Pedobiologia 50 (2006) 301–306

Available online at www.sciencedirect.com
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Pedo biologia
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Collembola population levels 7 years after installation of the North Carolina Long Term Soil Productivity Study

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Received 15 July 2005; accepted 27 March 2006

KEYWORDS
Collembola;
Forest soil;
Population dynamics;
Organic matter removal

Summary

Collembola are among the most abundant microarthropods in terrestrial ecosystems and have been shown to affect litter decomposition and nutrient release rates. Previous work on the Croatan National Forest Long Term Soil Productivity (LTSP) study indicated organic matter removal and vegetation control treatments affected collembolan populations. The present study isolated important factors within these treatments and determined if differences in collembolan populations by treatment persisted over time. Collembolans were extracted from litter and enumerated on both a per area and volume basis for 1 year. Litter volume, quality, and nutrient concentration, in addition to treatment effects of organic matter removal, soil compaction and vegetation control were tested against numbers of Collembola. Organic matter removal and vegetation control treatments had a significant negative effect on populations during the late spring, summer, and early fall months, whereas compaction had no significant effect. Physical litter characteristics, nitrogen, phosphorous, and carbon to nitrogen ratio were consistently significantly correlated to collembolan populations. Results indicate removal of the fermentation and humus (F, H) layers not only decrease the volume of living space but also make Collembola more susceptible to dry periods, and this effect continues even after reestablishment of the forest floor litter.

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Introduction

In many terrestrial ecosystems Collembola are the most abundant microarthropods (Hopkins, 1997) and, whereas the order is considered

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0031-4056/$ - see front matter Published by Elsevier GmbH.
doi:10.1016/j.pedobi.2006.03.002

omnivorous as a whole, a large number of species are classified as fungivores or detritivores (Hopkins, 1997; Filser, 2002). As widespread and abundant occupants of the detritivore niche, collembolans are critical to litter decomposition and nutrient turnover processes in forest ecosystems. Because Collembola affect decomposition and nutrient cycling processes, it is important to understand the environmental factors and site practices that affect their population levels. For example, Ponge et al. (2003) reported changes in Collembola abundance and diversity as a result of different land use, while Axelsen and Kristensen (2000) detected an increase in collembolan populations when green manure was introduced. Collembola abundance and litter decomposition rates decreased in Appalachian hardwood stands that had been clear-cut 8 years previous (Blair and Crossley, 1988). In this study, we investigate the effects of organic matter removal and soil compaction during pre-establishment of a loblolly pine plantation, and post-establishment vegetation control on the abundance of collembolans 7 years after stand establishment. Additionally, we examine the relationship of Collembola populations to litter quantity, quality, and nutrient levels. The Long Term Soil Productivity (LTSP) Study is an international undertaking designed to quantify the effects of organic matter removal, soil compaction and vegetation control on forest productivity (Powers et al., 1990) and provides an excellent venue for this study.

Materials and methods

Site description

The study site is located on the Croatan National Forest in eastern North Carolina, USA. This LTSP study was installed in 1992 using a $3 \times 3 \times 2$ factorial, split-plot design replicated in three randomized complete blocks. Main effect treatments are three levels of organic matter removal (bole only (OM0); whole tree (OM1); whole tree plus forest floor (OM2)) and three levels of soil compaction (none (C0); moderate (C1); severe (C2)). Each 0.4 ha main plot is split in half, with the split-plot treatments being no competitive vegetation control (H0) and total competitive vegetation control (H1). The three levels of soil compaction and organic matter removal were chosen to bracket disturbances, from minimal to extreme, typical of harvest operations and the vegetation control treatment was included to provide information about plant growth potential on the site (Powers et al., 1990). Application of treatments is further described in Eaton et al. (2004). This region is part of the lower coastal plain and typically has cool winters and hot, humid summers. Mean yearly rainfall is 1385 mm and the mean yearly temperature is approximately 17 °C (Goodwin, 1989). The soil in block one is classified as predominantly Goldsboro (Fine-loamy, siliceous, thermic Aquic Paledults; moderately well-drained) and the soil in blocks two and three as Lynchburg (Fine-loamy, siliceous, thermic Aeric Paleaquults; somewhat poorly drained). Loblolly pine (*Pinus taeda* L.) 1–0 seedlings were hand-planted on a 3×3 m spacing in late winter 1991.

Sampling and analysis

Litter samples were collected from each split-plot treatment monthly from February 1998 through January 1999. Previous sampling at this site indicated that Collembola were primarily located in the litter layer (Eaton et al., 2004). Samples were collected from three randomly located points per split-plot treatment by cutting the forest floor along the inside of a 14.1×14.1 cm square frame. The depth of the litter layer was measured at the middle of each side of the frame and used to estimate sample volume. Samples were kept separate by sample point. Collembola and other microarthropods were extracted by drying each sample under a 15 W incandescent bulb placed over a modified Berlese funnel for 10 days. Extracted microarthropods were stored in an 85% aqueous ethanol solution. Limited resources required that Collembola be examined as an order and were sorted out and counted using a dissecting microscope. Except for February samples, litter was weighed after the extraction and sub-sampled for nutrient [carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg)] content and concentration, adjusted for mineral soil content using loss on ignition. Litter quality was based on the C/N ratio per sample. Litter density was estimated using dry weight/estimated volume. Collembolan abundance was calculated by area and by volume for each sample.

Analysis of variance using SAS® for Windows, version 9.1 (SAS Inc, Cary, NC, 2002) tested treatment effects on normalized (square root+1) population counts (Steele and Torrie, 1980). All data shown are the actual counts while ANOVA statistical significance tests are based on normalized data at $P \leqslant 0.05$ level. ANOVA was conducted to determine main and split-plot treatment effects on monthly collembolan abundance, forest floor characteristics (depth, volume, weight, density, and quality), and nutrient status measured in concentration (%) and content (grams). The mean of the untransformed monthly Collembola densities were correlated with mean of the forest floor characteristics values and nutrient status using Kendall's correlation ($n = 54$).

Results

Organic matter removal significantly affected abundance of Collembola both by area for March–January, and volume for May–October (Figs. 1a and b). Abundance of Collembola in the OM2 treatment was consistently lower than in the other two treatments; there was no consistent trend in abundance between the OM0 and OM1 treatments by area or by volume. Soil compaction was a significant factor on Collembola abundance by volume only for August and September (Figs. 2a and b). Vegetation control significantly impacted abundance of collembolans by area during July–October but only in July by volume basis during the same time period (Figs. 3a and b). In each case, Collembola numbers on the H0 plots became higher in June and generally stayed higher for the rest of the year.

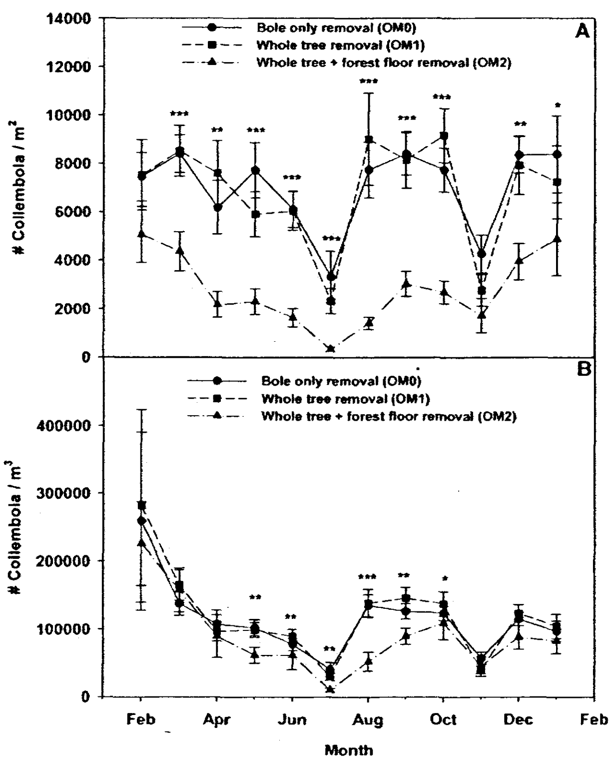

Figure 1. Monthly Collembola population levels at bole only (OM0), whole tree (OM1), and whole tree and forest floor (OM2) removal treatments per sample area (1A) and sample volume (1B). ***Significant difference at 0.001, **0.01, *0.05 levels.

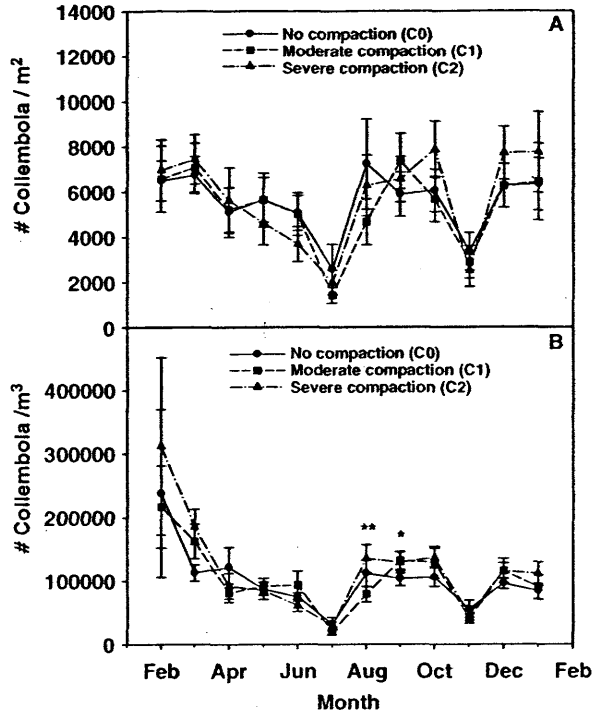

Figure 2. Monthly Collembola population levels at no (C0), moderate (C1), and severe (C2) compaction treatments per sample area (2A) and sample volume (2B). ***Significant difference at 0.001, **0.01, *0.05 levels.

Litter depth, weight, and volume were significantly affected by OM and vegetation control treatments. Litter characteristic results (litter depth, weight, and volume) were very similar and only litter volume data are presented. (Figs. 4 and 5). Litter from the OM2 treatments was significantly lower ($P<0.05$) in N and P concentrations, all nutrient content, and litter volume for nearly all months while the C/N ratio was significantly higher in the OM2 litter for nearly all months (data not shown). The litter from the H0 treatments was consistently higher than the H1 treatments in litter volume (Fig. 5) and N and P concentrations and had a lower C/N ration for nearly all months (data not shown). There were no consistent significant interaction effects in the ANOVAs (data not shown).

Although litter depth, weight, and volume, were significantly correlated ($P<0.05$) with numbers of Collembola for all months only litter volume is reported (Table 1). Other than N and P, litter nutrient concentrations were not consistently

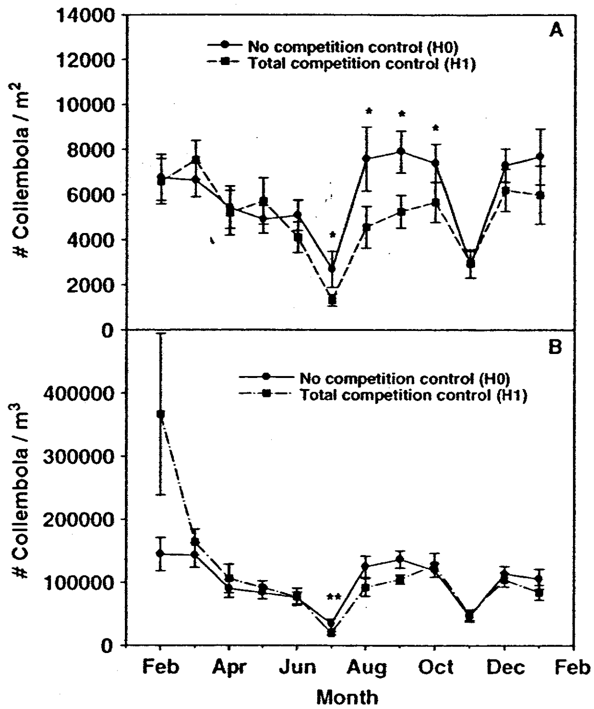

Figure 3. Monthly Collembola population levels at no (H0) and total (H1) competitive vegetation control treatments per sample area (3A) and sample volume (3B). ***Significant difference at 0.001, **0.01, *0.05 levels.

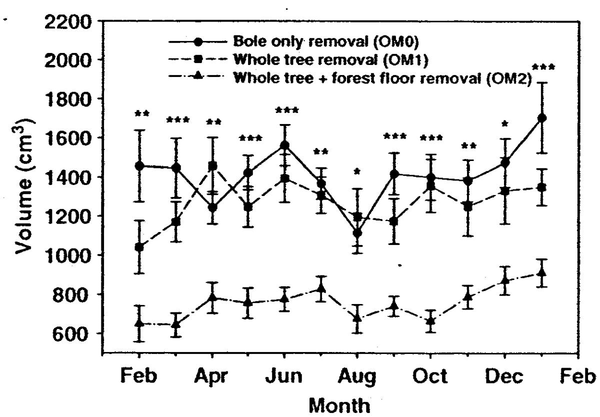

Figure 4. Monthly litter volume at bole only (OM0), whole tree (OM1), and whole tree and forest floor (OM2) removal treatments. ***Significant difference at 0.001, **0.01, *0.05 levels.

significantly correlated ($P<0.05$) with Collembola populations. Nitrogen and P concentrations were significantly correlated with collembolan abundance for all months except November and April, July, and December, respectively (Table 1). Litter quality, as measured by the ratio of carbon to nitrogen, was significantly negatively correlated

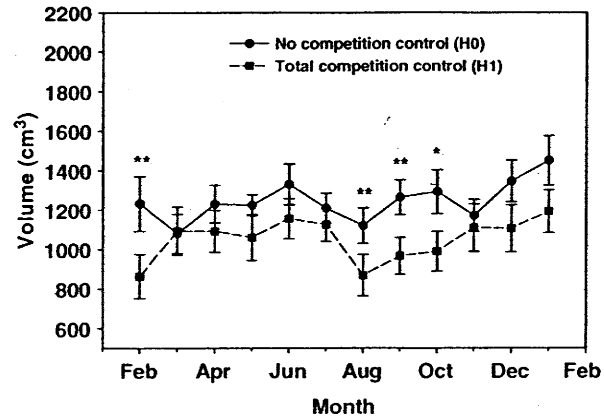

Figure 5. Monthly litter volume at no (H0) and total (H1) competitive vegetation control treatments. ***Significant difference at 0.001, **0.01, *0.05 levels.

Table 1. Uncorrected Kendall correlation values (τb and $P>r$) on mean untransformed Collembola abundance ($N=54$)

Month	% N	% P	C/N	Litter volume
Feb	–	–	–	0.3951
				<0.0001
March	0.2728	0.1987	−0.2406	0.3858
	0.0036	0.0341	0.0103	<0.0001
April	0.2838	0.1608	−0.4264	0.4736
	0.0025	0.0862	<0.0001	<0.0001
May	0.1843	0.2516	−0.1534	0.5471
	0.0497	0.0074	0.1022	<0.0001
June	0.3464	0.2582	−0.3828	0.5784
	0.0002	0.0059	<0.0001	<0.0001
July	0.3451	0.1824	−0.4041	0.5307
	0.0002	0.0523	<0.0001	<0.0001
Aug	0.3356	0.2405	−0.3663	0.6102
	0.0003	0.0103	0.0005	<0.0001
Sept	0.2820	0.3590	−0.4811	0.5492
	0.0029	0.0002	<0.0001	<0.0001
Oct	0.3887	0.2908	−0.3244	0.5095
	<0.0001	0.0019	0.0005	<0.0001
Nov	0.1540	0.2310	−0.2940	0.5427
	0.1007	0.0138	0.0017	<0.0001
Dec	0.5094	0.0943	−0.4382	0.5571
	<0.0001	0.3139	<0.0001	<0.0001
Jan	0.3439	0.3607	−0.3565	0.5151
	0.0002	0.0001	0.0001	<0.0001

with collembolan populations for all months except May (Table 1).

Discussion

We consistently observed lower numbers of Collembola in the plots that had the lowest litter amounts (OM2 treatment plots). The population trends on a per volume basis indicate differences in abundance are due to more than a simple reduction in the litter layer. These results support Wolters (1998) when he hypothesized annual fluctuations in Collembola densities could be the result of temperature effects on litter quality and quantity. Collembola are generally sensitive to relative humidity levels, preferring environments of high humidity (Christensen, 1964). Higher per volume populations in the OM0 and OM1 treatments reflect the application of the treatments, which generally left the forest floor layer intact and undisturbed. Following total removal of the forest floor (OM2), time was required for this material to re-accumulate and form the humus (H) and fermentation (F) layers. Both the F and H layers contain a high level of nutrients and provide protection from desiccation due to their higher moisture contents and resistance to moisture loss (Fisher and Binkley, 2000). Although there was no direct measurement of the forest floor material by layers, visual inspections indicated that only a thin layer of the F material had formed on the OM2 plots. Takeda (1995) hypothesized that Collembola vertically migrate to escape drought. Thus, lower per volume populations in the OM2 during the months of May–October may likely be the result of the reduction or absence of the layers that protect Collembola against the intense heat of summer. In addition, the F and H layers provide conditions favorable for colonization by bacteria and fungi. Because many Collembola rely on fungi and bacteria as a food, there is additional pressure on Collembola populations when these layers are removed or reduced. Although direct measurements of fungal and bacterial populations were not made, these results are consistent with those of Ponge (1993) and Chagnon et al. (2000) who describe variation of collembolan species abundance with changes in soil and vegetation conditions.

Higher nutrient contents for litter in the OM0 and OM1 plots, compared with the OM2 plots may also be a factor in collembolan population differences between the organic matter removal treatments. There was consistent correlation between litter nitrogen and, to a lesser extent, phosphorous concentrations and collembolan population levels for nearly all months (Table 1). Axelsen and Kristensen (2000) and Kaneda and Kaneko (2002) also reported a correlation between nutrient levels and Collembola populations. Choi et al. (2002) hypothesized that Collembola that were well-fed had a higher tolerance to periods of low soil moisture.

The spike in abundance of collembolans per area in the February sampling period is a result of aggregation in some of the smaller volumes. Previous measurements indicated that daytime litter temperatures on OM2 sites were warmer in the winter than on the OM0 and OM1 treatments (Eaton et al., 2004). We hypothesize that the thinner patches warmed quickly under direct sunlight and provided "islands" suitable for activity. The spikes in February appear to reflect these occurrences.

Soil compaction treatments significantly affected the abundance of Collembola on a per volume basis during August and September but there were no easily identifiable trends in the data. These results are similar to findings from an earlier study (Eaton et al., 2004). Soil bulk density measurements taken immediately post-treatment indicated a significant difference increase in bulk density on the treated plots. Although these differences had disappeared by year five (Dumrose-Page et al., 2006), soil compaction does not seem to have influenced collembolan abundance. Previous surveys on the site found few Collembola in the soil and, although the compaction treatment was applied over the forest floor when present, there is no evidence compaction affected the forest floor.

Differences in F and H layer development in response to vegetation control treatments further support the hypothesis that the F and H layers are critical in providing habitat for Collembola. The greater numbers of collembolans in the H0 plots during the months of August–October on an area basis (Figs. 3a and b) may be due to a significant difference in litter volume that also occurs during those months (Fig. 4). Although there was a difference in populations on a per volume basis it was not significant, except for July. Calculations on a per volume basis remove the impact of litter volume rather than that of the F and H layers and, thus, it is apparent that presence of these layers is important to the abundance of collembolans during these months.

Significant effects of the organic matter removal treatment on abundance of Collembola were evident 7 years after the organic matter removal treatments were applied. There is strong evidence that the effect is a result of the depth of the forest floor. Restoration of organic matter does not immediately ameliorate severe disturbance of the forest floor with regard to Collembola. Whereas gross measurements of forest floor depth and volume indicated a positive relationship with abundance of Collembola, the F and H layers are also needed to provide protection and a substrate for the food source for Collembola to thrive, especially during the warmer months. Although vegetation control is beneficial for tree growth, faster accumulation of forest floor on H0 plots corresponded to higher abundances of collembolans. Soil compaction did not affect litter-dwelling Collembola in any consistent way; possibly because compaction affected the mineral soil rather than the forest floor. Although it is not possible to discount nutrient content, concentration, or litter quality as factors impacting Collembola, they did not have a strong correlation to collembolan populations in this experiment. Additional research should focus on the relationship between the F and H forest floor layers and nutrient contents on Collembola and their contribution to decomposition and mineralization.

Acknowledgments

The author wishes to acknowledge the following people: Thomas Christensen; Susan Cohen; Damien Sherling; and Karen Sarsony for their help in field and lab work, Drs. Mary Barberchek; Kim Ludovici; Alex Mangini; Felipe Sanchez; and two unknown reviewers for their thoughtful comments, and Stan Zarnoch for his statistical advice.

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