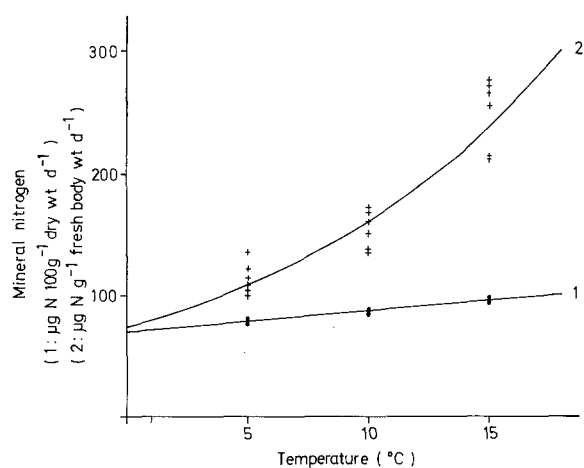


Fig. 2. Temperature dependence of nitrogen net mineralization of the soil (1) and N_L values caused by *Aporrectodea caliginosa* (2). For details of the plotted exponential equations see text

Table 1. The amount of mineral nitrogen (NH_4^+ and NO_3^-) in food substrate (soil) and faeces of *Aporrectodea caliginosa* (0–3 days old; mean of 3 replicates)

	Mineral nitrogen content (ppm)			
	NH_4^+		NO_3^-	
	Mean	1 S.D.	Mean	1 S.D.
Soil	2.08	0.18	63.91	1.38
Faeces	89.16	5.25	96.35	4.27

fraction, as has been reported for *A. rosea* by Bolton et al. (1976). Differences in mineral nitrogen content in faeces and soil should therefore be caused by processes during the gut passage and not by selective food consumption.

The ammonium content of the faeces exceeded that of the soil by 87.08 ppm N, the nitrate content by 32.44 ppm N (Table 1). Hence the amount of mineral nitrogen in faeces exceeded that of the soil by 119.52 ppm N, which is equivalent to an increase of 181%.

Field calculation

In 1981 number and biomass of the lumbricids of the study site were determined monthly by hand sorting and formalin extraction (Schaefer, unpublished work). By combining these data with the mean monthly temperature in 4.5 cm soil depth (Hövmeyer 1985) and equation (2) the mean additional monthly nitrogen mineralization caused by the population of *A. caliginosa* in the studied beechwood was calculated (Fig. 3).

The population of *A. caliginosa* which accounted in 1981 for only 17% of the biomass of the lumbricids at the study site caused an additional nitrogen mineralization of about 4.23 kg N ha⁻¹ a⁻¹. Almost half of this amount was produced during June and July.

Influence of litter quality

There was a pronounced effect of litter quality on net mineralization rate of nitrogen of the soil (Table 2). Net mineral-

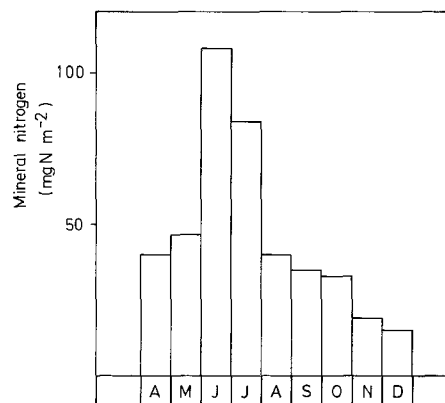


Fig. 3. Calculated additional amount of mineral nitrogen per month caused by the population of *Aporrectodea caliginosa* in a beechwood on limestone. For details of the calculation see text

ization exceeded that of the control (no litter) only in the soil under old beech leaf litter. Freshly fallen beech and ash leaves both caused a decrease of nitrogen net mineralization in the soil. The lowest value (about 25% of the control) was obtained in soil with fragmented ash litter.

Presence of litter caused a decrease of the N_L values in all cages with *A. caliginosa* (see Table 2). In most cases the effect of fragmented leaf litter exceeded distinctly that of intact leaves. The N_L value under ash leaves <2 mm reached only about 30% that of the control.

The N_L value obtained in the field (cages without litter) was 178.83 $\mu\text{g N g}^{-1}$ fresh wt d⁻¹. Using equation (2) and the mean monthly temperature determined in 1981 a value of 178.90 $\mu\text{g N g}^{-1}$ fresh wt d⁻¹ is obtained. The close similarity of the calculated values with the field data illustrates the usefulness of equation (2) for field calculations.

Discussion

Soil invertebrates are considered to be key components for the mineralization process of several elements, especially nitrogen (Anderson et al. 1984, 1985a, b; Coleman et al. 1983). More important than their direct influence through nitrogen excretion is thereby their role as driving variable for microbial mineralization and immobilization. By measuring the influence of lumbricids on nitrogen net mineralization both direct and indirect effects of the animals on mineralization were taken into account. This more natural approach enables a realistic quantification of the influence of the population of *A. caliginosa* on the net mineralization of nitrogen in the field.

The additional net mineralization rate caused by the activity of *A. caliginosa* was linearly correlated with the biomass of the lumbricids independently of their number. At 15°C the animals caused an increase of the mineralization rate by 243.3 $\mu\text{g N g}^{-1}$ fresh body wt d⁻¹. This very high amount cannot be explained exclusively by nitrogen excretion of *A. caliginosa* because N excretion is in the range of 67.2 (at 18°C) (Makeschin 1980) and 87.5 $\mu\text{g N g}^{-1}$ fresh wt d⁻¹ (at 23°C) (Needham 1957). In addition most of the N excretion consists of proteins (up to 52%; Haggag et al. 1959), whereas ammonium accounted only for 27% (Makeschin 1980).

Table 2. Influence of different litter types (whole leaves and fragmented leaves <2 mm) on nitrogen net mineralization of the soil and N_L values caused by *Aporrectodea caliginosa* in a field experiment (mean of 4 replicates)

		Nitrogen net mineralization ($\mu\text{gN } 100 \text{ g}^{-1} \text{ dry wt d}^{-1}$)		N_L values ($\mu\text{gN } \text{g}^{-1} \text{ fresh wt d}^{-1}$)	
		Mean	1 S.D.	Mean	1 S.D.
Litter type					
Freshly fallen beech leaves	intact	13.79	2.16	168.55	13.70
	<2 mm	14.87	0.68	115.20	3.75
Freshly fallen ash leaves	intact	19.41	4.69	172.70	42.78
	<2 mm	5.79	0.26	56.13	3.65
Old beech leaves	intact	31.71	2.34	153.20	32.80
	<2 mm	42.64	2.69	136.55	12.73
Without litter		22.54	0.14	178.83	20.20

The content of mineral nitrogen in 0–3 days old faeces of *A. caliginosa* exceeded that of the food substrate by 181%, about 75% of this increase was caused by ammonium.

At 15° C and sufficient soil moisture content *A. caliginosa* egests about 2,100 mg faeces g^{-1} fresh wt d^{-1} (Scheu 1987). The additional mineral nitrogen content therein should be about 251 $\mu\text{g N}$. This value is almost exactly the same as the determined N_L values for *A. caliginosa* at the same temperature (243 and 250 $\mu\text{g N } \text{g}^{-1}$ fresh wt d^{-1}). The increase of net nitrogen mineralization in the soil caused by the burrowing activity of *A. caliginosa* could therefore be explained by the gut passage of the soil material.

The amount of mineral nitrogen in faeces of earthworms has been frequently determined (Barley et al. 1959; El-Duweini et al. 1971; Graff 1971; Aldag et al. 1975; Dash et al. 1979; Syers et al. 1979; Makeschin 1980). However, the mineral nitrogen content of the food substrate of the earthworms was not determined in these studies the increase of mineral nitrogen caused by the gut passage remained unclear. Makeschin (1980) assumed that the additional amount of mineral nitrogen in faeces of lumbricids is caused by selective food consumption.

The ammonium contents of the soil in which *A. caliginosa* had burrowed were very low. The high amounts of NH_4^+ found in faeces of *A. caliginosa* therefore must have been nitrified quickly. An increase of nitrification activity in casts of earthworms has been reported by Day (1950) and Parle (1963). Loquet et al. (1977) found that the nitrifiers account for up to 42% of the aerobic bacteria in walls of earthworms burrows. Therefore one can assume that under more anaerobic conditions in the gut of lumbricids ammonification is strongly increased, whereas nitrification proceeds in the presence of oxygen in the faeces. The observed increase of pH in the gut of earthworms (Heran 1954) might be explained by this process. In the faeces one should expect a corresponding decrease in the concentration of protons.

With increasing temperature N mineralization showed an exponential response. The net mineralization in cages without earthworms, which should be a mainly microbial process, was only slightly temperature dependent ($Q_{10} = 1.22$). In contrast the additional N mineralization rate caused by the activity of *A. caliginosa* (N_L) was much more

affected by temperature ($Q_{10} = 2.18$). This Q_{10} value is in good agreement with Q_{10} values found for the metabolism of poikilothermic animals (Reichle 1977). The temperature dependent increase of N mineralization by *A. caliginosa* might therefore be explained by the increased metabolism of the animals. The very low Q_{10} value of the net mineralization rate in soil without lumbricids indicates that there are other limiting factors for the mainly microbial mineralization process.

The additional amount of nitrogen caused by the population of *A. caliginosa* at the studied beechwood in 1981 was calculated to be 4.23 kg N ha^{-1} . Almost half of this amount is produced in June and July, months with high nutrient requirement by plants. Net mineralization of nitrogen at the study site in 1981 has been calculated to be about 160 kg N ha^{-1} (Reichardt 1982). Considering that *A. caliginosa* only accounts for 17% of the total lumbricid biomass the contribution of earthworms to nitrogen mineralization cannot be neglected. For the calculation given above only the effect of living lumbricids was taken into account. Satchell (1967), however, emphasized that mineralization of dead earthworms might be an important mineral nitrogen source for the soil subsystem.

By introduction of litter quality as an additional variable in a field experiment a further step towards a more natural design of the experiments was done. This variable had a distinct effect on the nitrogen mineralization in both soil with *A. caliginosa* and soil without earthworms. The effect was most obvious in cages with fragmented litter. Net mineralization was increased up to 90% in soil covered with old beech leaf litter, whereas freshly fallen beech leaves caused a decrease of the nitrogen content of about 35%. Despite the very low C/N ratio (20.2) fragmented ash leaves caused a decrease of nitrogen mineralization by 75%. The N_L values in the cages with lumbricids showed a similar pattern.

The nitrogen content of litter changes during the process of decomposition. Three phases can be distinguished: Leaching, accumulation and mineralization (Berg et al. 1981). The fresh litter used in the experiments was presumably in the accumulation phase, which may have resulted in a transfer of mineral nitrogen from the soil to the litter. Fungi growing into the litter are considered to enable such a transfer (Dowding 1976). In contrast it can be assumed that the old beech leaf litter was in the mineralization phase,

which caused an increased net mineralization in the soil. The more pronounced effect of litter <2 mm on the nitrogen dynamics of the soil litter system may be explained by the better conditions for microbial growth provided by fragmentation. Further experiments are necessary to elucidate the function of this nitrogen transfer for litter decomposition and the modification of this process by soil invertebrates.

Acknowledgements. I thank Prof. M. Schaefer and D. Matthies for helpful comments on the manuscript. Partly supported by the Deutsche Forschungsgemeinschaft and the Bundesministerium für Forschung und Technologie.

References

- Aldag R, Graff O (1975) N-Fractionen in Regenwurmlosung und deren Ursprungsboden. *Pedobiologia* 15:151–153
- Allen SE (ed) (1974) Chemical analysis of ecological materials. Blackwell, London
- Anderson JM, Ineson P (1983) Interactions between soil arthropods and microorganisms in carbon, nitrogen and mineral element fluxes from decomposing leaf litter. In: Lee JA, McNeill S, Rorison JH (eds) Nitrogen as an ecological factor, the 22nd Symposium of the British Ecological Society Oxford 1981. Blackwell, Oxford London Edinburgh, pp 413–432
- Anderson JM, Ineson P (1984) Interactions between microorganisms and soil invertebrates in nutrient flux pathways of forest ecosystems. In: Anderson JM, Rayner ADM, Walton DWH (eds) Invertebrate-microbial interactions. Cambridge University Press, Cambridge, pp 59–88
- Anderson JM, Leonhard MA, Ineson P, Huish SH (1985a) Faunal biomass: A key component of a general model of nitrogen mineralization. *Soil Biol Biochem* 17:735–737
- Anderson JM, Huish SH, Ineson P, Leonhard MA, Splatt PR (1985b) Interactions of invertebrates, microorganisms and tree roots in nitrogen and mineral element fluxes in deciduous woodland soils. In: Fitter AH (ed) Ecological interactions in soil. Blackwell, Oxford New York Edinburgh, pp 377–392
- Barley KP, Jennings AC (1959) Earthworms and soil fertility. III. The influence of earthworms on the availability of nitrogen. *Aust J Agric Res* 10:364–370
- Berg B, Staaf H (1981) Leaching, accumulation and release of nitrogen in decomposing forest litter. In: Clark FE, Rosswall T (eds) Terrestrial nitrogen cycles. *Ecol Bull* 33, Stockholm, pp 163–178
- Bolton PJ, Phillipson J (1976) Burrowing, feeding, egestion and energy budgets of *Allolobophora rosea* (Savigny) (Lumbricidae). *Oecologia* (Berlin) 23:226–245
- Coleman DC, Reid CPP, Cole CV (1983) Biological strategies of nutrient cycling in soil systems. In: Macfadyen A, Ford ED (eds) Advances in ecological research 13. Academic Press, New York, pp 1–55
- Dash MC, Patra UC (1979) Wormcast production and nitrogen contribution to soil by a tropical earthworm population from a grassland site in Orissa, India. *Rev Ecol Biol Sol* 16:79–83
- Day GM (1950) Influence of earthworms on soil microorganisms. *Soil Science* 69:175–184
- Dowding P (1976) Allocation of resources, nutrient uptake and release by decomposer organisms. In: Anderson JM, Macfadyen A (eds) The role of terrestrial and aquatic organisms in decomposition process. Blackwell, Oxford, pp 169–183
- El-Duweini KA, Ghabbour SJ (1971) Nitrogen contribution by live earthworms to the soil. In: Organismes du sol et production primaire. Proc 4th Intern Soil Zool Coll, Dijon, pp 495–501
- Evans AC (1947) A method for studying the burrowing activities of earthworms. *Ann Mag Nat Hist* 14:1–13
- Graff O (1971) Stickstoff, Phosphor und Kalium in der Regenwurmlosung auf der Wiesenfläche des Sollingprojektes. *Ann Zool Ecol Anim, Special Publ* 4:503–512
- Haggag G, El-Duweini KA (1959) Main nitrogenous constituents of the excreta and tissue of earthworms. *Proc Egypt Acad Sci* 13:1–5
- Heran H (1954) Die Wasserstoffionenkonzentration im Darm von *Lumbricus terrestris* L. *Z Vergl Physiol* 36:55–65
- Hövemeyer K (1985) Die Zweiflügler (Diptera) eines Kalkbuchenwaldes: Lebenszyklen, Raum-Zeit-Muster und Nahrungsbiologie. Dissertation, Göttingen
- Lee KE (1983) The influence of earthworms and termites on soil nitrogen cycling. In: Lebrun P, Andre HM, DeMedts A, Gregoire-Wibo C, Wauthy G (eds) New trends in soil biology. Proc 8th Intern Coll Soil Zool, Louvain-la Neuve, pp 35–48
- Loquet M, Bhatnagar T, Bouché MB, Rouelle J (1977) Essai d'estimation de l'influence écologique des lombriciens sur les microorganismes. *Pedobiologia* 17:400–417
- Makeschin F (1980) Einfluß von Regenwürmern (Lumbricidae, Oligochaeta) auf den Boden sowie auf Ertrag und Inhaltsstoffe von Nutzpflanzen. Dissertation, Gießen
- Needham AE (1957) Components of nitrogenous excreta in the earthworms *Lumbricus terrestris* L. and *Eisenia foetida* (Savigny). *J Exp Biol* 34:425–446
- Parle JN (1963) A microbiological study of earthworm casts. *J Gen Microb* 31:1–11
- Reichardt C (1982) Stickstoff-Nettomineralisation im Boden eines Kalkbuchenwaldes. *Mitt Dtsch Bodenkundl Ges* 34:33–37
- Reichle DE (1977) The role of soil invertebrates in nutrient cycling. In: Lohm U, Persson T (eds) Soil organisms as components of ecosystems. *Ecol Bull* 25, Stockholm, pp 146–156
- Runge M (1970) Untersuchungen zur Bestimmung der Mineralstickstoffnachlieferung am Standort. *Flora Abt B* 159:233–257
- Satchell JE (1967) Lumbricidae. In: Burges A, Raw F (eds) Soil biology. Academic Press, London, pp 259–322
- Scheu S (1987) The role of substrate feeding earthworms (Lumbricidae) for bioturbation in a beechwood soil. *Oecologia* (Berlin) 72:192–196
- Syers JK, Sharpley AN, Keeney DR (1979) Cycling of nitrogen by surface casting earthworms in pasture ecosystems. *Soil Biol Biochem* 11:181–185

Received November 1, 1986