



Use of radiocarbon to estimate diet ages of earthworms across different climate regions

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ABSTRACT

Natural abundance of radiocarbon (^{14}C) has been applied to estimate the turnover time of soil carbon (C) across different climate regions. However, despite the important functional role played by soil animals in decomposition processes, little is known about variation in their ^{14}C concentrations across different climate regions. In this study, we measured ^{14}C concentrations of earthworms collected in three forests in Japan. In addition, we also reviewed ^{14}C data on earthworms that were previously reported. We used these data to test whether the diet ages (defined as time elapsed since C in the diet of earthworms was fixed from atmospheric CO_2 by photosynthesis) differed according to feeding habits and across study sites in various climate regions ranging from cool temperate forest to tropical savanna. Multiple regression analysis showed that the diet ages of earthworms were significantly affected by both feeding habits and study sites. The diet ages of endogeic (soil-feeding) earthworms (8.3 ± 0.4 years, mean \pm SE) were significantly older than those of epigeic (litter-feeding) earthworms (2.6 ± 0.5 years), with anecic (litter-/soil-feeding) earthworms (5.7 ± 0.9 years) having intermediate diet ages. When mean diet age was compared for each feeding habit, only that of endogeic earthworms differed significantly across the sites. However, it did not necessarily become younger in warmer climate regions. These results either suggest that the degree of decomposition of soil organic matter used by earthworms differs among the study sites, or that the difference in the turnover time of soil organic C used by earthworms across the sites is relatively small and variable due to factors other than temperature, such as soil texture and vegetation.

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1. Introduction

An increasing number of studies have examined the temperature sensitivity of soil organic carbon (SOC) decomposition because of the potential feedback to increased temperature through enhanced decomposition of SOC, which is the largest carbon (C) pool in terrestrial ecosystems (Schimel et al., 1994; Ise and Moorcroft, 2006; von Lützow and Kögel-Knabner, 2009). Natural abundance of radiocarbon (^{14}C) produced by atmospheric nuclear bomb testing has been used as a global C tracer to study the dynamics of SOC (Trumbore et al., 1996; Koarashi et al., 2009; Trumbore, 2009). Some radiocarbon studies have shown that the low-density SOC fraction has a faster turnover time in warmer climates than in colder climates, and that the temperature sensitivity was greater in the low-density fraction than the heavy-density fraction of SOC (Trumbore et al., 1996; Davidson et al., 2000; Trumbore,

2000). Meanwhile, other studies using laboratory incubations have demonstrated the temperature sensitivity of stable SOC is higher than that of the labile SOC fraction (Fierer et al., 2003; Leifeld and Fuhrer, 2005); thus a consensus on this issue has not yet emerged (Davidson and Janssens, 2006; von Lützow and Kögel-Knabner, 2009).

Earthworms play an important role in the decomposition process (Swift et al., 1979; Coleman et al., 2004; Bardgett, 2005; Lavelle and Spain, 2005). In addition, they are among the most abundant soil animals in many terrestrial ecosystems and are important prey for many predators (Macdonald, 1983; Lee, 1985; Curry, 2004). Earthworms likely digest labile organic matter, such as carbohydrates and proteins, and possibly cellulose and simple phenolic compounds as well through enzymatic activities from ingested soil microbes and endogenous origin (Curry and Schmidt, 2007; Nozaki et al., 2009).

Radiocarbon has been used to investigate the feeding ecology of terrestrial consumer organisms including earthworms (Beavan and Sparks, 1998; Briones and Ineson, 2002; Hobbie et al., 2002; Tayasu et al., 2002). By using the decreasing trend in the ^{14}C concentrations

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in atmospheric CO₂, diet age can be estimated with a precision of one to a few years (Hua, 2009). Diet age is defined as the time elapsed since C in the diet was fixed from the atmosphere by primary producers (Hyodo et al., 2006). As such, the measurement of ¹⁴C concentrations in earthworms collected from various climate regions would enable to estimate the turnover time of labile SOC that they consume and its response to differences in climate regions. Note that estimation of diet age using ¹⁴C does not require a vegetation shift between C3 and C4 plants (Tayasu et al., 2002), which has been used to calculate turnover time of SOC and ages of organic matter used by soil animals based on differences in stable C isotopic signatures (Balesdent et al., 1987; Martin et al., 1992). A laboratory experiment using ¹⁴C has demonstrated that increased temperature enhances the use of old C by enchytraeids, possibly because of the increased use of non-labile C (Briones et al., 2007). However, little is known about the variation in ¹⁴C concentrations in soil invertebrates and their diet ages under field conditions across different climate regions. Previous studies reported that the diet ages of earthworms with the same feeding habits collected from a temperate deciduous forest in the United Kingdom and from gallery forest and tropical savanna in Ivory Coast did not show clear differences between sites; approximately 5 years for epigeic (litter-feeding) earthworms and 10 years for endogeic (soil-feeding) earthworms (Briones et al., 2005; Hyodo et al., 2008).

In this study, we measured ¹⁴C concentrations in earthworms and soil organic matter, with which the feeding habits of the earthworms had been previously investigated on the basis of habitat preference, gut content analyses, and stable isotopic analyses (Uchida et al., 2004). The samples were collected from three climate regions in Japan which cover cool temperate broad-leaved, temperate evergreen, and subtropical forests (Uchida et al., 2004). In addition, we reviewed existing ¹⁴C data on earthworms (Briones et al., 2005; Hyodo et al., 2008; Toyota et al., 2010). These ¹⁴C data allow us to investigate variation in diet ages in earthworms across different climate regions ranging from cool temperate forests to tropical savanna. We hypothesized that the earthworms would show lower contemporary ¹⁴C concentrations, and thus younger diet ages as the climate became warmer because the turnover time of the low-density SOC fraction, which earthworms probably utilize, decreases as temperature increases (Trumbore et al., 1996). These studies would provide insights into not only the feeding ecology of earthworms but also the time scale of C turnover in terrestrial ecosystems in which earthworms directly participate.

2. Materials and methods

2.1. Study sites and sample collection

Earthworms were collected at three forest sites in 2001 by Uchida et al. (2004; Table 1). The first site was Tomakomai Experimental Forest of Hokkaido University (TOEF (B)). The forest was a cool temperate broad-leaved forest, dominated by deciduous oak, *Quercus crispula*. The second site, Manazuru Forest for fish conservation (MFF), was a temperate evergreen forest, consisting of *Cinnamomum camphora*. The third was Yona University Forest, University of the Ryukyus (YONA), in the northern part of Okinawa Island. This forest was a subtropical evergreen forest covered mainly by *Castanopsis cuspidate* var. *sieboldii*. The soil types (FAO) were Regosols, Andosols, and Acrisols, for TOEF, MFF, and YONA, respectively.

The samples of earthworms, soil and litter examined by Uchida et al. (2004) were also used for this study. The earthworms were sampled by digging and hand-sorting from litter layer and soil (0–5 cm) at TOEF, from litter layer and soil (0–20 cm) at MFF, and from midden and soil (0–20 cm) at YONA. They were brought back

to a laboratory in a cooler box, washed with distilled water, and then identified. They were kept at –30 °C until freeze-dried, and were ground after removing the guts. Litter samples were randomly collected at TOEF and MFF sites. At YONA site, where a litter sample was unavailable, a litter sample from middens was used. Soil samples at depths of 0–5, and 10–15 cm at the three sites were used for radiocarbon analyses. Those samples were oven-dried at 65 °C for 72 h. Litter samples were ground in a food blender. Soil samples were sieved through a 2-mm mesh, ground using a ball mill, and treated with 0.5 N HCl to remove carbonates. Three individuals of each earthworm species, and one sample for litter and soil from each study site were used for radiocarbon analysis (Table 2).

To examine the variation in diet ages in earthworms across different climate regions, we compiled published data that include at least two feeding habits (endogeic, epigeic, or anecic) and at least two replicate individuals of the same feeding habits. We also confined the data on earthworms to those from study sites where a vegetation shift was not reported, because it could be a confounding factor affecting diet ages. The earthworms used in this study were collected at the following four sites (Table 1): woodland (LAN) at Lancaster University campus in the United Kingdom in 2002 and 2004 (Briones et al., 2005), tropical gallery forest (LAMT(GF)) and tropical savanna (LAMT(S)) in Lamto Reserve in Ivory Coast in 2001 (Hyodo et al., 2008), and a cool temperate conifer forest dominated by *Picea jezoensis* (TOEF(C)) in Tomakomai Experimental Forest of Hokkaido University in Japan in 2007 (Toyota et al., 2010). The earthworms species used for this study were as follows: LAN, epigeic: *Lumbricus rubellus*, *n* = 3, endogeic: *Allolobophora caliginosa*, *n* = 3; anecic: *Allolobophora longa*, *n* = 3; LAMT(GF), epigeic: *Dichogaster agilis*, *n* = 2, endogeic: *Dichogaster terrae-nigrae*, *n* = 1, *Eudrilidae* spp., *n* = 2, *Millsonia anomala*, *n* = 1; LAMT(S), epigeic: *Dichogaster baeri*, *n* = 3; endogeic: *Eudrilidae* spp., *n* = 3, *D. terrae-nigrae*, *n* = 1, *M. anomala*, *n* = 3; TOEF(C), epigeic: *Amyntas yunoshimensis*, *n* = 3, *Metaphire hilgendorfi*, *n* = 1, endogeic: *Eisenia japonica*, *n* = 3. Note that *A. longa* is classically defined as an anecic earthworm (Schmidt et al., 1997), but recent studies show that it could have endogeic characteristics (Eisenhauer et al., 2008; Thakuria et al., 2010). Different earthworm species with the same feeding habits in LAMT(GF), LAMT(S), and TOEF(C) were treated as one group for each site, because the diet ages did not vary greater than the analytical precision (one to a few years; Hua, 2009).

2.2. Radiocarbon analyses

For radiocarbon analysis, samples (estimated to produce approximately 2 mg C) were combusted in evacuated and sealed Vycor tubes with CuO, Cu, and Ag wire at 850 °C for 2 h. After cooling, the Vycor tubes were cracked on a vacuum line, and the CO₂ was cryogenically purified. The purified CO₂ was graphitized under Fe catalysis at 650 °C for 6 h (Kitagawa et al., 1993). The graphite samples were sent to Rafter Radiocarbon Laboratory, Institute of Geological and Nuclear Sciences, New Zealand, for accelerator mass spectrometry measurements of radiocarbon. ¹⁴C concentrations are reported as Δ¹⁴C (‰), which is the part per thousand deviation from the activity of 19th century wood, and corrected for fractionation using stable C isotope ratios of the samples (Stuiver and Polach, 1977). The average analytical error was ±4.9‰.

2.3. Diet age determination

We estimated diet age from the difference between the sample collection year (2001) and the year (*t*) when the Δ¹⁴C value of a sample matched that of atmospheric CO₂, as previously done by Hyodo et al. (2008). The year (*t*) was calculated using a regression curve, year (*t*) = 2074 – 16.71 ln(Δ¹⁴C), which was estimated based on ¹⁴CO₂ data for the northern hemisphere from 1977 to 1999

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