



Romul_Hum—A model of soil organic matter formation coupling with soil biota activity. II. Parameterisation of the soil food web biota activity



Oleg Chertov^{a,*}, Alexander Komarov^b, Cindy Shaw^c, Sergey Bykhovets^b, Pavel Frolov^b, Vladimir Shanin^b, Pavel Grabarnik^b, Irina Pripulina^b, Elena Zubkova^b, Maxim Shashkov^b

^a Bingen University of Applied Sciences, Berlin Str. 109, Bingen, 55411, Germany

^b Institute of Physicochemical and Biological Problems in Soil Science, Russian Academy of Sciences, Institutskaya 2, Pushchino, Moscow Oblast, 142290, Russia

^c Northern Forestry Centre, Canadian Forest Service, 5320, 122nd Street Edmonton, AB, T6H 3S5, Canada

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ABSTRACT

A soil food web (FW) based approach to modelling the contribution of soil micro- and mesofauna to the formation of soil organic matter (SOM) was developed as an improvement to the soil organic matter model ROMUL, which is the predecessor of Romul.Hum. The main improvement is that the by-products (excrement and necromass) of soil micro- and mesofauna, and their important role as precursors to formation of stable SOM, that are not represented in any soil organic matter model, are now included in the Romul.Hum. First, parameters were compiled to explicitly and mechanistically model the foundational role of microbial communities in the soil FW by using a substrate C:N ratio based function that allows (a) the fungal to bacterial biomass ratio to vary from 3 to 15, (b) fungal C:N to vary from 8 to 30, and (c) bacterial C:N to vary from 5 to 8. These equations were used in model algorithms instead of fixed values that are used in the SOM models. Second, ordination was used on 15 published FWs biomass C datasets to define six FW patterns as combinations of two energy channels (fungal and bacterial) and three types of soil horizons (L, F + H, Ah or Ahe) in temperate and boreal forests. Third, FW analysis methods were used to quantify excrement and necromass C produced by soil micro- and mesofauna at different trophic levels. Soil heterotrophic respiration (expressed as the rate of SOM mineralisation), a core rate variable in all SOM models, was associated with the formation of the faunal by-products (excrement and necromass) using stoichiometric relationships between the production of faunal excrement, necromass and total FW biotic respiration. The ratios of “excrement mass/necromass C to soil heterotrophic respiration C” were key parameters incorporated into the Romul.Hum. The values of these ratios vary from 0.03 to 0.41 for the bacterial energy channels (with maximum in the F + H soil horizon) and from 0.02 to 0.17 in fungal energy channels (with maximum in the Ah/Ahe soil horizon). The well established mechanistic algorithm for available nitrogen (N) of the FW methodology was used to develop functions for the “ratio of available N to heterotrophic respiration C” depending on substrate C:N ranging from 5 to 120. The resulting algorithms, functions and new parameters for excrement and necromass production, as well as parameterisation of available N production, are described for all six FW patterns. The newly developed FW module was incorporated in the simulation model of SOM formation, Romul.Hum, allowing for the calculation of faunal organic matter contributions to SOM formation. This novel approach to including soil faunal activity in modelling of soil C dynamics takes advantage of the high degree of organisation within soil biotic communities in FWs and integrates the effects of microorganisms and soil fauna that govern the processes of organic residues transformation and mineralisation in the soil system.

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* Corresponding author. Present address: Albert-Schweitzer Str. 20, 26129 Oldenburg, Germany.

E-mail addresses: chertov@fh-bingen.de (O. Chertov), as.komarov@rambler.ru (A. Komarov), cindy.shaw@canada.ca (C. Shaw), s.bykhovets@rambler.ru (S. Bykhovets), ximikadze@gmail.com (P. Frolov), shaninvn@gmail.com (V. Shanin), gpya@rambler.ru (P. Grabarnik), irina.pripulina@gmail.com (I. Pripulina), elenazubkova2011@yandex.ru (E. Zubkova), max.carabus@gmail.com (M. Shashkov).

1. Introduction

The role of soil fauna in humus formation, formalised in the concepts of “humus forms” of Müller (1887) and others (Kubiěna, 1953; Duchaufour, 1960; Wilde, 1958), have been further articulated in recent decades by Chertov (1981), Klinka et al. (1981), Baritz (2003), Zanella et al. (2011) and Ponge (2013). Fundamental to the concept of humus forms is that they are comprised of identifiable horizons (L, fresh litter at the start of decomposition; F+H, the forest floor or the organic layer developed from partially to fully decomposed organic matter and Ah or Ahe, the top of mineral soil rich in humified organic matter and organo-mineral complexes) and in various forms these horizon types are used in forest soil classification globally (SCWG, 1998; Ponge, 1999; Baritz, 2003; Zanella et al., 2011). In Americal soil taxonomy, organic horizons defined now as follows: L=Oi, F=Oe and H=Oa (Soil Survey Staff, 2010). The relative amounts and combinations of these horizons are used to describe humus form (e.g., Mull, Moder and Mor). The link between organic and organo-mineral soil horizons and soil micro-, meso- and macro-biotic activity have been well documented and described in numerous morphological studies of humus forms (e.g., Bal, 1970, 1982; Pawluk, 1987; Galvan et al., 2006; Zanella et al., 2011) and FW studies (Schröter et al., 2003; Holtkamp et al., 2010). Protozoa and Nematoda dominate in the L horizon; Enchytraeidae, Protozoa, micro- and mesoarthropoda dominate in the F horizon; microarthropoda in the H horizon; and various groups in the Ah or Ahe horizon depending on soil properties. These well developed concepts constitute the theoretical foundation of the soil organic matter (SOM) dynamics model ROMUL (Chertov et al., 2001; Komarov et al., 2007). Over the last five decades experimental data has amassed in soil zoology on the quantitative evaluation of the role of different taxonomic and functional groups of soil fauna in the processes of SOM decomposition (Striganova, 1980, 2003; Hunt et al., 1987; Pokarzhenskii et al., 2007; de Vries et al., 2013), nitrogen (N) mineralisation, and plant nutrition (de Ruiter et al., 1993; Schroeter, 2001; Seeber et al., 2008). However, few studies exist that have quantified the role of soil micro- and mesofauna in humification or recalcitrant SOM formation (Fox et al., 2006; Ekschmitt et al., 2008).

In most soil science or ecology literature the word “decomposition” has generally meant “mineralisation” (Swift et al., 1979; Petersen and Luxton, 1982; Eijsackers and Zehnder, 1990; Schulze et al., 2005; Berg and McClaugherty, 2008; Holtkamp et al., 2011) or occasionally physical fragmentation (Braakhekke et al., 2011). This has led to an emphasis in SOM modelling on loss of SOM or carbon (C) and disregard for processes that transform or humify SOM that were a focus of soil science research in earlier decades (Kononova, 1966; Schnitzer and Khan, 1972; Stevenson, 1994), and continue to be researched today (Brock et al., 2013; Semenov et al., 2013; Jozefaciuk et al., 2015). The synonymous terms of “humification” and “recalcitrant SOM formation” for the development of a slowly decomposing, relatively stable, N-rich SOM (Kogel-Knabler and Matzner, 2008) define a core process for C sequestration in soil and terrestrial ecosystems. Explaining and quantifying C sequestration is important to understanding the role of soils in ecosystem C budgets and ultimately greenhouse gas emission estimation.

Here we used a soil food web (FW) analysis framework (Hunt et al., 1987; de Ruiter et al., 1993) as a promising approach to study the contribution of micro- and mesofauna in SOM formation. This approach allows for an assessment of C and N flows through soil faunal by-products from a multilayered trophic web of microorganisms, microbial grazers and micro- and mesofaunal predators. Soil macrofauna are not included in the FWs but the interplay between earthworms and this module is described in the companion papers by Komarov et al. (2016) and Chertov

et al. (2016). The FW features described here apply to humus form development dominated by microorganisms and mesofauna; namely, raw humus (mor) and moder (Baritz, 2003; Klinka et al., 1981; Culliney, 2013; Ponge, 2013; De Nicola et al., 2014) where macro- and micro-morphological humified and zoogenically transformed material (micro- and macroarthropod and enchytraeid excrement) in organic and organo-mineral horizons is diagnostic for different types of mor and moder humus forms (including tangel and amphi with litho-, psammo-, hydro- and histo- subforms (Galvan et al., 2006; Zanella et al., 2011)). For the sake of simplicity we use the singular term excrement to refer to all types of faunal pellets, faeces and casts. These humus forms are common in most undisturbed natural ecosystems including the large forested regions of Canada where the dominant agents of humus form development are microorganisms, micro- and mesofauna (Klinka et al., 1981; Pawluk 1987) because earthworms were extirpated from most of Canada during the last glaciation (Gates, 1982). Despite the proven role of soil mesofaunal excrement in soil structure development they are rarely studied as sites of SOM formation in soil microaggregates (Blaud et al., 2014; Lehmann et al., 2007; Six et al., 2004) and the role of faunal necromass is never considered. Both these faunal by-products have a fine, dispersed physical nature and play an important role in the development of SOM system and ecosystem functioning (Lavelle, 1997; Fox et al., 2006; Ekschmitt et al., 2008; Chertov, 2016). The high mobility of soil fauna provides the mechanism to distribute and increase the rate of contact between their by-products and the mineral soil matrix: conditions that favour recalcitrant SOM formation, namely humification.

The role of soil mesofauna excrement in humus formation is well known based on qualitative, not quantitative, studies (Kubiěna, 1953; Webb, 1977; Moldenke et al., 2000; Galvan et al., 2006; Ekschmitt et al., 2008; Culliney, 2013). The mass of mesofaunal excrement can be directly estimated using soil FW analysis (Hunt et al., 1987; de Ruiter et al., 1993) and an analysis and synthesis of published FW data showed that production of micro- and mesofaunal excrement and necromass varies significantly from 0.18 to 0.62 and 0.06 to 0.32 ton⁻¹ ha⁻¹ year⁻¹, respectively, in organic and organo-mineral horizons of various soils (Chertov, 2016). These values of transformed organic matter with high N content can account for as much as 8–38% of the annual forest litter fall but lower of rhizodeposition (Lynch and Whipps, 1990) that can account up to 40% of agricultural plant productivity and influence FW by activation of microorganisms' growth, however insufficient data for soil fauna faecal production in the rhizosphere makes this uncertain.

Most models of SOM dynamics do not take into account the role of soil fauna in SOM formation (Smith et al., 1997, 1998; Benbi and Richter, 2002; Manzoni and Porporato, 2009). Soil FW models (Hunt et al., 1987; Holtkamp et al., 2011; Larocque et al., 2016) do focus on faunal mediated processes related to the mineralisation of C and N but not C sequestration or SOM formation. Therefore, Chertov (2016) analysed and synthesised published FW data to develop an approach and algorithms to describe the role of FW faunal products (excrement and necromass) as precursors to SOM formation.

In this study we synthesised decades of published data and knowledge to develop a set of variables to model the role of micro- and mesofauna (Protozoa, Nematoda and Arthropoda) in SOM formation using published eco-physiological parameters within the FW analysis method of Hunt et al. (1987) and de Ruiter et al. (1993). We developed new parameters and algorithms for the contribution of micro- and mesofauna to humification of organic residues in soil and combined these with the algorithms of Chertov (2016) for incorporation into a new version of the well tested and widely used ROMUL SOM model (Chertov et al., 2001; Komarov et al., 2007)

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