



Contrasting effects of nitrogen limitation and amino acid imbalance on carbon and nitrogen turnover in three species of Collembola

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ARTICLE INFO

Article history:

Received 6 July 2010

Received in revised form

3 December 2010

Accepted 7 December 2010

Available online 23 December 2010

Keywords:

Energy and nutrient budgets

Diet quality

Isotope patterns of amino acids

Nutritional resources

Soil detritivores

Stable isotopes

Tissue replacement

ABSTRACT

Soil animal detritivores play an important role in facilitating decomposition processes but little information is available on how the quality of dietary resources affects their stoichiometry of carbon (C) nitrogen (N) and phosphorus (P), and turnover of C and N. This study investigated how a fungal diet, *Fusarium culmorum*, with a low N content and imbalanced amino acid (AA) composition affected the physiology of three soil-dwelling collembolans (*Folsomia candida*, *Protaphorura fimata* and *Proisotoma minuta*) in comparison to a control diet, *Saccharomyces cerevisiae*, with a high N content and balanced AA composition. We compared the elemental composition of animals, their growth rates and tissue replacement of C and N. We also measured the individual AA $\delta^{13}\text{C}$ to investigate the extent that Collembola may rely on endogenous sources to compensate for scarcity of essential AAs. The results showed that animal's N content tracked closely the composition of their diets, decreasing from around 10 to 7% N from the high to low N diet. They also had a significant increase of C and a decrease of P. *P. fimata* was less affected than *F. candida* and *P. minuta*. The total incorporation of C and N in the animals due to growth and tissue replacement decreased from 11–17 to 6–12% DM d⁻¹ on the high and low N diet respectively with *P. fimata* experiencing the smallest change. Essential AAs $\delta^{13}\text{C}$ did not always match perfectly between Collembola species and their diets; particularly on the low N diet. Isotope patterns of AAs indicate that bacteria may have been the alternative source of essential AAs. While the results of this study cannot be extrapolated directly to the dynamics of Collembola populations in the field, they serve to demonstrate their flexibility in adapting physiologically to the temporal and spatial patchiness of the soil environment.

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1. Introduction

The role of consumers in total ecosystem function has traditionally been viewed within the context of energy flow (Lindeman, 1942; Odum, 1957; O'Neill, 1968) allowing ecologists to use a common currency for estimating how consumers influence ecosystem

function (Kitchell et al., 1979; Visser et al., 1981). The concept of energy flows has been widely used to characterize and understand interactions in the soil food web (Petersen and Luxton, 1982; de Ruiter et al., 1995; Lavelle et al., 1997) demonstrating that while the autotrophs are responsible for determining the amount of carbon that enters the system, animal detritivores play a crucial role in governing the availability of nutrients required for plant productivity. Detritivores primarily exert their influence by microbial grazing and by masticating and translocating organic matter (Ingham et al., 1986; Lussenhop, 1992; Coleman, 2008), and these activities are in most ecosystems regulated by bottom-up control, i.e. by the quality and availability of dietary resources (Wardle, 2002; White, 2008; Pollierer et al., 2010).

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The stoichiometry of dietary carbon (C), nitrogen (N) and phosphorus (P) is in combination with the composition of biochemical compounds key for the nutritional value of the diet (Sterner and Elser, 2002; Moe et al., 2005). The majority of dietary C, N and P is supplied to cell metabolism in the form of amines, phosphate ions, sugars and other simple compounds. In addition, animals also need essential complex compounds from the diet that they cannot synthesize from simple precursors. Quantitatively, the most important essential biochemical compounds are the essential amino acids and fatty acids. While the requirements and dietary routing of fatty acids in soil detritivores have received considerable attention in recent years (e.g. Ruess et al., 2002, 2007; Evans et al., 2003; Chamberlain et al., 2004, 2005; Pollierer et al., 2010) only little attention has been paid to the amino acids (Rothstein, 1963; Anderson et al., 1983; Pokarzhevskii et al., 1997). This is surprising since amino acids (AAs) unlike other nutrients must comprise a large proportion of the diet for the consumer to achieve maximum growth and fecundity (e.g. Lii et al., 1975; Bowen, 1984; Kleppel and Burkart, 1995; Ramsay and Houston, 1998; Guisande et al., 1999; O'Brien et al., 2003; Boëchat and Adrian, 2006). It is likely that dietary AA composition also affects physiology and food preference of soil detritivores, as is the case for dietary N content (Booth and Anderson, 1979; Bengtsson et al., 1985; Lavy and Verhoef, 1996a; Hogervorst et al., 2003; Jensen et al., 2006) and for other invertebrates (Ventura and Catalan, 2010). The link between N and AAs is important because the majority of animal's N content is in the form of AAs (e.g. Ventura, 2006) and because the consumer is more homeostatic than their food in essential AAs (Sterner and Elser, 2002; Anderson et al., 2004). Comparison between organisms and their dietary AA composition has therefore been proposed as a stoichiometric argument for obtaining knowledge of the mechanisms underlying N limitation (Cowgill et al., 1986; Anderson et al., 2004; Ventura and Catalan, 2010).

Detritus-based systems are widely considered to be extremely nutrient limited, (Schulten and Schnitzer, 1997; Moe et al., 2005), and detritivores have therefore adapted different behavioural and physiological strategies to cope with temporal and spatial variations of dietary resources (Cross et al., 2003). One strategy is ingestion of the most digestible components in soil such as microorganisms involved in decomposition. Another strategy is ingestion of less nutritious components such as senescent plant material mixed with microorganisms living on these substrates (Plante et al., 1990). A feeding strategy on low nutrient diets requires morphological adaptations such large guts (Christiansen, 1964) and is demanding in terms of metabolic investments for maintaining a rich gut flora for digesting hardly decomposable materials (Sibly and Calow, 1986). Detritivores foraging on high nutrient diets are not only better adapted to sequester limiting nutrients by selective feeding but also more prone to stoichiometric mismatches between their own demands and dietary supply (Fagan and Denno, 2004). Several authors have proposed that scarcity of a specific nutrient in available food also can impact their physiology such as growth (Fink and Von Elert, 2006) and reproduction (Færøvig and Hessen, 2003), and consequently reduce consumer demands for that nutrient (Elser et al., 2000b, 2006; Kay et al., 2005). It has also been found that some animals are able to adjust their body C:N:P to the quality of resources (Elser et al., 2000a; Cross et al., 2003; Martinson et al., 2008) but it is not clear to what degree soil detritivores are able to adjust their stoichiometry to dietary N limitations and how it impacts their turnover of C and N.

To investigate how limitations in dietary N and AA imbalances affect the physiology of soil detritivores we investigated how a fungal diet (*Fusarium culmorum*) with a low N content and imbalanced AA composition affected body composition of C, N and P and turnover of C and N in three soil-dwelling Collembola species

(*Folsomia candida* Willem 1902; *Protaphorura fimata* Gisin 1952 and *Proisotoma minuta* Tullberg 1871) and compared them with those fed a control diet (*Saccharomyces cerevisiae*) with a high N content and balanced AA composition. While N-containing sugars such as chitin can constitute up to 45% of the organic fraction of fungal cell walls and structural membranes (Roberts, 1992) and be an important N source for Collembola (Borkott and Insam, 1990), this study focuses particularly on AAs as an N source for following reasons: chitin has a lower N content than AAs (6.6% vs. 16.5% N) and is in soil a less abundant N pool than the AAs (Schulten and Schnitzer, 1997), which in fungi typically constitute the major fraction of the total N (Kurkela et al., 1980). Moreover, essential AAs cannot be biosynthesized by metazoans and need to be provided from the diet or endosymbionts (Nation, 2002). The Collembola species selected for our study have previously been shown to have different dietary preferences. *P. fimata* has the largest dietary breadth of the three species and is able to function as a root herbivore as well as a detritivore (Ulber, 1983; Endlweber et al., 2009) in contrast to *F. candida* and *P. minuta*, that are thought to feed primarily on fungi and other highly nutritious sources (Harasymie and Sinha, 1974; Jørgensen et al., 2003; Larsen et al., 2007, 2008). The differences between the species were also demonstrated by Larsen et al. (2009b) who found that *P. fimata* primarily allocated nutrients to growth contrary to *P. minuta* that primarily allocated nutrients to metabolism and reproduction.

In this study we quantified the incorporation of C and N in Collembola by changing the isotopic (^{13}C and ^{15}N) composition of their diets after they had reached sexual maturity and followed growth, body composition of C, N and P, and the rate of isotopic change in their tissues during a period of 28 days. This design allowed us to partition between C and N allocations to growth and tissue replacement (Larsen et al., 2009b) and test the hypothesis that *F. candida* and *P. minuta* would decrease their rates of growth and tissue replacement relatively more than *P. fimata* on the low N diet. We also measured $\delta^{13}\text{C}$ of the AAs in the animals and their diets to determine whether the AA carbon skeletons were derived from the diet or were synthesized in the animals after assimilation. Similar $\delta^{13}\text{C}$ values between diet and animals would suggest that the AA carbon skeletons were primarily derived from the diet, whereas differences would indicate *de novo* synthesis. It has not been previously documented that gut bacteria in Collembola provide AAs to their hosts. For this reason, we hypothesized that the $\delta^{13}\text{C}$ values of amino acids essential for insects would match closely between Collembola and their diets (Sang and King, 1961; Davis, 1975; Nation, 2002; O'Brien et al., 2002).

2. Material and methods

2.1. Experimental diets and animals

The three Collembolan species, *F. candida*, *P. fimata* and *P. minuta* were obtained from a stock of established laboratory cultures raised on commercial freeze-dried *S. cerevisiae* (De Danske Spritfabrikker A/S, DK) for several (>10) generations. During the experiment the animals were raised on laboratory cultured fungi, *S. cerevisiae* as a high N reference diet and *F. culmorum* as a low N diet. *F. culmorum* was cultured in a broth medium with a low concentration of nitrogen to alter the C:N ratio: 1000 mg KH_2PO_4 (VWR), 1000 mg KNO_3 (VWR), 500 mg $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ (VWR), 500 mg KCl, 26.00 g D(+)-glucose, 2.4 g Potato Dextrose broth (Difco, Denmark), 1000 ml distilled water. We also cultured an isotopically enriched batch of *F. culmorum* by making the following substitutions of KNO_3 and glucose: 250 mg D-glucose- $^{13}\text{C}_6$ 99 atom%, 25.75 g D(+)-glucose. The growth medium for unlabelled *S. cerevisiae* was: 1.6 g yeast synthetic media with AAs (Fluka–Sigma Aldrich, Denmark), 5.0 g

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