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Influence of the larvae of *Athous subfuscus* (Müller, 1764) (Coleoptera, Elateridae) on the nutrient status of the microflora in three different beech forest soils*

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Mit 1 Abbilung und 1 Tabelle

Zusammenfassung
Am Beispiel der Larven des Schnellkäfers *Athous subfuscus* wurde die Wirkung humiphager Arthropoden auf den Nährstoffumsatz der streuzersetzenden Mikroflora in drei unterschiedlichen Buchenwaldböden (Mull, Moder, gekalkter Moder) untersucht. Die Larven verringerten in allen drei Böden die Immobilisation von Nährstoffen wie N, P, K und Ca durch eine Reduktion der mikrobiellen Biomasse. In dem Moderboden erhöhte *A. subfuscus* den Nährstoffbedarf der streubesiedelnden Mikroflora. Dies weist auf die große Bedeutung der Nährstoffverfügbarkeit für die Interaktion zwischen Tieren und Mikroflora in sauren Böden hin. In dem Mullboden verstärkte *A. subfuscus* die Akkumulation sticksoffreicher Verbindungen während er den Abbau dieser Verbindungen in dem Moderboden beschleunigte. In dem gekalkten Moderboden verschoben die Larven die Balance zwischen der edaphischen Mikroflora und der streubesiedelnden Mikroflora zu gunsten der edaphischen Mikroflora. Darüber hinaus verstärkte *A. subfuscus* die Akkumulation N-reicher Verbindungen in dem gekalkten Boden.

Abstract
The larvae of the elaterid beetle *Athous subfuscus* served as an example of the effect of humiphagous arthropods on the nutrient turnover of the decomposer microorganisms in three contrasting beech forest soils (mull, moder and limed moder). The larvae reduced the microbial immobilization of nutrients as N, P, K and Ca by reducing the size of the microbial biomass. In the moder soil, *A. subfuscus* increased the nutrient requirements of the litter-colonizing microflora. This points to the most important effect of nutrient availability on the interaction between fauna and microflora in acid soils. The effect of the larvae on the pronase-extractable ^{14}C-fraction (= labile N-rich organic compounds) shows that *A. subfuscus* promotes the accumulation (mull) or the rapid turnover (moder) of the nutrients contained in the tissue of the microflora in a soil specific way. In the limed moder soil, the humiphagous larvae shifted the balance between soil microflora and litter microflora towards the soil microflora. In addition, *A. subfuscus* accelerated the accumulation of N-rich compounds in the limed soil.

1. Introduction
The elaterid beetle *Athous subfuscus* (Müller, 1764) occurs in various ecosystems (e. g. CYKOWSKI 1977, KOPONEN 1985) but prefers woodland habitats (PRANCE 1985). The soil dwelling larvae of *A. subfuscus* greatly affect the decomposition process (WOLTERS 1889b) and form an important component of the decomposer food web in many soils (KORNALEWICZ 1977 a & b, KRISTEK 1979, NIELSEN 1974 & 1975, SCHAUERMANN 1986). They feed on dif-

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ferent kinds of food (BLUNCK & MÜHLMANN 1954, ESCHERICH 1923, MORITZ 1986, SCHAERFFENBERG 1942, SERGEEVA 1983, STREY 1972). According to the results of gut content analyses and microcosm experiments they seem to be humiphagous, even under extremely different soil conditions (WOLTERS 1989b). This unspecialized feeding behavior is typical to many soil arthropods. The widespread larvae of *A. subfuscus* are therefore well suited as an indicator for the reaction of edaphic fauna to variations in environmental conditions (KOLBE et al. 1988) and for a comparative analysis of the influence of soil arthropods on the edaphic microflora (WOLTERS 1989a).

In the following paper, data are presented on the influences of *A. subfuscus* on the nutrient demand and on the nutrient turnover of soil microflora. It is demontrated that humiphagous arthropods such as *A. subfuscus* larvae significantly affect the microbial immobilization of plant nutrients, the accumulation of N-rich C-compounds in the litter layer and the C-, N- und P-requirements of the microflora. Most of these influences are soil specific.

2. Methods

Samples were taken from three German beech forest soils with contrasting soil conditions in October 1986: I. A_h horizon of a 130 year old beech forest on mull soil (Göttinger Wald); II. F/H horizon of a 142 year old beech forest on moder soil (Solling); III. F/H horizon of an area close to the second site, which had been limed with a total amount of three tons onf lime per ha in 1973, 1975 and 1980. The study area in the Göttinger Wald is situated at an altitude of approx. 420 m and the study areas in the Solling are situated at an altitude of approx. 500 m. The experiment was carried out in 36 microcosms (specially designed perspex tubes with a diameter of 6 cm, which were fixed on a ceramic plate; for a more detailed description of the microcosm system see WOLTERS 1989b). The construction of the microcosms allows a continuous flow of soil water and thereby a nutrient ransfer, closely simulating natural conditions. The sieved soil samples (mull: 25 g soil, moder and limed moder: 10 g soil) were filled into the perspex tubes and then compressed to field density (if not otherwise stated, all data are expressed on an oven dry [OD] weight basis). Rainfall was simulated by daily watering with 7 ml water per microcosm. After 56 days, 2 *A. subfuscus* larvae were placed into each of 18 microcosms. The live weight of the larvae varied between 8.12 and 26.14 mg. On the 57th day, 60 mg of the non-labile residues of ^{14}C-labelled litter of beech leaves (corresponding to 25.2 mg C; for details see WOLTERS 1988 and 1989b) were placed on the surface of the 36 soil columns, replacing the litter layer. The microcosms were kept for 137 days at a temperature of 10 °C and at 100% air humidity in permanent darkness. Six replicates were set up per treatment.

The CO_2 and the $^{14}CO_2$ released by the soil was absorbed with 10 ml NaOH. CO_2 and $^{14}CO_2$ evolution from the soils was determined in 0.5 ml aliquots of the NaOH using standard methods. C- and ^{14}C-content of the microbial biomass was measured by the fumigation-incubation method at the end of the experiment (JENKINSON & POWLSON 1976; VANCE et al. 1987). The reaction of the microflora to additional nutrient supply was tested by adding either 8000 ppm glucose or 1600 ppm N (as NH_4NO_3) or 800 ppm P (as KH_2PO_4) to 1 g OD aliquots of mixed soil (3 replicates per treatment). The CO_2 and $^{14}CO_2$ released during a period of 7 days from the soils treated in this way was determined. The influence of the larvae on the physico-chemical state of the non-mineralized portion of the labelled leaf litter was determined by subsequently extracting 1 g OD aliquots of mixed soil with methanol-chloroform-water (12 : 5: 3; 4 h at 20 °C; soluble C-compounds), pronase (Pronase E [Serva, Heidelberg] in 0.05 M tris-buffer, 24 h at 30 °C; labile, N-rich C-compounds) and amyloglucosidase (Rohalase HT [Serva, Heidelberg] in 0.05 M KH_2PO_4, 24 h at 60 °C) (3 replicates per treatment). The influence of *A. subfuscus* and soil on the thus extractable C-compounds were tested by means of a two-way analysis of variance. Mean values were compared using the Tukey-test.

3. Results

3.1 The influence of *A. subfuscus* on the microbial immobilization of nutrients

At the end of the experiment, the size of the soil microbial biomass amounted to 2085 μgC g^{-1} OD soil in the An-horizon of the mull soil (= 2.61% of total-C), to 3073 μgC g^{-1} OD in the F/H-horizon of the moder soil (= 0.73% total-C) and to 9230 μgC g^{-1} OD (= 2.20% total-C) in the F/H-horizon of the limed moder soil. The feeding activity of the *A. subfuscus* larvae reduced the size of the microbial C-pool in all three soils: in the mull soil by 31.9%, in the moder soil by 31.7% and in the limed moder soil by 37.1%. This effect is inevitably connected with a reduced immobilization of nutrients in the soil microbial biomass. The C/N-value of the soil microflora amounts to 6.67, the C/P amounts to 8.62, the C/K amounts to 10.2 and the C/Ca amounts to 71.43 (Anderson and Domsch 1980). It can be calculated from these values that *A. subfuscus* mobilized 99.7 μg N g^{-1}OD soil, 77.2 μg P g^{-1}OD soil, 65.2 μg K g^{-1}OD soil and 9.31 μg Ca g^{-1}OD soil from the labile biomass pool of the microflora in the mull soil. In the moder soil, the estimated nutrient mobilization amounts to 146.1 μg N g^{-1}OD soil, 113 μg P g^{-1}OD soil, 95.5 μg K g^{-1}OD soil and 13.6 μg Ca g^{-1}OD soil. In the limed moder soil, *A. subfuscus* mobilized 513 μg N g^{-1}OD soil, 397.3 μg P g^{-1}OD soil, 335.7 μg K g^{-1}OD soil and 47.9 μg Ca g^{-1}OD soil.

3.2 The influence of *A. subfuscus* on the microbial transformation of beech leaf litter

In the 137 days of the experiment, 15.3% of the non-labile residues of the ^{14}C-labelled beech litter were mineralized in the litter layer of the mull soil, in that of the moder soil, 12.9% and in that of the limed moder soil, 18.8%. According to the results of the two-way analysis of variance, these soil specific differences in the efficiency of the litter colonizing microflora also affected the physico-chemical state of the non-mineralized remains of the ^{14}C-labelled beech litter. In the moder soil and in the limed moder soil, the proportion of water soluble ^{14}C-compounds was significantly higher than in the mull soil ($p < .05$, Tab. 1). Furthermore, there was a significant accumulation of pronase-extractable ^{14}C-compounds in the limed moder soil ($p < .05$).

Site	Göttinger Wald		Solling		Solling	
Soil type	mull		moder		limed moder	
A. subfuscus	-	+	-	+	-	+
M-C-W soluble ^{14}C (ppm)	29.0	27.2	36.7	34.5	36.9	36.1
influence of *A. subfuscus* (%)	- 6.2 (n.s.)		- 5.9 (n.s.)		- 2.1 (n.s.)	
Amyloglucosidase-extractable ^{14}C (ppm)	18.0	17.4	19.3	19.1	17.6	18.3
influence of *A. subfuscus* (%)	- 3.2		- 1.0		+ 4.0	
Pronase-extractable ^{14}C (ppm)	24.4	24.9	21.1	18.8	27.8	32.6
influence of *A. subfuscus* (%)	- 2.1		- 10.8**		+ 17.6**	

Tab. 1: Influence of soil conditions and *A. subfuscus* larvae on the physico-chemical state of ^{14}C-labelled beech litter, which was not mineralized during a timecourse of 137d (M-C-W soluble: methanol-chloroform-water (12 : 5 : 3) soluble; for further explanation see chapter on methods).

The influence of *A. subfuscus* was limited to the pronase-extractable C-coumpounds (Tab. 1). In the mull soil, the larvae had no influence on the proportion of this ^{14}C-fraction, whilst they significantly promoted its decomposition in the moder soil ($p < .05$). In the limed moder soil, however, *A. subfucus* reduced the decomposition of the pronase-extractable ^{14}C-fraction and so acclerated the accumulation of nitrogen-rich carbon compounds in the litter layer. This effect coincides with the inhibitory effect of *A. subfuscus* on the leaflitter decompostion in the lime ameliorated soil (compare WOLTERS 1989b).

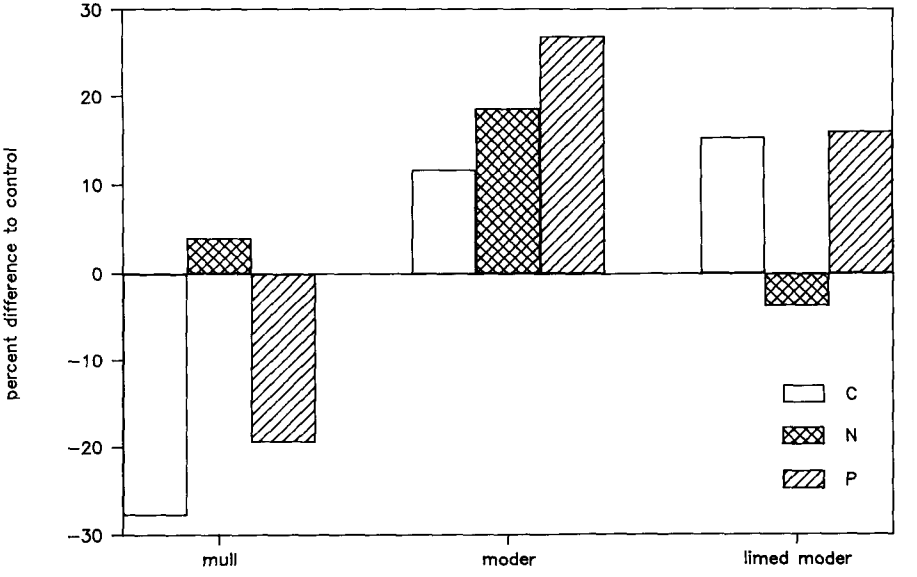

Fig. 1: Soil-specific influence of *A. subfuscus* larvae on the reaction of litter-microflora to additional carbon (C), nitrogen (N) and phosphorus (P) supply (measured as influence of fertilization on the ^{14}C-mineralization rate in three soils, which were kept for 137 in microcosms with and without larvae [= control]).

3.3 The effect of *A. subfuscus* on the nutrient requirements of the microflora

Differences in carbon mineralization clearly demonstrated that *A. subfuscus* larvae strongly influenced the C-, N- and P-requirements of the litter microflora and of the edaphic microflora. According to the influence of C-, N- and P-fertilization on ^{14}C-mineralization (Fig. 1), *A. subfuscus* reduced the nutrient requirements of the microflora living in the surface layer of the mull soil (C, P) or did not alter it at all (N). In the O_L-horizon of the moder soil, in contrast, the larvae markedly raised the C-, N- and P-demand of the litter-colonizing microflora. In the limed moder soil, *A. subfuscus* also raised the C- and P-demand of the litter microflora, but had no influence on N-requirements.

According to the influence of additional nutrient supply on soil respiration, *A. subfuscus* reduced N-requirements of the edaphic microflora in the Ah-horizon of the mull soil by 15% ($p < .1$). In the F/H-layer of the moder soil, *A. subfuscus* raised the N-demand of the edaphic microflora by 9% (n. s.). In the natural soils, the effect of the larvae on the nutrient demand of the edaphic

microflora was thus similar to the effect on the litter microflora. In the F/H-layer of the limed moder soil, however, the larvae lowered the P-requirements of the edaphic microflora by 42% ($p < .05$). This effect is opposite to the effect of the larvae on the P-requirements of the litter-colonizing microflora.

4. Discussion

The larvae of *A. subfuscus* served as an example of the effect of humiphagous arthropods on the nutrient turnover of the decomposer microorganisms. It is generally accepted that soil animals affect the turnover of bioelements in the soil in many ways (e. g. WERNER & DINDAL 1987). This is confirmed by the results of the experiments presented here. The influence of *A. subfuscus* on the mobilization of nutrients like N, P, K and Ca by reducing the size of the microbial biomass and by stimulating the metabolic activity of the microflora (see also WOLTERS 1989b) is remarkably high.

While the larvae had a general effect on the size of the microbial nutrient-pool, the influence on the reaction of the microflora to additional nutrient supply was soil specific. *A. subfuscus* greatly increased the nutrient requirements of the litter-colonizing microflora in the moder soil. This points to the most important effect of nutrient availability on the interaction between fauna and microflora, especially in acid soils. Because the availability of inorganic nutrients may also affect the structure of the decomposer community (van STRAALEN et al. 1987, WOLTERS 1989c), the results presented should make an important contribution to an understanding of the influence of soil acidification on soil-biological processes (ULRICH 1987, WOLTERS 1989d). Further studies are needed, to overcome the dichotomy between descriptive and functional approaches in soil ecology (WOLTERS et al. 1989).

The increased carbon and phosphor limitation brought about by *A. subfuscus* confirms the hypothesis of an increased competition for nutrients within the microbial community of the lime ameliorated moder soil (WOLTERS 1988). In limed substrate, the larvae also had a contrasting effect on the nutrient demand of the litter microflora and of the soil microflora. This points to a promotion of the autochthonous soil microflora as opposed to the zymogenous litter microflora through the burrowing activity of *A. subfuscus*. This confirms the postulated "shifting effect" of humiphagous soil arthropods on the balance between different functional groups of the microorganisms. It also offers an explanation for the inhibitory effect of *A. subfuscus* on litter decomposition in the limed soil (WOLTERS 1989b).

The overwhelming portion of the pronase-extractable ^{14}C-fraction was most probably of microbial origin. The effect of the larvae on these nitrogen-rich organic compounds shows that *A. subfuscus* promotes, in a soil-specific way, the accumulation (mull) or the rapid turnover (moder) of the nutrients contained in the tissue of the microflora. Thus, the humiphagous arthropods not only stimulate the short-term turnover of nutrients by the soil microflora but also affect the long-term turnover of nutrients by influencing the composition of soil organic matter (compare WOLTERS 1988 and 1989b). In the limed moder soil, the larvae accelerated the accumulation of N-rich compounds in the litter layer. In this substrate, in contrast to the mull and moder soil, *A. subfuscus* feeds directly on the freshly fallen leaf litter and/or on the litter-colonizing microflora (WOLTERS 1989b). This leads to the conclusion that the accumulated N-rich compounds in the limed moder soil (see LANG & BEESE 1985) are partly a result of the concentration of microbially transformed carbon compounds on and in the feces of soil animals. The accumulation of labile N-compounds in the organic layer of the limed moder soils confirms that the liming of acid forest soils does not necessarily lead to a stabilization of soil biological processes (WOLTERS & SCHAUERMANN 1989).

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