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Population dynamics and functional roles of Enchytraeidae (Oligochaeta) in hardwood forest and agricultural ecosystems

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Abstract

Population dynamics of enchytraeids are described for 2 montane forested watersheds in southwestern North Carolina (Coweeta) and an agricultural site under conventional (CT) and no-tillage (NT) management in the northeastern Georgia piedmont (Horseshoe Bend, HSB). Given that much of the taxonomy, ecology and community structure of enchytraeids is poorly known, our objective was to identify key "indicators" of enchytraeid community structure which could be used, in this case, to better understand their role in soil structure formation. Although population densities of enchytraeids were higher in the forested (Coweeta) than in the arable soils (HSB), the average ash free dry weight per enchytraeid at HSB was nearly double that found at Coweeta. Based on these measurements and an estimate of their gut transit time, we calculated that the enchytraeids at HSB transported 2180 g of soil per m^2 per year compared to 443 and 393 g m^{-2} yr^{-1} for watershed 18 and 27, respectively at Coweeta. We therefore hypothesize that enchytraeids have a larger influence on soil structure in agricultural fields than in forested areas, in spite of lower population densities. The ash free dry weight and ash wt. per enchytraeid may qualify as key "indicator" parameters of enchytraeid community structure which helps to understand their functional role in ecosystems, though more studies are called for.

Introduction

Little information is available on the role of Enchytraeidae (Oligochaeta, Annelida) in ecosystems. Enchytraeids, like soil fauna in general (Pokarzhevsky et al., 1989; Swift, 1977), may play an important role in the turnover of nutrients due to the quantity of nutrients stored in their tissue. Enchytraeids can indirectly affect decomposition processes by comminution of organic material, by mixing organic material and soil, by selective grazing on micro-organisms and through dispersal of spores (e.g. Ponge, 1984; Toutain et al., 1982; Toutain, 1987; Wolters, 1988). Enchytraeids can also have important influences on soil structure due largely to their high burrowing capacity (van Vliet et al., 1993), their production of fecal pellets (e.g Thompson et al., 1990; Zachariae, 1964) and the amount of mineral particles they transport through ingestion (e.g. Babel, 1968) or attached to the body surface (Ponge, 1984).

Although recorded from nearly all ecosystems, the largest populations have been reported from moors, moist coniferous forests and dune grasslands (Didden, 1993). In deciduous forests enchytraeid densities per m^2 can range from as low as 5,700 (Kairesalo, 1978) to as high as 108,000 (Ellenberg et al., 1986). In agricultural systems their abundance is much lower, ranging from 4,650 (Willard, 1974) to 30,000 per m^2 (Didden, 1991).

In natural ecosystems most enchytraeids are found in the upper 5 cm of the soil profile (Dash and Gragg, 1972; Nielsen, 1955b; Nurminen, 1967; O'Connor, 1957; Peachey, 1963; Springett, 1970). In conventionally tilled (CT) agricultural fields enchytraeids are more evenly distributed over the plow layer, while in minimum (MT) and no-tillage (NT) fields they are more abundant in the upper soil layer (Didden, 1991). This vertical distribution pattern is influenced by changes in soil moisture content, to which they can quickly respond (Nielsen, 1955b; O'Connor, 1967). The rapid loss of water by enchytraeids in low moisture soils may be prevented by deeper migration (Nielsen, 1955a). Springett et al. (1970) showed that enchytraeids were able to move vertically as the soil water content changed, covering up to 6 cm in a few hours. Dósza-Farkas (1973) showed that this vertical migration pattern is species specific. Her findings for a Hungarian forest revealed that *Stercutus niveus* Michaelsen 1888 had a pattern of distribution and migration differing substantially from that of other species present, pointing out the importance of knowing species composition and behavioral characteristics of the enchytraeid community.

Population size, species composition and seasonal dynamics will influence the importance of enchytraeids in ecosystem processes, especially nutrient cycling and soil structure formation. Unfortunately, the taxonomy of enchytraeids needs revision and elaboration, and there are relatively few scientists worldwide with taxonomic expertise in this group. In the U.S.A. the situation is particularly problematic because most species are not described at all. The objectives of this study were two-fold: 1) to describe the population dynamics and community structure of enchytraeids in 2 different ecosystems, i.e. a mixed hardwood forest in southwestern North Carolina and an agricultural site in northern Georgia, and 2) to look for "indicator" parameters which can aid in understanding the role of enchytraeids in soil structure formation.

Materials and methods

Site description

The Horseshoe Bend Experimental Area (HSB) at Athens, GA contains a welldrained sandy clay loam flood plain soil (fine-loamy, mixed, thermic Rhodic Kanhapludult). The area has been under continuous conventional (CT) and no-tillage (NT) management since 1978. In the winters of 1990–1991 and 1991–1992 the fields were planted with winter rye (*Secale cereale* L.) followed by a summer crop of grain sorghum (*Sorghum bicolor* L. Moench) in 1991 and corn (*Zea mays* L.) in 1992. During the winter of 1992–1993 the fields were kept fallow.

Additional sampling sites were located at the Coweeta Hydrologic Laboratory (a Long Term Ecological Research site), situated in the southern Appalachians near Franklin, North Carolina. Samples were collected from watershed 27 (WS 27) (1160 m altitude, 30–50 % slope) on a coarse-loamy mixed, mesic Typic Haplumbrept, and from watershed 18 (WS 18) (750 m altitude, 15–30 % slope) on a fine-loamy oxidic or mixed mesic Typic Hapludult. In each watershed samples were taken under rhododendron (*Rhododendron maximum* L.) and oak (*Quercus rubra* L.) to determine the influence of litter quality and microclimate on the enchytraeid community. The oak sites at both watersheds were more open than the rhododendron sites, allowing more light to reach the forest floor.

Some general characteristics of the soils and climates at these sites are listed in Table 1. Further details of these sites can be found in Beare et al. (1992) (HSB) and Swank and Crossley (1988) (Coweeta).

Methods

Enchytraeids were sampled at both sites with a 5.8 cm diameter soil corer to a depth of 15 cm. At the HSB site samples were taken monthly from Jan. 1991 until Jan. 1993. The Coweeta sites were sampled 10 times during the period from May 1989 until Oct. 1991. At each site and sampling date four replicates were taken, which were extracted separately.

Samples were extracted in 6 increments of 2.5 cm each, using a modified wet-funnel extraction method described by O'Connor (1955). The soil, resting on a sieve in a funnel filled with water, was exposed to light and heat. After 4 h of presoaking (saturated soils), the light intensity was increased gradually until the soil surface reached a temperature of 45 °C ($\approx$ 3 hrs). Enchytraeids responded to the light and heat by moving away from its source and passed through the sieve into the water below. After counting, the enchytraeids collected from each sample were composited by depth (0–5 and 5–15 cm), transferred to a drop of water, and freeze-dried for 48 hrs. To determine ash free dry weight (AFDW), the freeze-dried enchytraeids were ashed at 500 °C for 4 hrs. Average AFDW per enchytraeid and average ash weight (ash wt.) per enchytraeid were calculated by dividing the total sample AFDW and ash wt., respectively by the number of enchytraeids present in the sample. The number of enchytraeids, their AFDW and their ash weight were expressed as number m^{-2}, AFDW m^{-2} and ash wt. m^{-2}, respectively. Estimates of the amount of mineral soil transported were calculated by multiplying the ash wt. m^{-2} with the number of hours per year divided by the gut turnover time, as estimated by Didden (1990, 1991). Though not previously measured, Didden (1990, 1991) estimated the average gut

Table 1. Site characteristics

	HSB		Coweeta	
	CT*	NT*	WS*18	WS*27
Annual rainfall (mm)	1365		2190	2730
Avg. air temperature (°C)	17		14	13
Carbon content (g kg^{-1})				
0-5 cm	14	25	79	158
5-15 cm	11	10	36	30
Bulk density (Mg m^{-3})				
0-5 cm	1.3	1.1	0.5	0.1
5-15 cm	1.5	1.5	0.9	0.7
Soil type	Ultisol		Ultisol	Inceptisol

*CT - conventional tillage, NT - no-tillage, WS - watershed.

turnover time for an enchytraeid community to be ≈ 2 h. Because enchytraeids are small and very active worms, he based this estimate on the turnover time of *Allolobophora rosea* Savigny 1826, an endogeic earthworm, which is adapted to the rapid turnover of large quantities of soil and has a gut turnover time of 1–2.5 h (Bolton and Phillipson, 1976).

To compare seasonal variation between and within sites, all data were expressed per season: Winter (Dec-Feb), Spring (Mar-May), Summer (Jun-Aug) and Fall (Sep-Nov). SAS (ANOVA) (SAS®, 1988) was used for statistical analysis of the log transformed data.

Results

Average monthly temperatures and rainfall for the 4 seasons at Coweeta and HSB during the sampling years are shown in Figure 1. The climate at Coweeta was much cooler and wetter than at HSB. Temperatures at Coweeta were on average about 5 °C lower than at HSB; rainfall was about twice as much at Coweeta compared to HSB.

Figure 2 shows the overall average number of Enchytraeidae m^{-2} (0–15 cm) at all sites. The abundance of enchytraeids was significantly greater for the forested soils of Coweeta than the agricultural soils at HSB. No significant difference was found between populations in CT (15270 m^{-2}) and NT (16830 m^{-2}) soils.

Seasonal variation in enchytraeid populations (No. m^{-2}) differed by depth (0–5, 5–15 cm) in NT and CT (Fig. 3). In CT significantly more enchytraeids were found in the 5–15 cm than in the 0–5 cm layer. In NT the number of enchytraeids in summer was significantly lower than in other seasons.

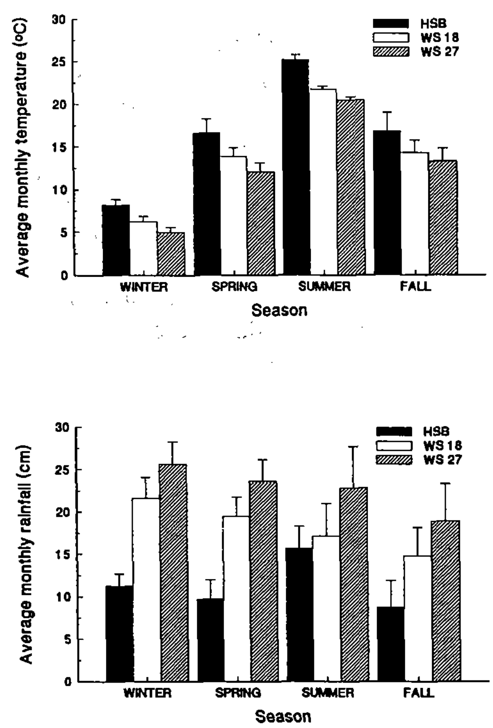

Fig. 1. Average monthly temperatures and rainfall by season at HSB and watershed 18 and 27 at Coweeta during the sampling periods. (For HSB: 1991–1992; For Coweeta: 1989–1991).

Although the depth distribution of enchytraeid biomass (AFDW m^{-2}) differed significantly for CT and NT (0–5 cm depth NT>CT; 5–15 cm depth

Table 2. Frequencies (in percentages) of Enchytraeidae genera found at HSB. Based on samples collected on 21 April, 1993

	No-tillage			Conventional tillage		
	0–5 cm	5–15 cm	0–15 cm	0–5 cm	5–15 cm	0–15 cm
Fridericia sp.						
Mature	31.8	45.1	39.3	25.0	31.4	29.1
Juvenile	55.6	22.0	36.6	37.5	21.4	27.3
Enchytraeus sp.						
Mature	1.6	1.2	1.4	2.5	1.4	1.8
Juvenile	7.9	19.5	14.5	15.0	5.7	9.1
Marionina sp.						
Mature	3.2	3.7	3.4	—	2.9	1.8
Juvenile	—	4.9	2.8	—	17.1	10.9
Acheata sp.						
Mature	—	—	—	10.0	7.1	8.2
Juvenile	—	2.4	1.4	10.0	12.9	11.8
Mesenchytraeus sp.						
Juvenile	—	1.2	0.7	—	—	—
Total number (n)[a]	63	82	145	40	70	110

[a]Area = 0.01 m^2.

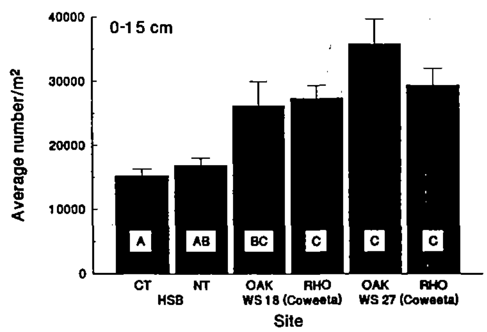

Fig. 2. The overall average abundance of enchytraeids at the 6 sampled sites. Different letters in the bars indicate significant differences at $p<0.05$ (ANOVA/Tukey).

CT>NT) (Fig. 4) no significant differences were found between the two tillages when their total biomasses (0–15 cm) were compared. In summer, AFDW m^{-2} was at a minimum of $\approx$ 200 mg m^{-2} at both depths in NT and CT. Combining the data of Figures 3 and 4 we concluded that at both depth intervals individual enchytraeids had lower biomass in summer than in other seasons. No significant differences were found in the AFDW per enchytraeid between the 2 tillage systems.

Based on the relative frequencies of enchytraeid genera at HSB (Table 2), it appeared that *Fridericia* sp. were more common in NT than CT soils. *Fridericia* sp. are often large worms, which can carry a high quantity of soil in their gut. Smaller enchytraeids such as *Achaeta* sp. and *Marionina* sp. were more common in CT soils.

The seasonal variation in enchytraeid densities at the Coweeta sites is shown in Figure 5. During winter and spring significantly more enchytraeids were found in WS 27 than WS 18, most of them occurring in the upper 5 cm. The high organic matter content of the upper soil layer, particularly at WS 27 (Table 1) is probably responsible for this difference in abundance at the 2 depths. Significant seasonal differences were found in WS 27 under oak at the upper depth, where densities were low in the fall and high in the spring. At the 5–15 cm depth, densities of enchytraeids were significantly higher under oak at WS 27 than at the other Coweeta sites in spring. No seasonal differences in AFDW m^{-2} at were present at Coweeta (Fig. 6). A quantitative analysis of the enchytraeid community was not completed at Coweeta, due to difficulties in identifying many of the juvenile organisms. The genera identified from a qualitative study performed in August 1991, were *Fridericia, Cognettia, Achaeta, Marioni-*

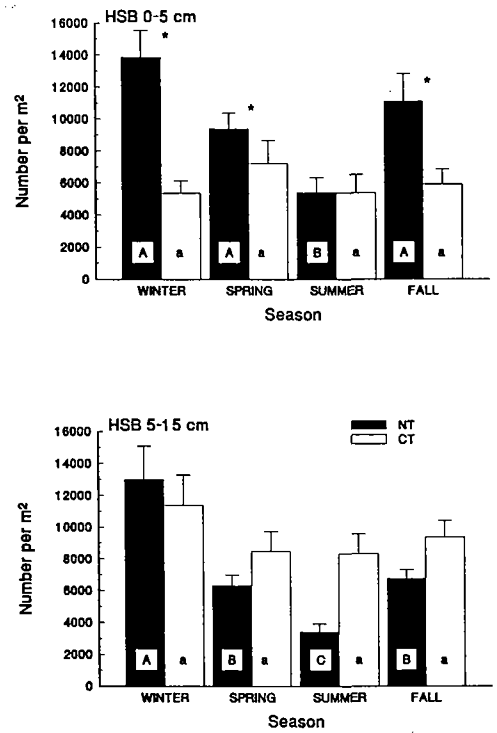

Fig. 3. The average number of Enchytraeidae per m^2 in No-Tillage (NT) and Conventional Tillage (CT) soils at HSB by season. Significant seasonal differences ($p<0.05$) for each ecosystem are shown with different letters in the bars (capital letters for NT, small letters for CT). An '∗' indicates that NT and CT are significantly different within season and depth ($p<0.05$).

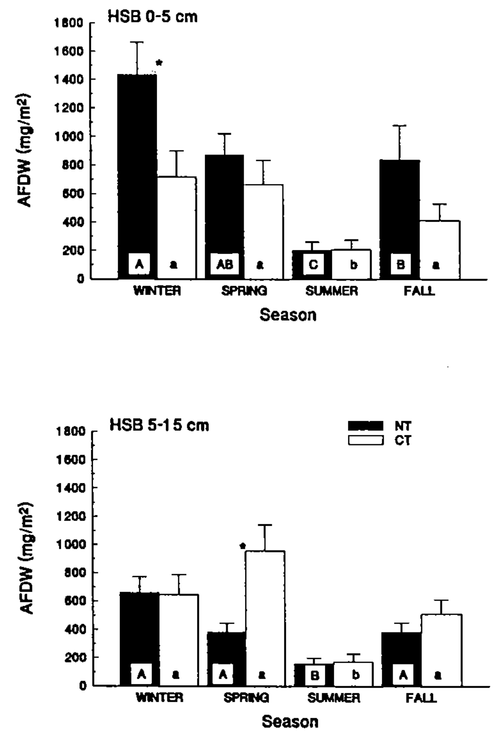

Fig. 4. Enchytraeid Ash Free Dry Weight (AFDW) in mg m^{-2} in No-Tillage (NT) and Conventional (CT) soils at HSB per season Significant seasonal differences ($p<0.05$) for each ecosystem are shown with different letters in the bars (capital letters for NT, small letters for CT). A significant difference between NT and CT within season and depth is indicated by an '∗'.

na, *Mesenchytraeus*, *Guaranidrilus*, *Hemienchytraeus* and *Bryodrilus*.

Discussion

On average, enchytraeid density was significantly lower at HSB than at Coweeta (Table 3). The high carbon content of the soil, and the cooler and wetter climate made Coweeta a more favorable habitat for enchytraeids than HSB (O'Connor, 1957). The densities at HSB are higher than in most other agricultural soils (e.g. Didden, 1991; Ryl, 1977; Willard, 1974). No significant correlations were found between seasonal rainfall (Fig. 1), seasonal minimum and maximum temperature and enchytraeid densities at HSB. Notably, during the summer period, enchytraeid densities decreased significantly in NT, while in CT no seasonal effects were present. However, the relative distribution of enchytraeids with depth in NT did not change markedly (i.e. density 0–5 cm/density 5–15 cm): Fall 1.7; Spring 1.5; Summer 1.6; Winter 1.1). Although significant correlations between soil moisture and enchytraeid density at the 0–5 cm (Pearson Correlation Coefficient = 0.69; $p<0.06$) and 5–15 cm depths (Pearson Correlation Coefficient = 0.66; $p<0.08$) were found, the decrease in overall (0–15 cm) abundance in the summer in NT cannot be explained by soil moisture alone. Differences in depth distribution of enchytraeids between NT and CT are mainly due to organic matter distribution in the soil. In CT organic matter is more evenly distributed throughout the soil profile, while more of the organic matter is concentrated near the surface in NT. According to Whitfield (1977), MacLean (1980) and Didden (1991), enchytraeids can be considered as 80 % microbivorous and 20 % saprovorous. The lower density of enchytraeids in the NT in the summer might be attributed to a combination of factors, including fluctuations in microbial activity, soil moisture and temperature as well as other biotic activity. The higher microbial activity associated with buried residues may be primarily responsible for the generally higher and

Table 3. A comparison of selected enchytraeid measurements between the different ecosystems[a]. Total depth of coverage is 15 cm

	HSB[b]	Coweeta WS 18[c]	Coweeta WS 27[c]
Number m^{-2}	16051a	2681b	32630 b
AFDW m^{-2} (mg)[d]	1125.9	732.6	828.4
Ash wt. m^{-2} (mg)	497.8	101.1	89.8
AFDW/enchytraeid (μg)	69.0	36.7	30.1
Ash wt./enchytraeid (μg)	32.5	5.5	3.6
Mineral soil transported (g m^{-2} yr^{-1})	2180	443	393
No. of sampling dates	22	6 (10 for number m^{-2})	

[a]Values followed by different letters within each measurement are significantly different at $p<0.05$. The absence of letters indicates no significant differences between sites.
[b]CT and NT combined.
[c]Oak and rhododendron combined.
[d]AFDW = Ash Free Dry Weight.

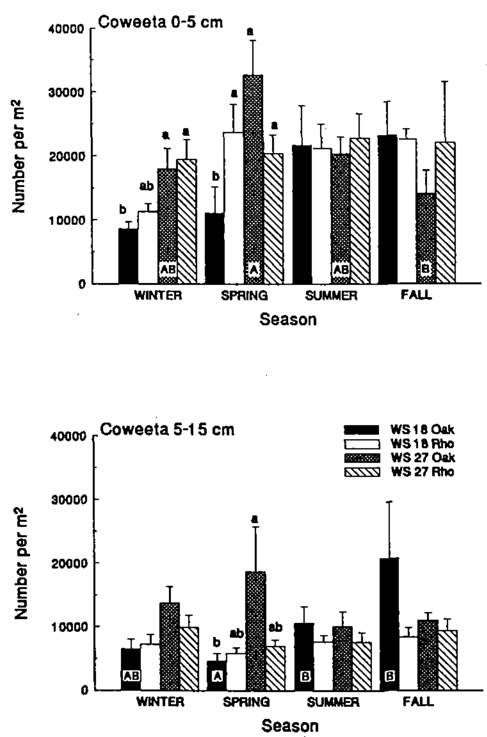

Fig. 5. The number of Enchytraeidae per m^2 per season under rhododendron (Rho) and oak at watershed 18 (WS 18) and 27 (WS 27) at Coweeta. Significant seasonal differences ($p<0.05$) for an ecosystem are shown with different letters in the bars. Significant differences between the different ecosystems within season and depth are indicated by letters above the bars.

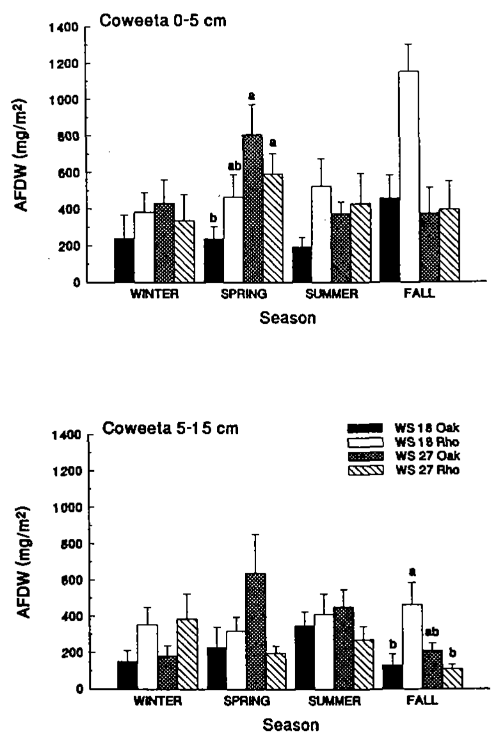

Fig. 6. Enchytraeid Ash Free Dry Weight (AFDW) in mg m^{-2} per season under rhododendron (Rho) and oak at watershed 18 (WS 18) and 27 (WS 27) at Coweeta. No significant seasonal differences ($p<0.05$) for the ecosystems were present. Significant differences between the different ecosystems within season and depth are indicated by letters above the bars.

less variable numbers of enchytraeids at the 5–15 cm depth in CT.

Many studies have shown that enchytraeid abundance is high in organic matter rich soils, and that it is strongly influenced by environmental conditions (e.g. O'Connor, 1957; Peachey, 1963). Organic matter content and environmental conditions also influence the vertical distribution of enchytraeids. More enchytraeids were found in the 0–5 cm layer, which contained significantly more carbon than the 5–15 cm layer at the 4 Coweeta sites and in the NT field at HSB (Table 1).

Although watershed 27 contained far more organic matter than watershed 18 (Table 1), only in the winter and spring were significantly more enchytraeids present. Therefore we conclude that not only organic matter content, but also other factors affect enchytraeid abundance. No overall significant differences were found between the oak and the rhododendron sites at the 2 watersheds. Apparently the difference in litter quality and microclimate does not affect enchytraeid abundance although, it may have affected species abundance. More information about the species composition at these sites is needed before further conclusions can be drawn.

Our findings for the Coweeta forests can be compared to few studies, due to the very different climatic conditions at Coweeta relative to other sites. During this study WS 18 and WS 27 at Coweeta received 2190 and 2730 mm of precipitation per year, respectively (average from Jan. 1989 till Dec. 1991). The average air temperature during the sampling period was 14 °C and 13 °C for WS 18 and WS 27, respectively. According to O'Connor (1957) seasonal trends in enchytraeid numbers can be predicted from climatological data. In a temperate oceanic climate, soil moisture would be sufficient for reproduction during the complete year, resulting in a generally high density of enchytraeids, which would be decreasing in winter, due to temperatures too low for reproduction. A south continental climate would have low abundances in summer and fall when temperature are too high and moisture too low to be suitable for reproduction. Maximum densities would occur in winter and spring. Coweeta's climate is classified as Marine Humid Temperature (Critchfield, 1966), with mild temperatures and high rainfall (Fig. 1). Because of the rainfall distribution during the year soil moisture will not be a limiting factor for enchytraeid reproduction. However, in winter temperatures are low, resulting in lower densities at both watersheds.

The AFDW biomass and ash wt. of enchytraeids per m^2, as well as average enchytraeid AFDW and Ash wt. did not significantly differ between HSB and watersheds 18 and 27 at Coweeta (Table 3), due to low summer values at HSB. For all other seasons, these parameters were significantly higher at HSB compared to Coweeta.

Although enchytraeid densities at HSB were one-half to one-third as high as those at Coweeta, AFDW per enchytraeid was much higher at HSB, resulting in a larger AFDW m^{-2} at HSB. Applying an average gut passage time of 2 h to the enchytraeid populations recovered in this study, we estimate that enchytraeids from HSB pass 4.9 to 5.5 times more soil than those under rhododendron or oak canopies at Coweeta. Based on these estimates, enchytraeids transported 1 %, 0.4 and 0.5 of the soil volume (0–15 cm) at HSB and WS 18 and 27 at Coweeta, respectively. These estimates are 40 to 100 times higher than those of Didden (1990), which can be attributed to two facts. First of all, Didden's method of determining the amount of mineral material in the gut was not as accurate as the ashing method, therefore he probably underestimated the amount of soil transported by enchytraeids. Secondly, the enchytraeid community at HSB was composed for more than 50 percent of large *Fridericia* enchytraeids, which can contain large quantities of soil in their guts. Marinissen and Didden (1994) collected excrements of *Buchholzia appendiculata* Buchholz 1862 enchytraeids, which were kept in small microcosms under laboratory conditions during a six week period. They estimated that the enchytraeids (at least 6900 m^{-2},) ingested at least 655 g of soil per m^2 per year. Their determination underestimated the amount of ingested soil because only excrements on top of the soil were collected.

Based on our findings we hypothesize that enchytraeids have a larger influence on soil structure in agricultural fields than in forested areas, in spite of their lower population densities. It is also apparent that abundance estimates alone are not sufficient to draw conclusions about the importance of enchytraeids for soil processes.

No major conclusions can be drawn from the genera lists for these sites. Both inventories are based on a one time sampling and additional inventories are necessary to link AFDW per enchytraeid with the size and presence of certain genera (species). The richness of enchytraeid genera appears to be higher at Coweeta than at HSB. This is also true for other organisms; conventionally tilled agricultural soils often have a lower soil fauna diversity than mature forest or grassland ecosystems (e.g., Altieri, 1991; Crossley et al., 1992).

More information about the biology and ecology of enchytraeids is needed. Accurate estimates of species specific gut transit times, effects of temperature and moisture changes on activity and feeding patterns and taxonomic inventories from a broad range of ecosystems are lacking. This knowledge is necessary to determine if AFDW per enchytraeid and ash wt. per enchytraeid can be used as "indicator" parameters for understanding the influence of enchytraeids on soil structure.

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