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Original article

Plant species effects on soil macrofauna density in grassy arable fallows of different age

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ABSTRACT

The density of soil macrofauna groups in nine grassy arable fallows of different age were investigated in a factorial design with the factors 'plant species' (legume: *Medicago sativa*, herb: *Taraxacum officinale*, grass: *Bromus sterilis*) and 'age class' (A1: 2–3/3–4, A2: 6–8/7–9, A3: 12–15/13–16 years in 2008/2009). Four plots were selected randomly at each fallow. In May 2008 and May 2009, within each plot five *M. sativa*, *T. officinale* and *B. sterilis* plants were extracted with their associated soil using steel cylinders. The material from each plant species was used for extraction of soil macrofauna and for determination of environmental parameters.

The main results were (i) the density of the saprophagous macrofauna was significantly higher in *B. sterilis* than in *M. sativa* and *T. officinale* samples indicating that this group possibly benefited from the particularly high amount of fine roots in the *B. sterilis* samples; (ii) densities of Gastropoda and predatory beetles were highest in the 7–9 yr old fallows indicating that predators may have benefited from the increased availability of their prey in the medium stage of grassland succession; (iii) focusing on the results of the CCAs (2008, 2009), the water content had the strongest influence of the measured soil parameters on the structure of the soil macrofauna assemblages.

1. Introduction

Grasslands comprise diverse ecosystems, spanning intensively-managed species poor pastures (e.g. *Trifolium–Lolium* mixtures) to extensive-utilized pastures and meadows with high biodiversity [13]. Plant species diversity and composition of grasslands has long been recognized as an important determinant of the density and species richness of organisms at higher trophic levels [50,52,64]. In agricultural landscapes species richness of animals and plants has declined in recent decades [27] due to intensive farming practices which have increased the productivity of arable land at the expense of other organisms. Moreover, recent field and microcosm studies showed that plant species loss of grasslands leads to a decline in plant biomass [42,68] probably dropping the abundances of animal communities. To counteract this development, semi-natural habitats like wildflower areas or grassy arable fallows (semi-natural habitats characteristic of agricultural landscapes in Eastern Austria) have been established to enhance overall arthropod diversity and to increase densities of beneficial spiders and insects like Staphylinidae and Carabidae [20,21]. Although the importance of grassy arable fallows within ecological research has increased in recent years [e.g. 26] there is little information available about above-/below-ground interactions (e.g., interactions between plants and soil macrofauna). In most studies focusing on biotic interactions in grassland ecosystems only the relationship between plant communities and above-ground invertebrate herbivores was investigated, neglecting the response of soil invertebrates [4,31,50]. If the response of soil invertebrates was included, most studies focused on the relationship between plant diversity and soil fauna diversity [e.g. 24,60], whereas the influence of single plant species on the structure of the soil fauna community has generated little attention [19,52]. However, frequent plant species in grassland ecosystems (e.g., grass species like *Bromus sterilis* and *Trisetum flavescens*, herb species like *Taraxacum officinale* and *Plantago lanceolata*, legume species like *Medicago sativa* and *Trifolium repens*) may have a strong influence on the structure of soil macrofauna assemblages at the micro-scale [5,11,70] due to their provision of a unique food source (living plant tissue, litter, root associated mycorrhizal fungi) and microhabitat (e.g. microclimate conditions, soil pores caused by the growth of fine roots).

In many other field studies similar to those of Felzmann [19] and Salamon et al. [52] (both part of the BIODEPTH experiment), the soil

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fauna of "artificial" experimental plots was investigated, with the grassland communities being re-established by sowing mixtures of specific plant species (e.g., the CLUE project [24] and the Cedar Creek experiment [66]). In the present study, however, we investigated the influence of single plant species (*M. sativa* (legume), *T. officinale* (herb), *B. sterilis* (grass)) on the density of the soil macrofauna in more natural grassland ecosystems of different ages (three 2–3 (3–4), three 6–8 (9–7) and three 12–15 (13–16) year old grassy arable fallows in 2008 and 2009), where the plants had the opportunity to spread out naturally. *M. sativa*, *T. officinale* and *B. sterilis* (in the following text abbreviated as Ms, To and Bs) were selected as target plant species because they were frequent in all three age classes of the investigated fallows, allowing us to minimize the neighbor effects of non-target plant species by removing the Ms, To and Bs plants from the centre of plant species aggregations within the fallows. To investigate the "micro-scale correlations" between single plants and their associated macrofauna assemblages, we extracted single plants with all of the associated soil from the root area and extracted the macrofauna using a heat extraction method, which is a novel ecological approach of the present study just once used before [55]. These "micro-scale correlations" were often investigated in laboratory studies by sowing plant species in microcosm systems and adding different macrofauna species (mostly earthworm species) [e.g. 7,39]. However, transferring the results of these laboratory studies to the field is difficult and reinforces the importance of additional field studies to investigate the "micro-scale" habitat selection of soil macrofauna taxa within grassland ecosystems.

Gastropoda, Symphyla, Lumbricidae, Julidae and Isopoda were selected as target soil fauna groups in the present work because they are important herbivores (Gastropoda; [44,65]) and/or important primary and secondary decomposers (Gastrodopa, Symphyla, Lumbricidae, Julidae, Isopoda [10,15,59,62]) and performing key functions in terms of regulating litter decomposition and nutrient cycling [25,35,40]. Moreover, the distribution patterns of predatory macrofauna groups (Staphylinidae, Carabidae, Formicidae and Chilopoda) were investigated because they feed on herbivores [14,43,71] and decomposers [33,46,59] and thus presumably indirectly depend on the presence of single plant species or age classes of fallows. It has to be emphasized that in the present work only the distribution patterns of the selected macrofauna groups were investigated without including studies about their feeding behaviour. However, measuring of microbial soil parameters (microbial biomass, ergosterol content) allowed us to search for potential positive correlations between saprophagous macrofauna/gastropod taxa and microbial parameters within the investigated fallows. Overall, the study is designed to test the following hypotheses:

1) The presence of a legume species (in this study Ms) containing a high nitrogen content [38] causes a bottom-up effect propagating through the food web leading to high densities of mainly herbivorous (Gastropoda) and saprophagous groups (Isopoda, Lumbricidae, Julidae) [16,40,61] and their potential predators (Carabidae, Staphylinidae, Chilopoda, Formicidae) [e.g.19,71].
2) Densities of Gastropoda and saprophagous macrofauna increase with increasing age of the fallows due to the increasing number of plant species [55] providing diverse food sources (different types of living plant material and litter [8,12]). In turn, densities of predatory macrofauna groups increase with advancing age of fallows because they benefit from the high density of prey in the old fallows [21,72].

2. Material and methods

2.1. Sites and sampling

The Marchfeld plain, an area of intensive arable agricultural production north-east of Vienna characterized by a continental eastern European climate (mean annual temperature 9.6 °C, mean annual precipitation 490 mm) [17] served as study area. In May 2008 and May 2009, the study was performed in three 2–3 (3–4), three 6–8 (9–7) and three 12–15 (13–16) yr old grassy arable fallows (altogether nine sites) each including the plant species *M. sativa* (Ms) (as legume), *T. officinale* (To) (as non-legume herb) and *B. sterilis* (Bs) (as grass). Within the grassy fallows the dominating soil type is a black earth (chernozem) in different variations (Table 1). In each of the nine sites two plots (5 × 5 m) spaced at least 40 m apart from each other were selected at random. In order to avoid autocorrelation large spacing was chosen, thus assuming samples to be independent [30]. The minimum distance of the plots to the margin of the fallow was 15 m to minimize effects of neighboring sites (arable fields or other grassy arable fallows). In May 2008 and May 2009, at each plot five Ms, Bs and To plants were dug out with their associated soil from the centre of aggregations of the respective target plant species with the help of steel cylinders (5.6 cm × 5.6 cm × 10 cm depth) to minimize neighbor effects of non-target plant species.

Table 1
Characteristics of the 9 investigated sites (grassy arable fallows) in the Marchfeld area (Austria).

Sites	Grassy arable fallow since	Soil type	GPS position (latidude: lat; longitude: lon)	Size of the fallow (m^2)
Site 1 (age class: 2–3 yr)	2006	Wet chernozem	lat N: 48.225 lon E: 16.871	1709
Site 2 (age class: 2–3 yr)	2006	Parachernozem	lat N: 48.300 lon E: 16.668	2092
Site 3 (age class: 2–3 yr)	2006	Parachernozem	lat N: 48.307 lon E: 16.490	1969
Site 4 (age class: 6–8 yr)	2001	Wet chernozem	lat N: 48.225 lon E: 16.872	2366
Site 5 (age class: 6–8 yr)	2000	Chernozem	lat N: 48.306 lon E: 16.591	1454
Site 6 (age class: 6–8 yr)	2002	Parachernozem/ chernozem	lat N: 48.280 lon E: 16.783	28,907
Site 7 (age class: 12–15 yr)	1994	Chernozem	lat N: 48.341 lon E: 16.723	1168
Site 8 (age class: 12–15 yr)	1996	Calcareous tilled soil	lat N: 48.366 lon E: 16.570	1277
Site 9 (age class: 12–15 yr)	1993	Chernozem	lat N: 48.201 lon E: 16.574	10,413

Within each plot the soil material of two steel cylinders per plant species was mixed and united into one sample to obtain sufficient material for the determination of microbial and abiotic soil parameters (altogether 54 samples per sampling time: nine sites (three 2–3/3–4, three 6–8/7–9 and three 12–15/13–16 yr old fallows in 2008/2009) * two plots * three plant species). The samples were sieved in the laboratory (2 mm), thereafter the measurements of the abiotic and microbial soil parameters were performed [2,58]. Soil organic matter content (in the following abbreviated as SOM) was just measured for the samples of May 2008 (for a detailed description see [55]). Soil moisture content was determined gravimetrically after drying at 105 °C for 24 h. N- and C-contents in soil materials were determined from dried and powdered samples using an elementar analyser (Carlo Erba, Milan). Microbial respiration was measured using an automated respirometer based on electrolytic O_2 microcompensation [58]. Basal respiration was measured in fresh soil materials equivalent to 3.5 g dry wt by averaging respiration rates of the hours 10–20 after starting of the measurements. Microbial biomass was calculated from the maximum initial respiratory response (MIRR; μg O_2/g dry wt hr) following glucose addition (substrate induced respiration method; [3]) of fresh soil samples equivalent to 3.5 g dry wt. Microbial carbon was calculated as 38.0 X MIRR [3] from oxygen uptake of soil samples supplemented with 4000 μg glucose (g dry wt)$^{-1}$ assuming a respiratory quotient of 1.0 [51]. Glucose was added as a solution to increase the water content to 100% of dry wt [9]. The inclusion of a Bachelor project to this study enabled us to determine the ergosterol content of the 54 soil samples of May 2009. Quantitative determination of ergosterol was performed for each sample (1 g dry wt) by reserved-phase HPLC analysis according to Zelles et al. [73].

Within each plot the material of further three steel cylinders per plant group was united into one sample to gain sufficient soil material for the extraction of soil macrofauna resulting in a total of 54 samples per sampling time (nine sites (three 2–3/3–4, three 6–8/7–8 and three 12–15/13–16 yr old fallows in 2008/2009) * two plots * three plant species). Soil macrofauna was extracted with a Berlese-Tullgren funnel apparatus [41,63] into 10% aqueous sodium benzoate solution and identified to different levels. Isopoda were identified to species/genus level. Formicidae, Chilopoda, Carabidae and Staphylinidae (with exception of the subfamily Aleocharinae) were identified to genus level. Because of the high amount of juvenile Gastropoda in the samples, this group was identified to different taxonomic levels (species, genus or family level). Moreover, because of the high amount of juveniles within the Lumbricidae and Julidae, these groups were just identified to family level. For GLM analyses (see below) taxa were divided into the different feeding groups:

1) Saprophagous macrofauna [see 15,59]: Isopoda (*Oniscus asellus*, *Trachelipus* sp.), juvenile Julidae, juvenile Lumbricidae.
2) Phytophagous/fungivorous Symphyla [see 15].
3) Phytophagous/fungivorous/saprophagous Gastropoda [see 62]: Valloniidae, Zonitidae, Vitrinidae, *Truncatellina* sp., *Columnella* sp., *Vertigo* sp., *Aegopinella* sp., *Punctum pygmaeum*, *Succinella oblonga*, *Pyramidula rupestris.*
4) Predatory Chilopoda [see 46,47]: *Geophilus* sp., *Lithobius* sp..
5) Predatory/omnivorous Coleoptera [see 22,59]: Staphylinidae (*Tachinus* sp., *Quedius* sp., *Xantholinus* sp., *Heterothops* sp., *Neobisnius* sp., *Tachyporus* sp., *Leptacinus* sp., *Philonthus* sp., *Stenus* sp., *Sepedophilus* sp., *Bryoporus* sp., Aleocharinae) and Carabidae (*Amara* sp., *Harpalus* sp., *Calathus* sp., *Clivina* sp., *Brachinus* sp., *Dromius* sp.).
6) Predatory/omnivorous Formicidae [see 11,48]: *Myrmica* sp., *Lasius* sp., *Solenopsis* sp., *Ponera* sp., *Leptothorax* sp., *Tetramorium* sp., *Strongylognathus* sp..

2.2. Statistical analysis

For detecting differences in densities of soil macrofauna groups (saprophagous macrofauna, Gastropoda, Symphyla, predatory Coleoptera, Chilopoda, Formicidae) and environmental parameters (microbial biomass, water content, C-to-N ratio) General Linear Models (GLMs) were used connecting the results of the years 2008 and 2009 with "year" (2008, 2009), "age class" (A1 = 2–3/3–4 yr, A2 = 6–8/7–9 yr and A3 = 12–15/13–16 yr) and "plant species" (Ms, To, Bs) as factors including interactions ("year × age class", "year × plant species", "age class × plant species", "year × age class × plant species") and "site" (1–9) as random effect nested within "age class". The ergosterol content was just measured in May 2009, thus the factor "year" was not included in the appropriate GLM. Tukey test was used to detect differences between means at the 5% probability level. Microbial biomass and ergosterol content were measured and then analysed with GLMs to compare the distribution pattern of the saprophagous macrofauna, Symphyla and Gastropoda with the distribution pattern of their potential food source (microbial and fungal biomass [1,10,15,28,37,49,59,62]). Water content and C-to-N ratio were analysed with GLMs because both abiotic parameters are important structuring forces of soil macrofauna assemblages [15,54].

The structure of the soil macrofauna assemblages of the investigated grassy arable fallows was analysed separately for the two sampling dates (May 2008, May 2009) by canonical correspondence analysis (CCA) using the software package CANOCO [69]. Only taxa which were at least found in 3 samples were included into the analysis. The following environmental factors were used for the macrofauna of both sampling times: C-to-N ratio, water content and microbial biomass. Additionally, the density of Collembola (data of May 2008 [see 55]) and the soil organic matter content (SOM) were included in the CCA of May 2008, whereas the ergosterol content (determined within the Bachelor Project 2009) as a measure of the fungal biomass was included in the CCA of May 2009. Moreover, the age of the grassy arable fallows and the presence of grasses, herbs and legumes were included as centroids in the CCAs.

3. Results

3.1. Density of macrofauna groups (connected data of 2008 and 2009)

The density of the saprophagous macrofauna differed significantly between the plant species (Fig. 1a) but not between the age classes (Fig. 1b) and years (data not shown). The density was significantly higher in the Bs than in the To samples with the Ms samples being intermediate (GLM: $SS = 46.7$, $F = 3.57$, $p < 0.05$, Fig. 1a). Moreover, the density tended to be higher in A2 than in A1 and A3. The density of Gastropoda differed significantly between the age classes (Fig. 1d) but not between the plant species (Fig. 1c) and years (data not shown). The density was significantly higher in A2 than in A1 with A3 being intermediate (GLM: $SS = 41.3$, $F = 3.94$, $p < 0.05$, Fig. 1d). The density of predatory beetles differed significantly between the age classes (Fig. 1f) and years but not between the plant species (Fig. 1e). Similar to the Gastropoda the density was significantly higher in A2 than in A1 with A3 being intermediate (GLM: $SS = 49.7$, $F = 3.97$, $p < 0.05$, Fig. 1f). Moreover, densities were significantly higher in May 2009 (386 ind. m^{-2}) than in May 2008 (104 ind. m^{-2}) (GLM: $SS = 49.7$, $F = 27.8$, $p < 0.001$). The density of Symphyla differed significantly between the years but not between the age classes and plant species (data not shown). The density was significantly higher in May 2008 (69 ind. m^{-2}) than in May 2009 (4 ind. m^{-2}) (GLM: $SS = 33.4$, $F = 10.6$, $p < 0.01$).

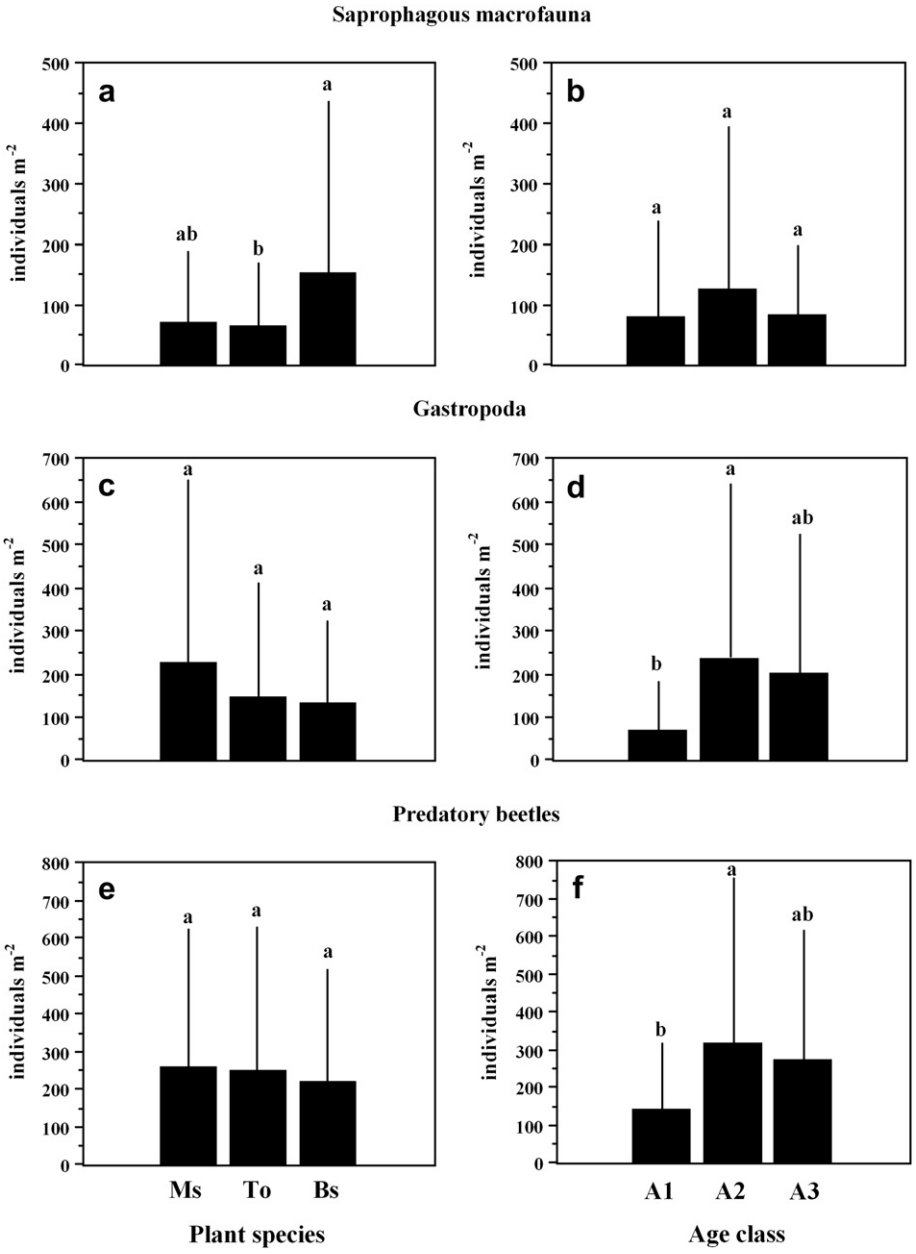

Fig. 1. Density of the saprophagous macrofauna (Lumbricidae, Isopoda, Dilopoda), Gastropoda and predatory beetles (Carabidae, Staphylinidae) in *Medicago sativa* (Ms), *Taraxacum officinale* (To) and *Bromus sterilis* (Bs) samples (a, c, e) and in the three age classes of the grassy fallows (A1, A2, A3) (b, d, f) ($n = 9$). Means with 1 SD (connected data of 2008 and 2009); bars that share the same letter are not significantly different from each other ($p < 0.05$, Tukey test).

The density of Chilopoda and Formicidae neither significantly responded to year and age class nor to the presence of the plant species (data not shown). Moreover, there were few significant interactions within the GLM results (saprophagous macrofauna, Gastropoda and predatory beetles: "year × age class"; Symphyla: "year × plant species").

3.2. Microbial biomass (data of 2008 and 2009) and ergosterol content (data of 2009)

The microbial biomass was significantly higher in May 2009 (1024.1 μg Cmic g^{-1} dw) than in May 2008 (790.5 μg Cmic g^{-1} dw) (GLM: SS = 72.7, $F = 30.2$, $p < 0.001$). Moreover, microbial biomass and ergosterol content differed significantly between the age classes (Fig. 2b, d) but not between the plant species (Fig. 2a, c). Microbial biomass and ergosterol content were significantly higher in A3 and A2 than in A1 (GLM microbial biomass: SS = 72.7, $F = 25.1$, $p < 0.001$, Fig. 2b; GLM ergosterol content: SS = 89.8, $F = 36.0$, $p < 0.001$, Fig. 2d). There were no significant interactions within the GLM results.

3.3. Water content and C-to-N ratio (connected data of 2008 and 2009)

Water content and C-to-N ratio differed significantly between the age classes (Fig. 3b, d) but not between the plant species (Fig. 3a, c). Both parameters significantly increased in with increasing age of the fallows (Fig. 3b, d) (GLM water content: SS = 80.4, $F = 14.8$, $p < 0.001$; GLM C-to-N ratio: SS = 57.8, $F = 23.4$, $p < 0.001$). Moreover, the water content was significantly higher in

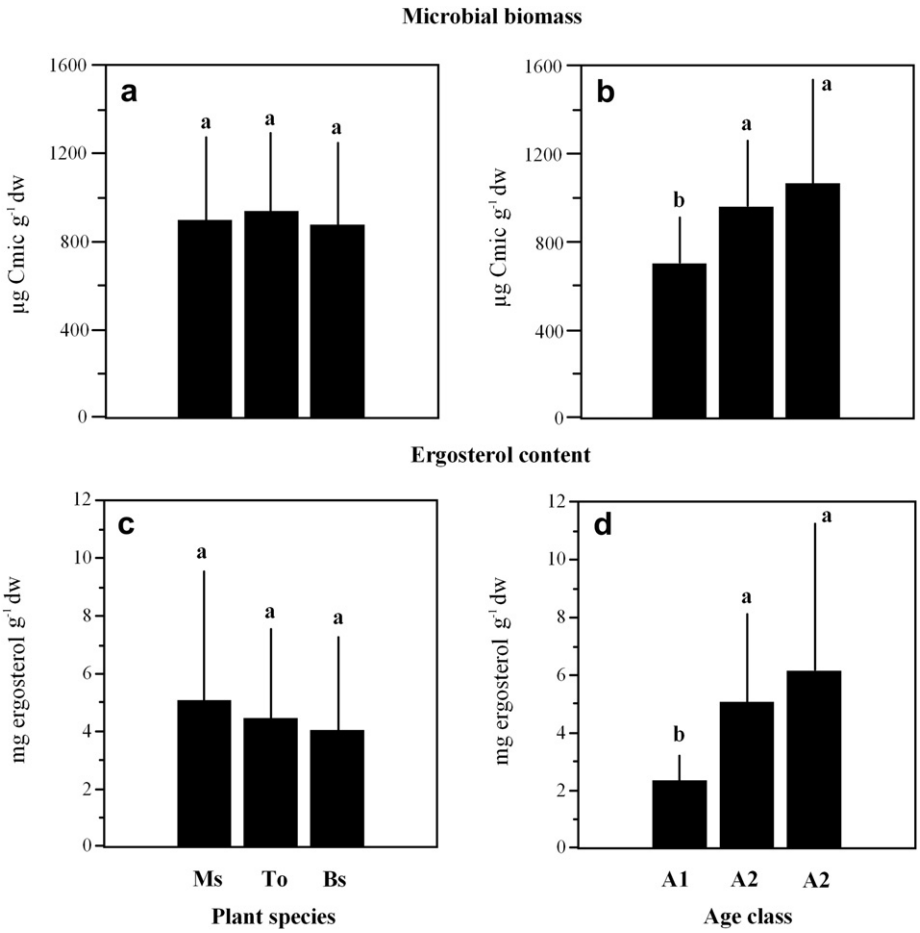

Fig. 2. Microbial biomass (connected data of 2008 and 2009) and ergosterol content (data of 2009) in *Medicago sativa* (Ms), *Taraxacum officinale* (To) and *Bromus sterilis* (Bs) samples (a, c) and in the three age classes of the grassy fallows (A1, A2, A3) (b, d) ($n = 9$). Means with 1 SD; bars that share the same letter are not significantly different from each other ($p < 0.05$, Tukey test).

May 2008 (16.04% dw) than in May 2009 (10.14% dw) (GLM: SS = 80.4, $F = 116.5$, $p < 0.001$). In contrast, the C-to-N ratio did not differ significantly between the years (data not shown).

3.4. Soil macrofauna assemblage

3.4.1. May 2008

CCA explained 16.3% of the total variance of the macrofauna assemblage (Fig. 4). SOM (5.5%), water content (3.7%) and microbial biomass (3.2%) contributed significantly to the macrofauna assemblage and explained 12.4% of the total variance.

Axis 1 mainly represents the SOM and the C-to-N ratio and separates A2 from A3 and A1 (Fig. 4). Axis 2 mainly represents the microbial biomass and the water content. Microbial biomass strongly correlated with *Taraxacum* samples. The ant taxa *Myrmica* sp. and *Ponera* sp. were associated with *Taraxacum* samples and obviously preferred plots with a high microbial biomass. The water content and the density of Collembola correlated with *Bromus* samples. The predatory taxa *Xantholinus* sp., *Lithobius* sp. and *Geophilus* sp. and the saprophagous Julidae and Symphyla were associated with *Bromus* samples and correlated positvely with the water content and Collembola density. Moreover, several predatory taxa were associated with A3 (*Lasisus* sp., *Tachinus* sp., *Solenopsis* sp.) whereas several saprophagous taxa were associated with A1 (Lumbricidae) or A2 (*Oniscus asellus*, *Succinella oblonga*, *Columnella* sp., *Pyramidula rupestris*).

3.4.2. May 2009

CCA explained 17.43% of the total variance of the macrofauna assemblage (Fig. 5). Ergosterol content (7.1%), water content (4.6%) and microbial biomass (3.4%) contributed significantly to the macrofauna assemblage and explained 15.1% of the total variance. Axis 1 mainly represents the ergosterol content and separates A2 from A3 and A1 (Fig. 5), as already observed in 2008. Axis 2 mainly represents the water content. Similar to 2008 the water content correlated with *Bromus* samples and also the taxa *Geophilus* sp. and Julidae were associated with *Bromus* samples and correlated positively with the water content. The ergosterol content, the microbial biomass and the C-to-N ratio correlated with A3. All gastropod taxa (Vitrinidae, *Punctum pygmaeum* and *Truncatellina* sp.) and the predatory taxa *Ponera* sp., *Tachinus* sp.and *Heterothops* sp. were associated with A3 and correlated positively with the microbial biomass and ergosterol content (as a measure of the fungal biomass). Moreover, several perdatory taxa (Aleocharinae, *Xantholinus* sp., *Myrmica* sp., *Amara* sp., *Solenopsis* sp., *Lithobius* sp., *Neobisnius* sp.) were associated with the cluster To samples plus A2.

4. Discussion

This study aimed at investigating the response of the soil macrofauna community to the presence of different plant species within grassy arable fallows and to the aging of these fallows. Moreover, connecting the results (densities of different macrofauna

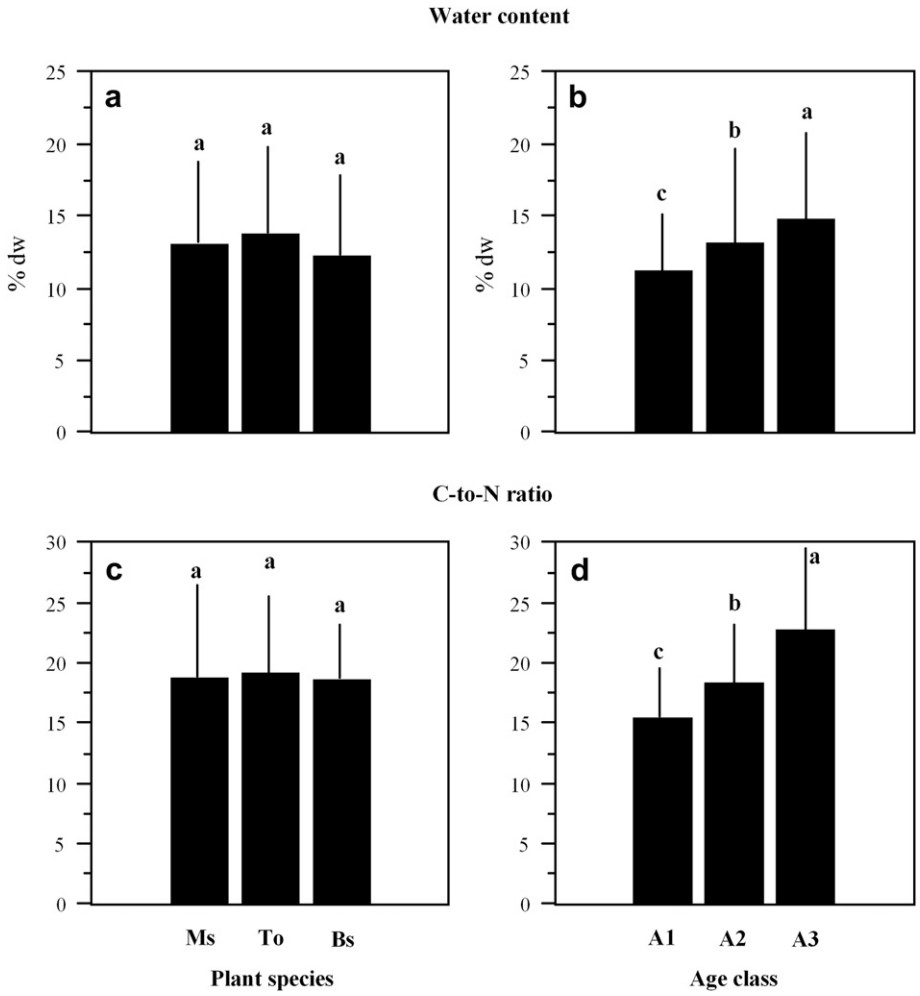

Fig. 3. Water content and C-to-N ratio in *Medicago sativa* (Ms), *Taraxacum officinale* (To) and *Bromus sterilis* (Bs) samples (a, c) and in the three age classes of the grassy fallows (A1, A2, A3) (b, d) ($n = 9$). Means with 1 SD (connected data of 2008 and 2009); bars that share the same letter are not significantly different from each other ($p < 0.05$, Tukey test).

groups, microbial biomass, water content, C-to-N ratio) of two years (May 2008, May 2009) allowed us to investigate potential yearly fluctuations in macrofauna densities and environmental parameters within the investigated fallows. Focusing on the response of the environmental parameters, microbial biomass was significantly higher in May 2009 whereas soil water content was higher in May 2008. However, within the soil macrofauna groups only the densities of predatory beetles (Carabidae, Staphylinidae) (higher densities in May 2009) and Symphyla (higher densities in May 2008) significantly differed between the years. The euedaphic hygrophilous Symphyla [15] may benefited from the higher soil water content in May 2008 whereas a part of the predominant predatory beetles (e.g. partly fungi feeding Aleocharinae [36,56]) may benefited from the higher microbial biomass in May 2009.

Contrary to our expectations, none of the investigated macrofauna groups positively responded to the presence of Ms in the investigated fallows, thus disproving this hypothesis 1 ("highest densities of the soil macrofauna groups in the Ms samples"). Moreover, in contrast to hypothesis 1, the density of the saprophagous macrofauna (Lumbricidae, Julidae, Isopoda) was significantly higher in Bs than in Ms samples. Thus, the saprophagous macrofauna possibly benefited from the particularly high amount of fine roots in the upper soil layers of Bs samples compared to Ms and To samples [34], indicating the importance of fine roots as attractive food source for saprophagous taxa (e.g. Diplopda, [see 45]). Similar to the results of the present work, in the field study of Bezemer et al. [6] plant identity (legume: *Lotus corniculatus*, non-legume herb: *Plantago lanceolata*) had strong effects on decomposing organisms (e.g. soil macrofauna), widely believed to be generalistic feeders. The authors concluded that species-specific differences in plant root traits (e.g. differences in secondary compounds in root tissues) contributed to differences that were observed in soil community composition underneath the individual plants.

Considering the results of the CCAs of both years, juvenile Julidae (see Figs. 4 and 5) and Symphyla (see Fig. 4) were associated with Bs samples, indicating that these hygrophilous taxa [15] presumably benefited from the high water content and the high amount of fine roots in the Bs samples [34,45]. Similar to the saprophagous taxa, the predatory taxa *Geophilus* sp. was associated with the Bs samples and also benefited from the high water content (see Figs. 4 and 5) and additionally from the high density of potential prey (Collembola, see Fig. 4; juvenile Julidae, see Figs. 4 and 5) in the Bs samples. In this connection Poser [46,47] and Scheu and Falca [59] emphasized that Collembola and juvenile Julidae are important prey groups of Geophilidae. In contrast to *Geophilus* sp., several ant taxa were associated with the To samples in May 2008 (*Myrmica* sp., *Ponera* sp.) and 2009 (*Myrmica* sp., *Solenopsis* sp.) and possibly benefited from the high amount of surrounding *Taraxacum* seeds, which are an attractive food source for many ant species [48]. Moreover, the results of the CCA (May

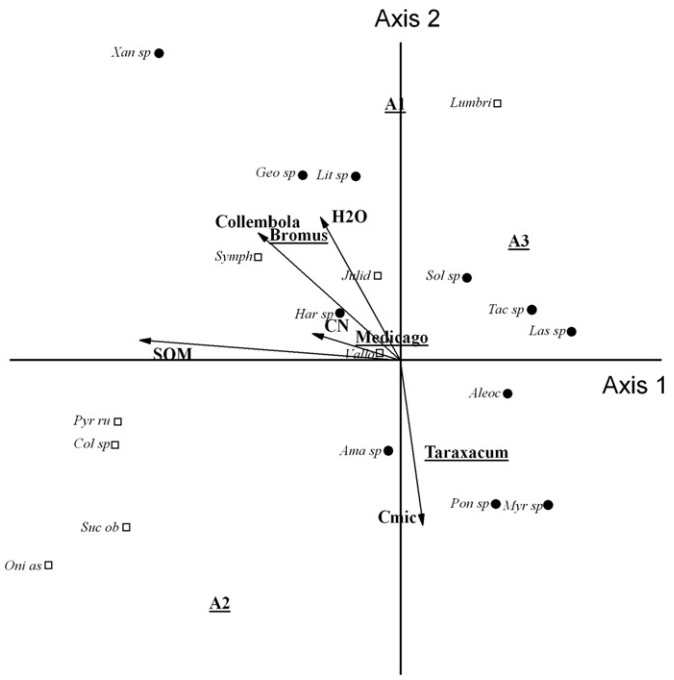

Fig. 4. Ordination bi-plot of the canonical correspondence analysis (CCA) with mean abundances of macrofauna taxa and different environmental factors (May 2008). Age of the grassy arable fallows (A1 = 2–3 yr, A2 = 6–8 yr, A3 = 12–15 yr) and presence of *Medicago sativa*, *Taraxacum officinale* and *Bromus sterilis* are included as centroids. Environmental variables: Cmic (microbial biomass), CN (C-to-N ratio), H2O (water content), SOM (soil organic matter content), Collembola (density of Collembola). Saprophagous/herbivorous/fungivorous macrofauna taxa (marked with □): Lumbri = juvenile Lumbricidae, Julid = juvenile Julidae, Isopoda (Oni as = *Oniscus asellus*), Symph = Symphyla, Gastropoda (Vallo = Vallonidae, Pyr ru = *Pyramidula rupestris*, Col sp = *Columnella* sp., Suc ob = *Succinella oblonga*). Predominant predatory macrofauna taxa (marked with ●): Coleoptera (Xan sp = *Xantholinus* sp., Tac sp = *Tachinus* sp., Aleoc = Aleocharinae, Har sp = *Harpalus* sp. Ama sp = *Amara* sp.), Chilopoda (Geo sp = *Geophilus* sp., Lit sp = *Lithobius* sp.), Formicidae (Sol sp. = *Solenopsis* sp., Las sp. = *Lasius* sp., Myr sp = *Myrmica* sp., Pon sp = *Ponera* sp.).

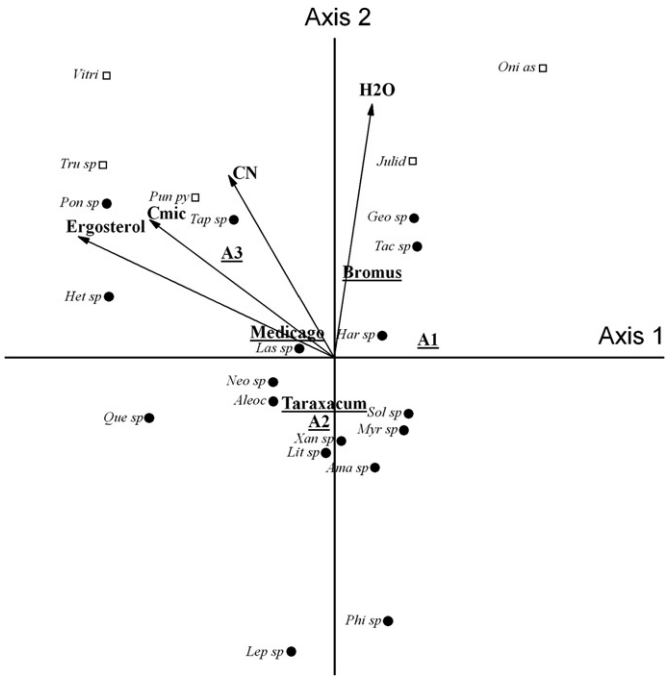

Fig. 5. Ordination bi-plot of the canonical correspondence analysis (CCA) with mean abundances of macrofauna taxa and different environmental factors (May 2009). Age of the grassy arable fallows (A1 = 3–4 yr, A2 = 7–9 yr, A3 = 13–16 yr) and presence of *Medicago sativa*, *Taraxacum officinale* and *Bromus sterilis* are included as centroids. Environmental variables: Cmic (microbial biomass), CN (C-to-N ratio), H2O (water content), Ergosterol (ergosterol content. Saprophagous/herbivorous/fungivorous macrofauna taxa (marked with □): Julid = juvenile Julidae, Isopoda (Oni as = *Oniscus asellus*), Gastropoda (Vitri - = Vitrinidae, Tru sp = *Truncatellina* sp., Pun py = *Punctum pygmaeum*). Predominant predatory macrofauna taxa (marked with ●): Coleoptera (Xan sp = *Xantholinus* sp., Que sp = *Quedius* sp., Tac sp = *Tachinus* sp., Tap sp = *Tachyporus* sp., Aleoc = Aleocharinae, Het sp = *Heterothops* sp., Neo sp = *Neobisnius* sp., Xan sp = *Xantholinus* sp., Har sp = *Harpalus* sp. Ama sp = *Amara* sp., Phi sp = *Philonthus* sp.), Chilopoda (Geo sp = *Geophilus* sp., Lit sp = *Lithobius* sp.), Formicidae (Sol sp = *Solenopsis* sp., Las sp = *Lasius* sp., Myr sp = *Myrmica* sp., Lep sp = *Leptothorax* sp., Pon co = *Ponera* sp.).

2008) indicated that the ant taxa *Myrmica* sp. and *Ponera* sp. additionally profited from the relatively high microbial biomass in the To samples, supporting that the microbial (fungal) biomass is an important food source for *Myrmica* sp. [32].

Focusing on the response of microbial (ergosterol content and microbial biomass) and abiotic soil parameters (water content and C-to-N ratio) to aging of the fallows, all measured soil parameters significantly increased with increasing age of the fallows. However, densities of the investigated soil macrofauna groups (e.g. saprophagous macrofauna, Gastropoda) did not gradually increase with the age of the fallows in spite of an increase of potential food sources (bacterial and fungal biomass, number of plan species [55]) and a potential improvement of the physically environment (increasing water content) disproving hypothesis 2 ("increase of the density of Gastropoda and saprophagous macrofauna with increasing age of the fallows"). Thus it is obvious that microbial and fungal biomass were no limiting factors for the density of saprophagous macrofauna and Gastropoda in the investigated fallows supporting the results of other studies [53,57].

In contrast to hypothesis 2, densities of Gastropda and predatory beetles were significantly higher in A2 than in A1 with A3 being intermediate. Moreover, the density of the saprophagous macrofauna also tended to be highest in A2. Supporting these results of the GLMs, in May 2008 several gastropod taxa (*Columnella* sp., *Succinella oblonga*, *Pyramidula rupestris*) and the saprophagous macrofauna species *Oniscus asellus* correlated positively with A2. However, causal factors responsible for this pattern are poorly known. We suppose that the high density of Gastropoda and saprophagous macrofauna in A2 was partly caused by the high amount of attractive fine roots provided by grasses like *B. sterilis* and *Bromus tectorum* [34] in this age class taking into account that several saprophagous macrofauna and gastropod taxa partly feed on fine roots [29,45]. Supporting this conclusion, in two of the three fallows of A2 the coverage of *B. sterilis* plus *B. tectorum* was higher than 40% (Wissuwa et al., unpublished data). The fact that the number of predatory beetles was also comparatively high in A2 (see Fig. 1c) indicates that predators may have benefited from the increased availability of their prey (e.g. Gastropoda, Lumbricidae and Julidae) (see Fig. 1b, d). Gastropoda, Lumbricidae and Julidae are known to be important prey groups for Staphylinidae and Carabidae [15,18,23,33,59,67]. We thus conclude that changes in the resource base (e.g. the amount of fine roots) may be propagated through the food web and had a potential impact on specific predaceous arthropod taxa.

In conclusion, focusing on the different stages of grassland succession, we found significant changes in the soil macrofauna at the level of individual groups: Densities of Gastropoda and predatory beetles flourished in the "medium stage" (A2) of grassland succession. However, it is difficult to state more precisely the causal factors (e.g. fine root biomass) responsible for this pattern. Focusing on the "micro-scale" response of the soil macrofauna groups to the presence of different plant species (Ms, To, Bs), the importance of

the food source "belowground biomass" (death and living fine roots) was possibly higher than the importance of the litter type/quality [see 45], leading to higher abundances of the saprophagous macrofauna in the Bs than in the Ms and To samples because of the higher amount of fine roots in the upper soil layers of Bs compared to Ms and To samples [34]. Focusing on the results of the CCAs of both years, within the measured abiotic and microbial soil parameters the water content had the strongest influence on the structure of the macrofauna assemblages: Several taxa (juvenile Julidae, Symphyla, *Geophilus* sp.) were associated with Bs samples and presumably benefited from the high water content in the root-associated soil of Bs.

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