Biol Fertil Soils (2017) 53:563–571
DOI 10.1007/s00374-017-1200-6

ORIGINAL PAPER

Effect of Collembola on mineralization of litter and soil organic matter

Min Wang[1,2,3] · **Weixin Zhang**[4] · **Hanping Xia**[1] · **Jinhua Huang**[5] · **Zhifeng Wu**[6] · **Guoliang Xu**[6]

Received: 26 September 2016 / Revised: 20 March 2017 / Accepted: 30 March 2017 / Published online: 19 April 2017

Abstract Although soil Collembola are known to contribute to soil carbon (C) cycling, their contribution to the mineralization of C sources that differ in bioavailability, such as soil organic C (SOC) and leaf litter, is unknown. Stable C isotopes are often used to quantify the effects of both soil C and litter C on C mineralization. Here, ^{13}C-labeled litter was used to investigate the effects of Collembola (*Folsomia candida*) on the mineralization of both SOC and litter C in laboratory microcosms. The three microcosm treatments were soil alone (S); soil treated with δ^{13}C-labeled litter (SL); and soil treated with δ^{13}C-labeled litter and Collembola (SLC). The presence of Collembola did not significantly affect soil microbial biomass or litter mass loss and only had a small effect on CO_2 release during the first week of the experiment, when most of the CO_2 was derived from litter rather than from SOC. Later, during the experiment (days 21 and 63), when litter-derived labile C had been depleted and when numbers of Collembola had greatly increased, Collembola substantially increased the emission of SOC-derived CO_2. These results suggest that the effect of Collembola on soil organic C mineralization is negatively related to C availability.

Keywords Collembola · Stable isotope · C mineralization · C availability

✉ Guoliang Xu
xugl@gzhu.edu.cn

[1] South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China

[2] Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, China

[3] University of Chinese Academy of Sciences, Beijing 100049, China

[4] College of Environment and Planning, Henan University, Kaifeng 475001, China

[5] Postdoctoral Scientific Research Stations, Chinese Academy of Agricultural Engineering, Beijing 100125, China

[6] School of Geographical Sciences, Guangzhou University, Guangzhou 510006, China

Introduction

Collembola and other soil fauna play essential roles in the transformation of soil organic matter and in nutrient cycling (Rusek 1998). Although their direct contribution to energy flow is small, Collembola have a large indirect effect on the soil ecosystem (Petersen 2002; Ponge 2015) because they can regulate soil respiration, the leaching of dissolved organic carbon (C), and the mineralization of nitrogen (N) (Filser 2002; Ke et al. 2005; Lussenhop and BassiriRad 2005; Neher et al. 2012). However, the effects of Collembola on mineralization and stabilization of soil organic C (SOC) are poorly known. Microbial respiration and microbial biomass, for example, were increased (Addison et al. 2003; Coleman et al. 2004; Cragg and Bardgett 2001) or not affected by Collembola (Kaneda and Kaneko 2008; Kaneko et al. 1998).

According to the availability of C, the C pool in soil can be divided into stabilized C, potentially mineralizable C, and readily mineralizable C, and soil organisms can enhance the transformation of potentially mineralizable C into readily mineralizable C (Zhang et al. 2013).The contributions of soil fauna to C dynamics may be greatly affected by resource availability and/or quality. For instance, Yang and Chen (2009) reported that soil fauna enhanced soil organic C (SOC) decomposition to a greater extent in systems with less available resource (Yang and Chen 2009). Earthworms had a greater effect on the transformation of less labile C, such as SOC and litter C, than on the transformation of readily

mineralizable C, such as the C in root exudates (Huang et al. 2015). Therefore, we wondered whether C availability also regulates the effects of Collembola on C transformations in soil. Given that labile C content may decrease and recalcitrant C content may increase over time as a C source incubates in soil, we hypothesized that Collembola would promote microbial activity and stimulate C mineralization of both litter C and SOC with the depleting of available C during an incubation experiment. We used a microcosm experiment to test this hypothesis in the current study. The use of labeled litter is a general method (Vidal et al. 2016, 2017) to distinguish between litter- and soil-derived C in emitted CO_2. We chose the typical soil and typical leaf at an evergreen broad-leaf forest in subtropical China to evaluate the effect of Collembola on litter C and SOC mineralization.

Materials and methods

Soil, litter, and Collembola

Mineral soil, collected (0–10 cm) from a pine and broad-leaf mixed forest at the Dinghushan Biosphere Reserve (Guangdong Province, subtropical S China: 112° 10′ E, 23° 10′ N), is classified in the Ultisol group and Udult subgroup according to the USDA soil classification system (Huang et al. 2013); soil samples were air-dried, sieved (<2 mm) and sterilized in autoclaving at 121 °C for 30 min. The soil is a typical evergreen broad-leaf forest soil of subtropical China and had the following characteristics: pH 3.54, SOC 5.96%, and soil readily oxidized organic C (ROC after oxidation with 333 mM KMnO4) 1.31%.

Leaf litter of *Schima superba* (Gardner & Champ), a common plant of subtropical China, was used. *S. superba* seedlings were grown in pots in a growth chamber. When the seedlings were 50-cm high, they were transferred to greenhouse. From 12:00 hours to 13:00 hours every day for 7 days, $^{13}CO_2$ (99 atom% ^{13}C, Cambridge Isotope Laboratories, Inc., USA) was pumped into the greenhouse atmosphere. Fully expanded leaves were then collected, oven-dried, and chopped into small pieces (2-3 mm), which were used as the litter in the experiment. The $\delta^{13}C$ value of this litter was 1151.54‰. The method used to determine the $\delta^{13}C$ value is described below. The Collembola *Folsomia candida* was cultured in the laboratory on dried yeast (Løkke 1998).

Microcosms

Microcosms consisted of 150-ml beakers containing 100 g of soil (dry weight), which was dry when placed in the beakers. The 36 microcosms were placed in a plastic container (10.5-cm internal diameter × 12-cm height, one microcosm per container), that could be sealed with airtight lids. A 50-ml beaker with 20 ml 1 M NaOH was also placed in each container which was sealed. The NaOH was used to adsorb evolved CO_2 (see "CO_2 emission" section). To inoculate the soil with an assemblage of microorganisms, 30 g of fresh soil were mixed with 300 ml of sterile water. After most of the soil particles had settled, the supernatant was passed through a 23-μm sieve to permit the passage of microorganisms; then, 10 ml were added to each microcosm. An additional 30 ml of sterile water were then added to each microcosm to increase the water content to 60% of maximum holding capacity. The soil water content was maintained constant by weighing each beaker and adding sterile water as needed every other week. A 1-g quantity of labeled litter ($\delta^{13}C$ = 1151.54‰) was placed on the soil surface of each of 24 of the 36 microcosms. Thirty mature Collembola (*F. candida*) were then added to 12 of the microcosms that contained litter. The experiment included three treatments: soil alone (S), soil treated with $\delta^{13}C$-labeled litter (SL), and soil treated with $\delta^{13}C$-labeled litter and Collembola (SLC). Each treatment was replicated 12 times, microcosms were incubated in a climate chamber under the darkness at 25 °C. Four replicate microcosms of each treatment were destructively sampled at 7, 21, and 63 days.

Analyses

CO_2 emission

The CO_2 evolved from each microcosm was trapped in the 20 ml 1 M NaOH. Every 2 weeks, the NaOH was exchanged and the trapped CO_2 was measured by titration with 0.5 M HCl after carbonate was precipitated with 5 ml saturated $BaCl_2$ solution. To determine the $\delta^{13}C$ values of carbonate, the solution with the precipitate was transferred to 50-ml centrifuge tubes. The tubes were shaken by hand and centrifuged for 2 min at 2500×*g*. After centrifugation, the supernatant was discarded, and the tubes with pellets of $BaCO_3$ were immediately filled again with H_2O and then closed, shaken, and centrifuged (2500×*g*). This washing procedure was repeated until the pH of the supernatant was 6.8–7.0, thereby preventing further trapping of CO_2 from the air. The samples were then dried in an oven at 80 °C for 48 h (Marhan et al. 2007); $\delta^{13}C$ values were measured with an IsoTope 100 stable isotope ratio gas mass spectrometer, IsoPrime, UK.

Sampling of soil, litter, and Collembola

Before a microcosm was destructively sampled, the litter was carefully removed from the soil surface, dried at 60 °C, and then pulverized in a ball mill. We considered a homogenous distribution of Collembola in the microcosms; the soil of each microcosm was then vertically divided into two parts: one part was used for extraction of Collembola, and the other part was used for analysis of microbial phospholipids fatty acids (PLFAs), SOC,

and ROC. Collembola were extracted using Tullgren dry funnels for 48 h; the extracted specimens were stored in alcohol and then counted. PLFAs were analyzed as described by Bossio and Scow (1998). Concentrations of each PLFA were standardized relative to the 19:0 internal reference concentration. Bacterial biomass was represented by i14:0, i15:0, i16:0, a15:0, i17:0, a17:0, 15:0 3OH, 16:1 2OH, 16:1ω5c, 16:1ω9c, 18:1ω5c, 18:1ω7c, 18:1ω9c, cy17:0, cy19:0, 14:0, 15:0, 17:0, and 18:0 and fungal biomass was represented by 18:2ω6,9 and 18:3ω6,9,12c (Baath 2003; Bossio and Scow 1998; Frostegard et al. 2011). The ratio of cy17:0 to 16:1ω7c was used to indicate the activity of bacteria, with the higher ratio values indicating bacterial stress (Grogan and Cronan 1997). SOC and ROC were analyzed by the $K_2Cr_2O_7$ oxidation-external heating method and by the $KMnO_4$ oxidation method, respectively (Blair et al. 1995, 1997).

Identification of the C sources in released CO_2 using stable isotopes

When *n* isotope systems are used to determine the proportional contributions of $n + 1$ sources to a mixture, standard linear mixing models can be used to mathematically solve for the unique combination of source proportions that conserves mass balance for all *n* isotopes (Phillips and Gregg 2003). In our study, with one isotope system and two sources (C from litter and C from soil organic carbon), the following mass balance equation can be solved to determine the proportions (f_{litter}, f_{soil}) of source isotopic signatures (δ_{litter}, δ_{soil}) that coincide with the observed signature as the

$$\delta_{CO2} = f_{litter} \times \delta_{litter} + f_{soil} \times \delta_{soil} \quad (1)$$

and

$$f_{litter} + f_{soil} = 1 \quad (2)$$

where f_{litter} and f_{soil} refers to the proportion of litter-derived and soil-derived CO_2, respectively; and δ_{litter} and δ_{soil} refers to the isotope abundance ($\delta^{13}C$) of litter and soil, respectively.

Statistics

To assess the effect of Collembola on mineralization of litter, mineralization of SOC, and soil microbial PLFAs, we used a one-way ANOVA, with litter dry weight being the dependent variable, and repeated measures ANOVAs, with ROC, PLFAs, CO_2, and $\delta^{13}C$ values of CO_2 being the dependent variables. When ANOVA gave significant differences, we also determined differences among means using LSD post hoc multiple comparisons. The significance level in all analyses was $P < 0.05$. All data passed the homogeneity of variance test, and all statistical analyses were carried out using SPSS 16.0. Figures were drawn with Origin 2016.

Results

Collembola numbers were about 17-fold higher on days 21 and 63 than on days 0 and 7 (Fig. 1). By day 63, litter mass on the soil surface had declined by about 33% but the decline was unaffected by Collembola ($F = 0.011$, $P = 0.918$, Fig. 2). During the whole experiment, the C content of the litter did not change significantly ($F = 0.832$, $P = 0.489$, Fig. 3a), whereas the N content of the litter significantly increased from 1.76 ± 0.07% on day 0 to 2.66 ± 0.41% on day 63 ($F = 105$, $P < 0.01$, Fig. 3b). There were no significant differences in C or N contents of litter (% C: $F = 0.005$, $P = 0.947$; % N: $F = 1.138$, $P = 0.297$, Fig.3), or in C/N ratio of litter between microcosms with or without Collembola ($F = 1.126$, $P = 0.299$, Fig. 4).

Bacterial biomass did not significantly differ among the three treatments during the incubation ($F = 1.944$, $P = 0.205$, Fig. 5a). Although fungal biomass differ significantly at different sampling time ($F = 7.177$, $P = 0.014$, Fig. 5b) it did not differ significantly among the three treatments (day 7: $F = 1.291$, $P = 0.321$; day 21: $F = 0.641$, $P = 0.549$; day 63: $F = 1.138$, $P = 0.362$; Fig. 5b). At any sampling time, soil microbial biomass did not significantly differ among the three treatments ($F = 0.312$, $P = 0.740$; Fig. 5c), but ratio of fungal biomass to bacterial biomass differ significantly at different sampling time ($F = 6.024$, $P = 0.030$, Fig. 5d). The ratio of cy17:0 to 16:1ω7c did not differ among treatments during the incubation ($F = 0.897$, $P = 0.441$; Fig. 6).

The presence of Collembola and litter did not significantly affect the SOC content of microcosms (data not shown) ($F = 0.591$, $P = 0.547$). The ROC content did not differ among treatments on day 7 but it did differ among treatments on day

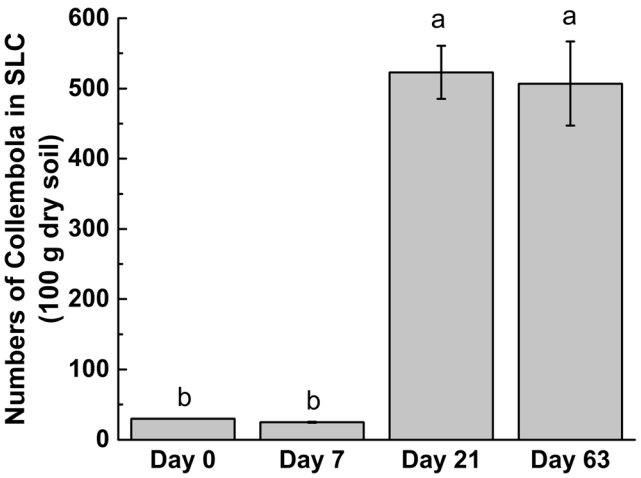

Fig. 1 Collembola numbers in soil microcosms, containing $\delta^{13}C$-labeled litter (treatment SLC) as affected by incubation time. This is an estimation value according to the number of Collembola in a part of soil of the microcosm. Values are means ± SE ($n = 4$). Means with the different letters are significantly different ($P < 0.05$)

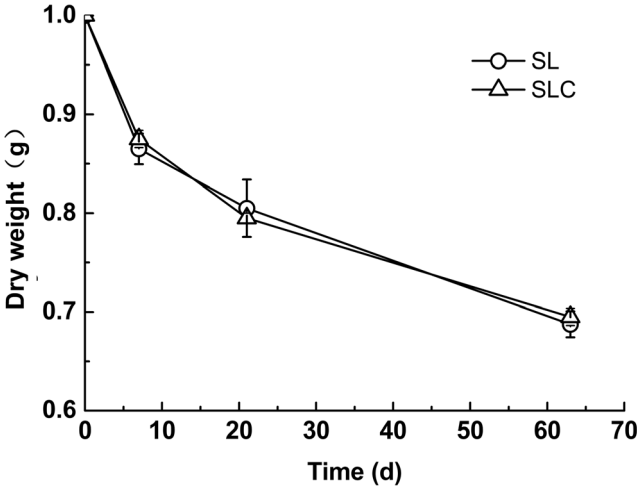

Fig. 2 Changes in litter mass remaining on the soil surface of soil treated with δ^{13}C-labeled litter (SL); and soil treated with δ^{13}C-labeled litter and Collembola (SLC). Values are means ± SE (n = 4)

21 (F = 158, P < 0.01), when the ROC content was significantly increased in S microcosms, unchanged in SL microcosms and decreased in SLC microcosms (Fig. 7). ROC content did not differ among treatments on day 63, but the ROC content increased when litter was added and again when litter and Collembola were added. ROC content in SL and SLC microcosms were significantly higher on day 63 than on day 21.

The cumulative release of CO_2 showed significant difference among treatments (F = 96, P < 0.01, Table 1). Early during the incubation, CO_2 emission rate was much greater in SL and SLC microcosms than in S microcosms (Fig. 8). CO_2 emission rate did not significantly differ between SL and SLC microcosms before day 35 but then it was higher in SLC microcosms than in SL microcosms, perhaps because numbers of Collembola had greatly increased during this period.

The δ^{13}C values of CO_2 were significantly higher in SL and SLC microcosms than S microcosms but this difference gradually decreased over time (F = 1012.14, P < 0.01, Fig. 9). The δ^{13}C values of CO_2 did not significantly differ between SL and SLC microcosms at days 7 to 21. But the δ^{13}C values was lower in SLC than in SL microcosms from day 35 to the end of experiment and this suggests that increases in numbers of Collembola were associated with a decrease in the proportion of litter-derived C in the CO_2 emission.

According to the amount (mg of C) of CO_2 and f_{litter} and f_{soil} values, we calculated the amounts (mg of C day^{-1}) of litter- and soil-derived CO_2 and the net effect of Collembola (Table 2). This indicated that soil organisms other than Collembola mineralized the litter-derived C and that most of the litter-derived CO_2 was generated by soil organisms other than Collembola. In other words, Collembola had little effect on litter-derived CO_2. The net contribution of Collembola to soil-derived CO_2 was substantial on day 63 (Table 2). In others, the net effect of Collembola to the mineralization of soil C was about 0 on day 7 but increased to 26% on day 21 and to 24.16% on day 63. In other words, Collembola substantially increased the emission of soil-derived C with the incubation time.

Discussion

In our experiment, the Collembola *F. candida* had no significant effect on the C and N contents and thus to C/N ratio in the microcosms. The Collembola also had no effect on litter mass loss or litter C mineralization. These results are consistent with previous studies (Andren and Schnurer 1985; Aslam et al. 2015; Chamberlain et al. 2006). Because *F. candida* is a fungivorous (Chahartaghi et al. 2005; Haubert et al. 2006; Scheu and Simmerling 2004), it does not directly assimilate C from litter but indirectly affects litter decomposition by feeding on microorganisms and by altering the soil microenvironment (Addison et al. 2003; Filser 2002). In other studies, however, mechanical fragmentation of litter, which was done in the current research, facilitated the interaction between

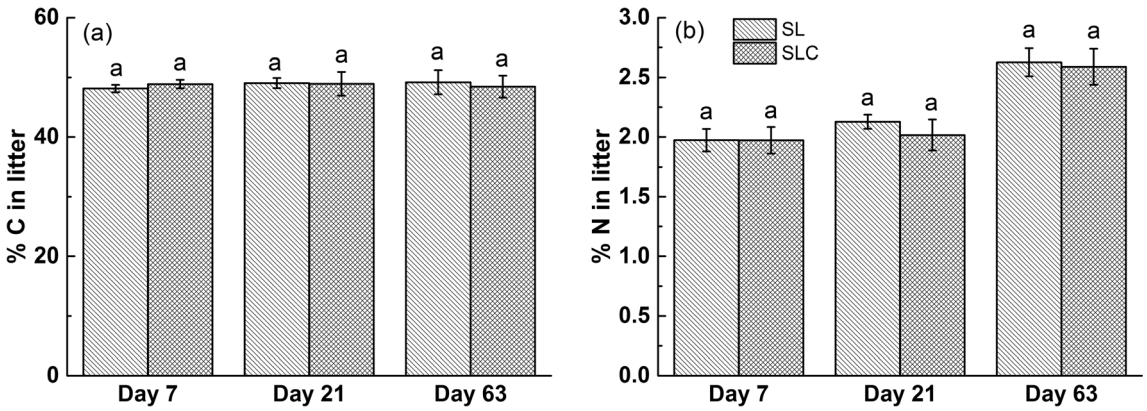

Fig. 3 The C (**a**) and N contents (**b**) of litter of soil treated with δ^{13}C-labeled litter (SL); and soil treated with δ^{13}C-labeled litter and Collembola (SLC). Values are means ± SE (n = 4). Means with the different letters are significantly different (P < 0.05)

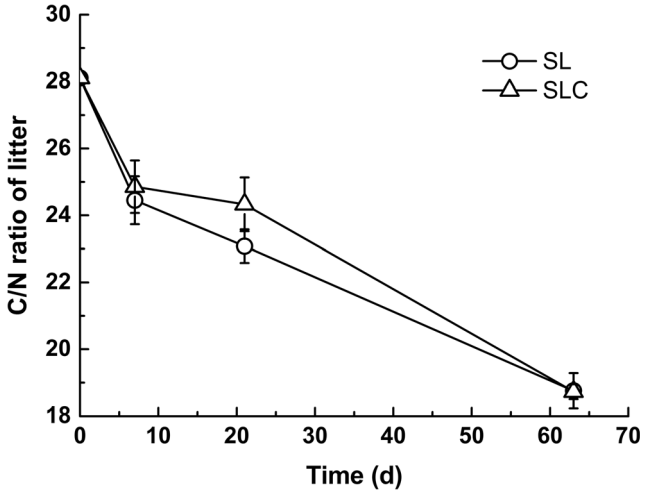

Fig. 4 Changes in C/N ratio of litter of soil treated with δ^{13}C-labeled litter (SL) and soil treated with δ^{13}C-labeled litter and Collembola (SLC). Values are means ± SE (n = 4)

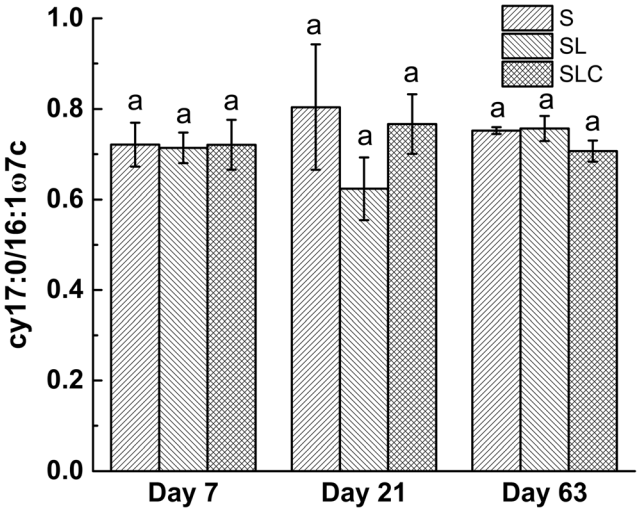

Fig. 6 The ratio of cy17:0 to 16:1ω7c in soil (S); soil treated with δ^{13}C-labeled litter (SL); and soil treated with δ^{13}C-labeled litter, and Collembola (SLC). Values are means ± SE (n = 4). Means with the different letters are significantly different ($P < 0.05$)

Collembola and microorganisms, which in turn accelerated litter decomposition (Hunter et al. 2003; Pieper and Weigmann 2008; Seeber et al. 2006; Yang et al. 2012). However, the litter used in our study was not obtained from senescence leaves. The nutrient content of the litter was higher than the dead leaves, especially the content of phosphorus (Gusewell and Verhoeven 2006; Liu et al. 2007). The difference on litter may explain these differences. Thus, whether Collembola indirectly accelerate litter decomposition this might depend on litter quality and Collembola species.

We also found that CO_2 emissions at day 7 were mainly derived from the litter. In previous reports, C was mineralized more rapidly from litter than from SOC (Kuzyakov 2011;

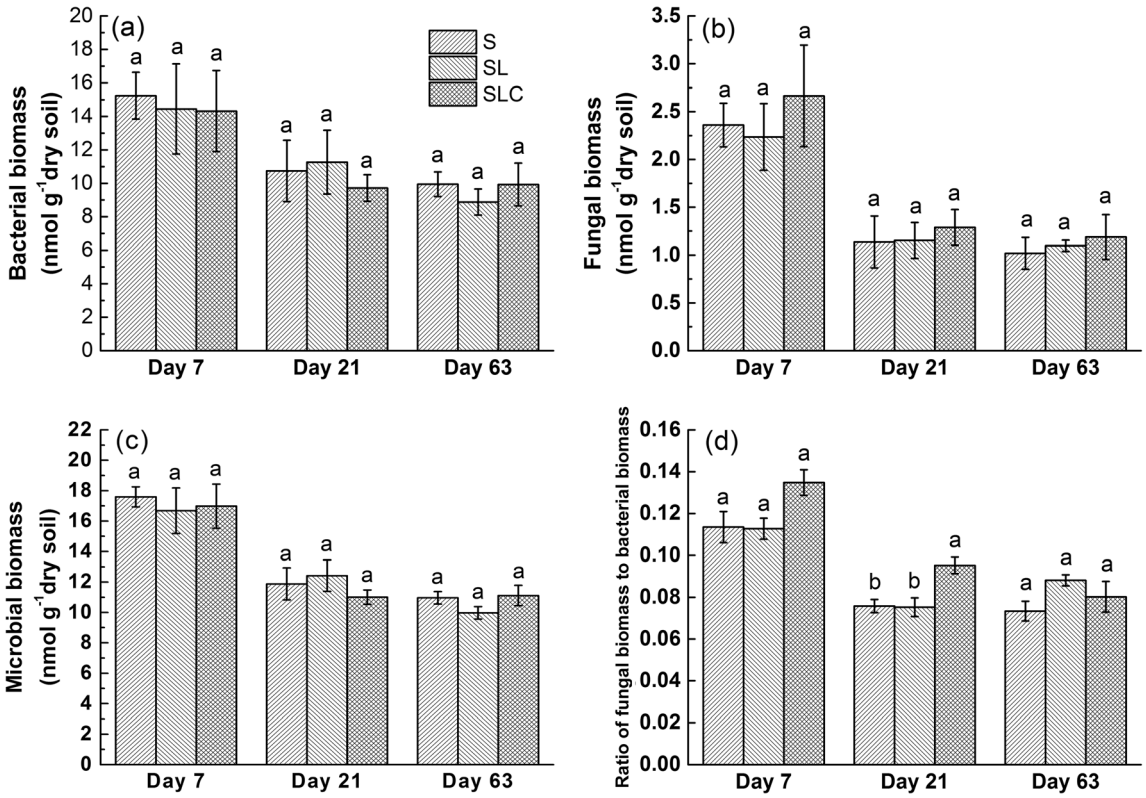

Fig. 5 Bacterial biomass (**a**), fungal biomass (**b**), total microbial biomass (**c**), and ratio of fungal biomass to bacterial biomass (**d**) in soil (S); soil treated with δ^{13}C-labeled litter (SL); and soil treated with δ^{13}C-labeled litter, and Collembola (SLC). Values are means ± SE (n = 4). Means with the different letters are significantly different ($P < 0.05$)

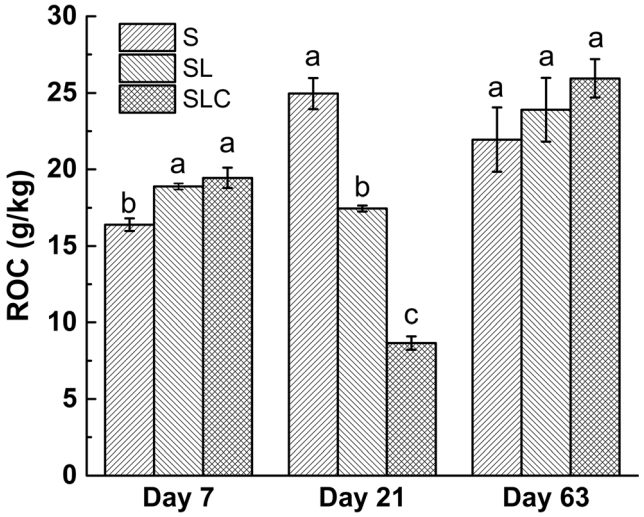

Fig. 7 The content of readily oxidized organic C (ROC) in soil (S); soil treated with δ^{13}C-labeled litter (SL); and soil treated with δ^{13}C-labeled litter, and Collembola (SLC). Values are means ± SE (n = 4). Means with the different letters are significantly different (P < 0.05)

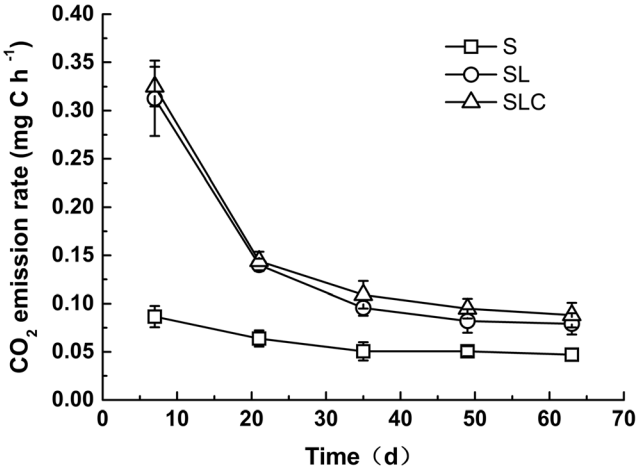

Fig. 8 Changes in CO_2 emission rate in soil (S); soil treated with δ^{13}C-labeled litter (SL); and soil treated with δ^{13}C-labeled litter, and Collembola (SLC). Values are means ± SE (n = 4)

Pausch and Kuzyakov 2012; Schlesinger and Lichter 2001). Because our results indicated that litter decomposition was not directly affected by *F. candida*, we infer that most of the litter mass loss and C mineralization was caused by microbial decomposition of the available C in the litter.

Along with mites, Collembola constitute an important mesofauna component of almost all terrestrial ecosystems (Rusek 1998). Collembola can increase nutrient cycling, improve soil physical and chemical characteristics, regulate soil microbial composition, and enhance soil fertility (Chen et al. 2007). However, their direct contribution to energy flow is limited and they mostly appear to have indirect effects on soil processes (Petersen 2002). In previous studies, for example, Collembola affected soil C turnover mainly by affecting soil structure and microbial activity (Addison et al. 2003; Cragg and Bardgett 2001; Endlweber et al. 2009; Lavelle 1997). In our study, Collembola had no significant effect on the total C pool in soil, but they affected ROC and the relative quantities of C in the different C pools, and also enhanced the mineralization of soil-derived C. In SL microcosms on day 21, soil microorganisms may have preferentially used litter C rather than SOC. In SLC microcosms on day 21, litter C was also preferred by soil microorganisms and Collembola; meanwhile, the numbers of Collembola had greatly increased and may have mineralized soil-derived C and thereby decreased ROC. At day 63, when the labile C in soil had been depleted and Collembola numbers were also high, Collembola would transfer soil C from stable to more labile pools. Thus, the increased content of ROC occurred at day 63 when Collembola numbers were high, suggesting that the Collembola may have increased the release of soil-derived C by increasing the pool of labile C in soil. Because Collembola promoted the release of soil-derived C, they reduced the δ^{13}C values of CO_2 from days 35 to 63 (Fig. 9). Previous studies (Fox et al. 2006; Johnson et al. 2005) also found that Collembola enhanced the mineralization of soil C. For example, Fox et al. (2006) confirmed that cumulative CO_2 emissions from soil were significantly increased when Collembola were present and that this resulted from the transfer of soil C from stable to more labile pools.

Table 1 Cumulative CO_2 respired from microcosms over the 63-day experimental period. Values are means (SE) (n = 4). Different letters indicate significant differences (P < 0.05)

Microcosm	Cumulative CO_2(mg C–CO_2)
S (soil)	86.0 (10.5)b
SL (soil and litter)	181.0 (13.4)a
SLC (soil, litter, and Collembola)	199.1 (12.9)a

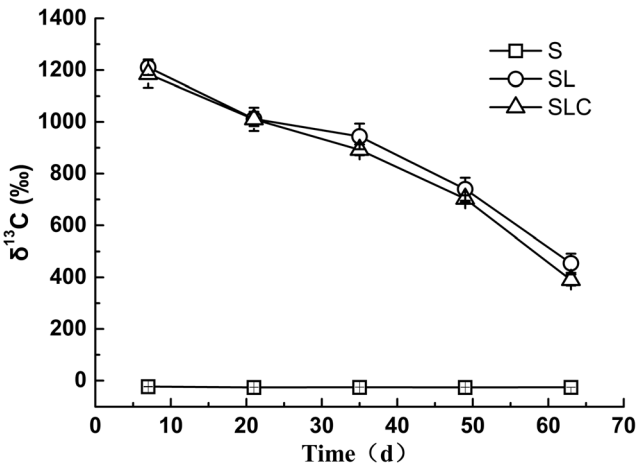

Fig. 9 The δ^{13}C values of CO_2 in soil (S); soil treated with δ^{13}C-labeled litter (SL); and soil treated with δ^{13}C-labeled litter, and Collembola (SLC). Values are means ± SE (n = 4)

Table 2 Effects of Collembola on litter- and soil-derived CO_2 (mg C day^{-1}) on days 7, 21, and 63. SL microcosms contain soil and $\delta^{13}C$-labeled litter. SLC microcosms contain soil, $\delta^{13}C$-labeled litter, and Collembola. Values are means (SE) ($n = 4$)

	$CO_{2litter}$			CO_{2soil}		
Microcosm	Day 7	Day 21	Day 63	Day 7	Day 21	Day 63
SL (with litter)	7.85	2.84	0.79	0	0.37	1.13
	(0.36)	(0.31)	(0.38)	(0)	(0.18)	(1.00)
SLC (with litter and Collembola)	8.04	2.84	0.80	0	0.50	1.49
	(0.36)	(0.74)	(0.57)	(0)	(0.26)	(0.47)
Net effect of Collembola (%)	2.36	0	1.25	0	26	24.16
	(0.05)	(0)	(0.85)	(0)	(1.5)	(0.24)

In this study, we did not measure the respiration of Collembola, and thus could not quantify the contribution of Collembola to C mineralization. Some studies had shown that Collembola respiration accounts for 1% of total soil respiration (Coulson and Whittaker 1978), while Collembola respiration may not be ignored when the population size of Collembola, e.g., in this study, was much greater than those in common soil situations. Thus, we made a rough calculation of the Collembola respiration according to dataset from literatures (Lagerlöf and Andrén 1985; Persson et al. 1980). However, the estimated respiration of Collembola was even bigger than the total soil respiration. So, we are wondering whether this method of respiration estimation of Collembola is suitable to our laboratory experiment. Another laboratory experiment found that CO_2 flux did not differ between soils with and without abundant Collembola (5 individuals g^{-1} dry soil) (Chamberlain et al. 2006). Therefore, it was also possible that the respiration of a large-sized population of Collembola still accounted for a small part of the total respiration. Nevertheless, the aim of this study is to evaluate the effects of Collembola presence on C mineralization, rather than an estimation of Collembola respiration. It suggests that total C mineralization was controlled by C availability and conversion of soil C was enhanced by the soil food web. Litter addition at the start of our experiment increased microbial respiration rapidly probably due to the rapid mineralization of the labile C of the litter (Fig. 8). Also, during the early stages of incubation, CO_2 emissions were derived mostly from litter C rather than from SOC (Table 2). Later, during the incubation, however, C mineralization depended more on SOC than on litter C, especially when Collembola were present. Collembola can affect soil C processes by affecting soil physical, chemical, and microbiological properties (Addison et al. 2003; Filser 2002). Indeed the effects of Collembola on C and N mineralization may be mediated by their effects on microbial community composition (Kaneda and Kaneko 2008; Seastedt 1984; Teuben 1991).

Conclusions

Collembola significantly increased the mineralization of SOC at the late stage of incubation when litter labile C was depleted. There was no evidence that Collembola affected the litter decomposition rate or microbial biomass. In this study, we only focused on the effects of Collembola (*F. candida*) on the mineralization of SOC and leaves of an evergreen broad-leaf forest in subtropical China. Future studies should investigate the effects of Collembola on C processes in different types of soil and litter.

Acknowledgements The present study was supported by the National Natural Sciences Foundation of China (31270560, 41571247) and High Level University Construction Project of Guangdong Province (Regional Water Environment Safety and Water Ecological Protection).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Addison JA, Trofymow JA, Marshall VG (2003) Functional role of Collembola in successional coastal temperate forests on Vancouver Island. Canada Appl Soil Ecol 24:247–261. doi:10.1016/S0929-1393(03)00089-1

Andren O, Schnurer J (1985) Barley straw decomposition with varied levels of microbial grazing by Folsomia-Fimetaria (L) (Collembola, Isotomidae). Oecologia 68:57–62. doi:10.1007/Bf00379474

Aslam TJ, Benton TG, Nielsen UN, Johnson SN (2015) Impacts of eucalypt plantation management on soil faunal communities and nutrient bioavailability: trading function for dependence? Biol Fert Soils 51:637–644

Baath E (2003) The use of neutral lipid fatty acids to indicate the physiological conditions of soil fungi. Microbial Ecol 45:373–383. doi:10.1007/s00248-003-2002-y

Blair GJ, Lefroy RDB, Lise L (1995) Soil carbon fractions based on their degree of oxidation, and the development of a carbon management index for agricultural systems. Aust J Agric Res 46:1459–1466. doi:10.1071/Ar9951459

Blair GJ, Lefroy RDB, Singh BP, Till AR (1997) Development and use of a carbon management index to monitor changes in soil C pool size and turnover rate. In: Cadisch G, Giller KE (eds) Driven by nature: plant litter quality & decomposition. pp 273–282

Bossio DA, Scow KM (1998) Impacts of carbon and flooding on soil microbial communities: phospholipid fatty acid profiles and substrate utilization patterns. Microbial Ecol 35:265–278

Chahartaghi M, Langel R, Scheu S, Ruess L (2005) Feeding guilds in Collembola based on nitrogen stable isotope ratios. Soil Biol Biochem 37:1718–1725. doi:10.1016/j.soilbio.2005.02.006

Chamberlain PM, McNamara NP, Chaplow J, Stott AW, Black HIJ (2006) Translocation of surface litter carbon into soil by Collembola. Soil Biol Biochem 38:2655–2664. doi:10.1016/j.soilbio.2006.03.021

Chen JX, Ma ZC, Yan HJ, Zhang F (2007) Roles of springtails in soil ecosystem. Biodivers Sci 15:154–161. doi:10.1360/biodiv.060288

Coleman DC, Crossley DA, Hendrix PF (2004) Fundamentals of soil ecology (second edition)

Coulson JC, Whittaker JB (1978) Ecology of moorland animals. Springer, Berlin Heidelberg

Cragg RG, Bardgett RD (2001) How changes in soil faunal diversity and composition within a trophic group influence decomposition processes. Soil Biol Biochem 33:2073–2081. doi:10.1016/S0038-0717(01)00138-9

Endlweber K, Ruess L, Scheu S (2009) Collembola switch diet in presence of plant roots thereby functioning as herbivores. Soil Biol Biochem 41:1151–1154. doi:10.1016/j.soilbio.2009.02.022

Filser J (2002) The role of Collembola in carbon and nitrogen cycling in soil: proceedings of the Xth international colloquium on Apterygota, České Budějovice 2000: Apterygota at the beginning of the third millennium. Pedobiologia 46:234–245

Fox O, Vetter S, Ekschmitt K, Wolters V (2006) Soil fauna modifies the recalcitrance-persistence relationship of soil carbon pools. Soil Biol Biochem 38:1353–1363. doi:10.1016/j.soilbio.2005.10.014

Frostegard A, Tunlid A, Baath E (2011) Use and misuse of PLFA measurements in soils. Soil Biol Biochem 43:1621–1625. doi:10.1016/j.soilbio.2010.11.021

Grogan DW, Cronan JE Jr (1997) Cyclopropane ring formation in membrane lipids of bacteria. Microbiol Mol Biol Rev 61:429–441

Gusewell S, Verhoeven JTA (2006) Litter N: P ratios indicate whether N or P limits the decomposability of graminoid leaf litter. Plant Soil 287:131–143. doi:10.1007/s11104-006-9050-2

Haubert D, Haggblom MM, Langel R, Scheu S, Ruess L (2006) Trophic shift of stable isotopes and fatty acids in Collembola on bacterial diets. Soil Biol Biochem 38:2004–2007. doi:10.1016/j.soilbio.2005.11.031

Huang WJ, Liu JX, Wang YP, Zhou GY, Han TF, Li Y (2013) Increasing phosphorus limitation along three successional forests in southern China. Plant Soil 364:181–191. doi:10.1007/s11104-012-1355-8

Huang JH, Zhang WX, Liu MY, Briones MJI, Eisenhauer N, Shao YH, Cai X, Fu SL, Xia HP (2015) Different impacts of native and exotic earthworms on rhizodeposit carbon sequestration in a subtropical soil. Soil Biol Biochem 90:152–160. doi:10.1016/j.soilbio.2015.08.011

Hunter MD, Adl S, Pringle CM, Coleman DC (2003) Relative effects of macroinvertebrates and habitat on the chemistry of litter during decomposition. Pedobiologia 47:101–115

Johnson D, Krsek M, Wellington EMH, Stott AW, Cole L, Bardgett RD, Read DJ, Leake JR (2005) Soil invertebrates disrupt carbon flow through fungal networks. Science 309:1047–1047. doi:10.1126/science.1114769

Kaneda S, Kaneko N (2008) Collembolans feeding on soil affect carbon and nitrogen mineralization by their influence on microbial and nematode activities. Biol Fert Soils 44:435–442. doi:10.1007/s00374-007-0222-x

Kaneko N, McLean MA, Parkinson D (1998) Do mites and Collembola affect pine litter fungal biomass and microbial respiration? Appl Soil Ecol 9:209–213

Ke X, Winter K, Filser J (2005) Effects of soil mesofauna and farming management on decomposition of clover litter: a microcosm experiment. Soil Biol Biochem 37:731–738. doi:10.1016/j.soilbio.2004.10.005

Kuzyakov Y (2011) How to link soil C pools with CO_2 fluxes? Biogeosciences 8:1523–1537

Lagerlöf J, Andrén O (1985) Succession and activity of microarthropods and enchytraeids during barley straw decomposition. Pedobiologia 28:343–357

Lavelle P (1997) Faunal activities and soil processes: adaptive strategies that determine ecosystem function. Adv Ecol Res 27:93–132. doi:10.1016/S0065-2504(08)60007-0

Liu P, Sun OJ, Huang JH, Li LH, Han XG (2007) Nonadditive effects of litter mixtures on decomposition and correlation with initial litter N and P concentrations in grassland plant species of northern China. Biol Fert Soils 44:211–216. doi:10.1007/s00374-007-0195-9

Løkke H (1998) Handbook of soil invertebrate toxicity tests. John Wiley & Sons, Chichester

Lussenhop J, BassiriRad H (2005) Collembola effects on plant mass and nitrogen acquisition by ash seedlings (*Fraxinus pennsylvanica*). Soil Biol Biochem 37:645–650. doi:10.1016/j.soilbio.2004.08.021

Marhan S, Langel R, Kandeler E, Scheu S (2007) Use of stable isotopes (^{13}C) for studying the mobilisation of old soil organic carbon by endogeic earthworms (Lumbricidae). Eur J Soil Biol 43:S201–S208

Neher DA, Weicht TR, Barbercheck ME (2012) Linking invertebrate communities to decomposition rate and nitrogen availability in pine forest soils. Appl Soil Ecol 54:14–23. doi:10.1016/j.apsoil.2011.12.001

Pausch J, Kuzyakov Y (2012) Soil organic carbon decomposition from recently added and older sources estimated by δ13C values of CO2 and organic matter. Soil Biol Biochem 55:40–47

Persson T, Bååth E, Clarholm M, Lundkvist H, Söderström BE, Sohlenius B (1980) Trophic structure, biomass dynamic and carbon metabolism of soil organisms in a scots pine forest. Ecol Bull 32:419–459

Petersen H (2002) General aspects of collembolan ecology at the turn of the millennium: proceedings of the Xth international colloquium on Apterygota, České Budějovice 2000: Apterygota at the beginning of the third millennium. Pedobiologia 46:246–260

Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261–269. doi:10.1007/s00442-003-1218-3

Pieper S, Weigmann G (2008) Interactions between isopods and collembolans modulate the mobilization and transport of nutrients from urban soils. Appl Soil Ecol 39:109–126. doi:10.1016/j.apsoil.2007.11.012

Ponge JF (2015) The soil as an ecosystem. Biol Fert Soils 51:645–648. doi:10.1007/s00374-015-1016-1

Rusek J (1998) Biodiversity of Collembola and their functional role in the ecosystem. Biodivers Conserv 7:1207–1219. doi:10.1023/A:1008887817883

Scheu S, Simmerling F (2004) Growth and reproduction of fungal feeding Collembola as affected by fungal species, melanin and mixed diets. Oecologia 139:347–353. doi:10.1007/s00442-004-1513-7

Schlesinger WH, Lichter J (2001) Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO_2. Nature 411:466–469. doi:10.1038/35078060

Seastedt TR (1984) The role of Microarthropods in decomposition and mineralization processes. Annu Rev Entomol 29:25–46. doi:10.1146/annurev.en.29.010184.000325

Seeber J, Scheu S, Meyer E (2006) Effects of macro-decomposers on litter decomposition and soil properties in alpine pastureland: a mesocosm experiment. Appl Soil Ecol 34:168–175. doi:10.1016/j.apsoil.2006.02.004

Teuben A (1991) Nutrient availability and interactions between soil arthropods and microorganisms during decomposition of coniferous litter—a Mesocosm study. Biol Fert Soils 10:256–266. doi:10.1007/Bf00337376

Vidal A, Remusat L, Watteau F, Derenne S, Quenea K (2016) Incorporation of ^{13}C labelled shoot residues in Lumbricus terrestris

casts: a combination of transmission electron microscopy and nanoscale secondary ion mass spectrometry. Soil Biol Biochem 93:8–16

Vidal A, Quenea K, Alexis M, Tu TTN, Mathieu J, Vaury V, Derenne S (2017) Fate of ^{13}C labelled root and shoot residues in soil and anecic earthworm casts: a mesocosm experiment. Geoderma 285:9–18

Yang XD, Chen J (2009) Plant litter quality influences the contribution of soil fauna to litter decomposition in humid tropical forests, southwestern China. Soil Biol Biochem 41:910–918. doi:10.1016/j.soilbio.2008.12.028

Yang XD, Yang Z, Warren MW, Chen J (2012) Mechanical fragmentation enhances the contribution of Collembola to leaf litter decomposition. Eur J Soil Biol 53:23–31. doi:10.1016/j.ejsobi.2012.07.006

Zhang W, Hendrix PF, Dame LE, Burke RA, Wu J, Neher DA, Li J, Shao Y, Fu S (2013) Earthworms facilitate carbon sequestration through unequal amplification of carbon stabilization compared with mineralization. Nat Commun 4:324–327