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Modelling the impact of microbial grazers on soluble rhizodeposit turnover

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Abstract

Rhizodeposition represents a relatively large carbon flow from a plant's root into the surrounding soil. This carbon flow may have important implications for nitrogen mineralisation and carbon sequestration, but is still poorly understood. In this paper we use a simple compartment model of carbon flow in the rhizosphere to investigate the proposed benefits of rhizodeposition and the effect of microbial grazers. Model parameters were fitted to published, experimental data. Analysis of the model showed that dead organic matter (necromass) had a much longer time-scale than the other carbon pools (soluble, microbial and grazer carbon), which allowed an approximate, mathematical solution of the model to be derived. This solution shows that the level of necromass in the soil is an important factor in many processes of interest. The short-term carbon and nitrogen turnover increases with the level of necromass. Microbial grazers decrease carbon turnover at high levels of necromass, whilst at lower, and possibly more realistic, levels of necromass grazers increase turnover. However, the largest effect of grazers was to increase carbon turnover by 10%, suggesting that grazers are relatively unimportant in larger scale models of soil organic matter turnover. The marginal benefits of rhizodeposition increase with the level of necromass. The model suggests that the short-term benefits of rhizodeposition to a plant are marginal, but long-term benefits may still occur.

Introduction

The rhizosphere (Hiltner, 1904) is the primary site of plant-soil interactions, and a major contributor to nutrient cycling in terrestrial ecosystems. For example, its ability to sequester carbon has implications for the greenhouse effect (Darrah, 1996; Paterson et al., 1996; Rattray et al., 1995). The rhizosphere is defined as the zone of soil surrounding a plant root whose microbial population is more active than the surrounding bulk soil (Curl and Truelove, 1986). This increased microbial activity is due to the rhizodeposition from a growing root tip, which releases organic material into the surrounding soil (Uren, 2001). A plant can generally lose between 5–15% of its total assimilation through rhizodeposition (Johansson, 1992; Lambers, 1987; Swinnen et al., 1995), with losses being up to 40% in some cases (Lynch and Whipps, 1990). The factors influencing rhizodeposition have been extensively studied (Curl and Truelove, 1986; Lynch and Whipps, 1990), but they are still poorly understood. Some rhizodeposits are known to have specific functions (Uren, 2001), but most have no known function. The apparent inability of a plant to control its losses from rhizodeposition raises two fundamental questions: Does rhizodeposition benefit the plant? What are the long-term consequences of rhizodeposition?

The dominant hypothesis for a possible benefit of rhizodeposition is the nutrient-availability hypothesis, which suggests that rhizodeposition increases the nutrient availability to a plant. Nutrient availability could be increased through a priming effect (Fontaine et al., 2003; Kuzyakov et al., 2000), where rhizodeposition increases microbial activity which in turn increases nutrient mineralisation. Rhizodeposition has been shown to increase microbial growth (Curl and

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Truelove, 1986; Meharg and Killham, 1988; 1991; 1995), but it is unclear whether this increases nutrient availability, because the nutrients bound up in microbial cells need to be released for them to be available to the plant. The nutrients contained within the microbial cells will be released through the slow process of death and subsequent decomposition of microbes, which means there will be a long time-delay between rhizodeposition and any benefits. This process may be accelerated by the presence of microbial grazers (e.g. bacteriophagous nematodes, collembolans or protozoa) by increasing the turnover of microbial cells (Bonkowski et al., 2000; Wardle, 1999). Indeed, studies have shown that excluding grazers slows down nitrogen turnover, and decreases plant growth (Alphei et al., 1996; Clarholm, 1985; Kuikman et al., 1990a), but to properly test the nutrient-availability hypothesis the nutrient flow through this complex system of several trophic levels must be understood.

The long-term effect of rhizodeposition on carbon turnover is of interest because carbon sequestration in the soil has been proposed as a means of fighting the greenhouse effect (Paustian et al., 1998; Smith et al., 1997, 2000). Not only may rhizodeposition be a first step in an important pathway of carbon sequestration in soil, but also a plant's belowground allocation and rhizodeposition may be increased in a CO_2 enriched atmosphere (Darrah, 1996; Paterson et al., 1996; Rattray et al., 1995). As with the nutrient-availability hypothesis of rhizodeposition, microbial grazers may play a role in carbon sequestration. Experiments have shown that, under controlled laboratory conditions, microbial grazers increase the rate of carbon release from the soil (Kuikman et al., 1990a, b). However, under field conditions the effect of microbial grazers on soil organic carbon content is difficult to measure directly because measurable differences in soil organic carbon take a long time to develop. Indirect evidence from field observations is provided from an increase of nitrogen mineralization as soil pore-spaces increase in size (allowing grazers greater access to the microbial carbon), and a positive correlation between the percentage of soil volume enclosed by pore-spaces of 0.2–1.2 μm diameter (from which grazers are excluded) and the bacterial biomass (Hassink et al., 1993). These results suggest that partial exclusion of microbial grazers slows down carbon turnover and increases carbon sequestration.

To understand the possible benefits of rhizodeposition and its long-term consequences it is important to understand the dominant mechanisms at work within the rhizosphere. Experimental progress is slow because the rhizosphere is difficult to sample and manipulate (Toal et al., 2000), so a fruitful approach would seem to be a combination of modelling and experimentation. Many authors have pointed out that models of rhizosphere processes would be useful (Sylvia et al., 1998) and despite many difficulties (Toal et al., 2000) several models have been developed (Darrah, 1991a, b; Kuzyakov et al., 1999; Newman and Watson, 1977; Robinson et al., 1989; Zelenev et al., 2000). Most of these models consider microbial activity in time and space along the root. Such models easily become complicated, making a thorough analysis difficult, if not impossible. Simple models lack many of the details found in reality, but their simplicity does mean that: they provide a general overview of the system, there are fewer parameters (which is especially important when there are large uncertainties in estimating parameters), a full analysis and understanding of the model is feasible, and any general conclusions are likely to be robust. Toal et al. (2000) considered a simple model for soluble exudates which was based upon the more complex, spatially-explicit model of Darrah (1991a, b). In this current study we extend the model of Toal et al. (2000) by considering the effect of microbial grazers and develop an analytical solution of the system. The solution describes the flow of soluble carbon on both short and intermediate time-scales (i.e. days to months). The model is validated using published, experimental data. We then use the model to highlight the different time-scales in the system, to quantify the effect of grazers on both the rate of carbon turnover, and the benefits of rhizodeposition through the marginal return of carbon and nitrogen to a plant. The results show that amount of organic matter in the soil has an important influence on the turnover of carbon, the effect of grazers on this carbon turnover, and on the benefits of rhizodeposition.

Methods

We extended the model of Toal et al. (2000) to include microbial grazers. The model describes the carbon flow between four carbon pools in the rhizosphere: soluble carbon, (C_s), microbial carbon, (C_m), necromass carbon, (C_n) and microbial-grazer carbon (C_g) (Figure 1). For a description of the soluble, microbial and necromass carbon pools see Toal et al. (2000). Protozoa and nematodes account for the majority of microbial-grazers in the soil (Bonkowski et al., 2000;

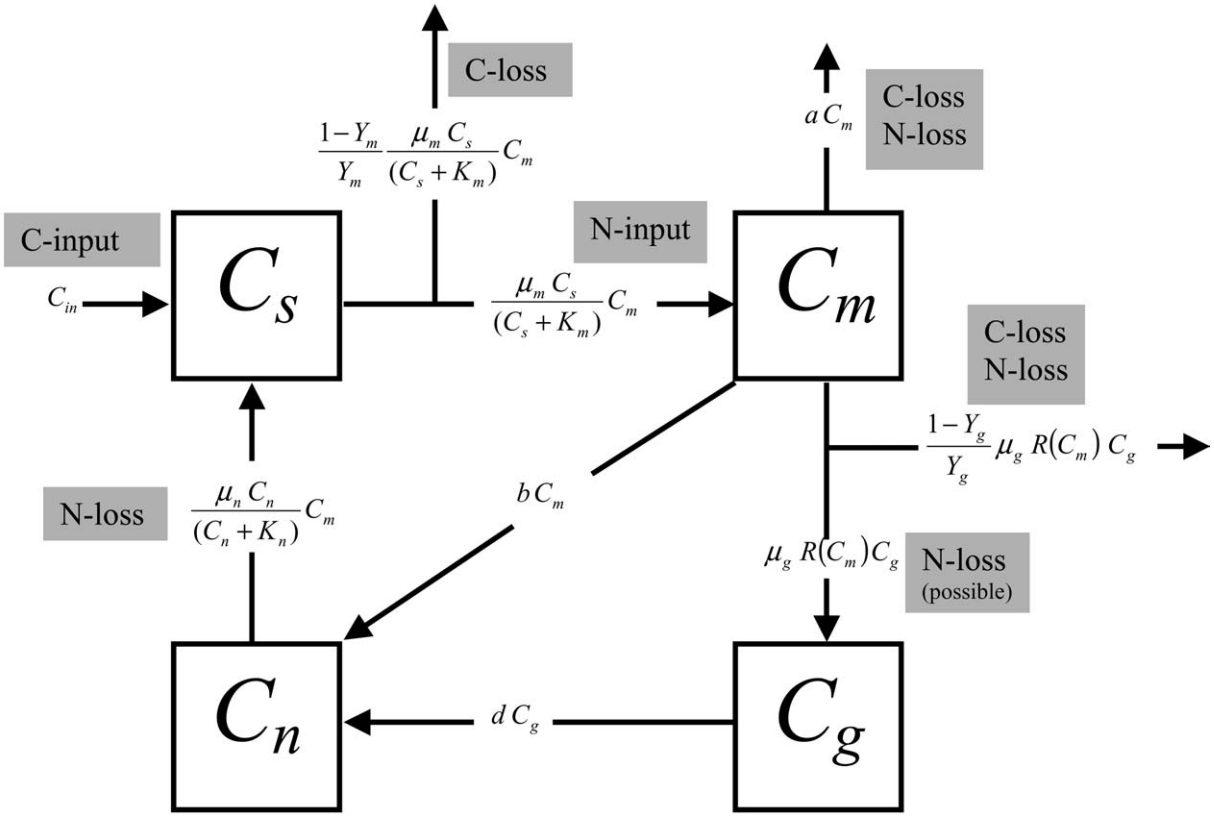

Figure 1. Flow diagram showing the four carbon pools and the fluxes of carbon. The points of input and release of carbon and nitrogen are indicated next to the relevant flow.

Zwart and Brussard, 1991), and the addition of a microbial-grazer carbon pool describes the presence of these microbe feeding protozoa and nematodes. It is unclear whether such grazers remain confined within a single rhizosphere (in which case their density would be regulated by conditions in the local rhizosphere), or whether they disperse more widely through the soil (in which case their density would not be strongly regulated by the local conditions of the rhizosphere). To allow for these two scenarios we analysed two models. In Model I the density of microbial grazers was treated as a dynamic variable, which implies that their density is regulated by the environment of the local rhizosphere. In Model II the density of microbial grazers was treated as a constant parameter, implying that their density is regulated on a larger spatial-scale than the local rhizosphere (this will be called external regulation). For example, model II would be applicable to grazers who arrived due to chemotactic attraction, because the density of grazers would not necessarily be related to the changes in microbial carbon density. Both models allow for the possibility that soil microsites act as microbial refuges, preventing the microbial grazers from feeding on all the microbial carbon (Hassink et al., 1993; Rutherford and Juma, 1992). The microbial carbon accessible to grazers is given by

$$R(C_m) = \begin{cases} 0 & \text{if } C_m < r \\ C_m - r & \text{if } C_m \geq r \end{cases}, \tag{1}$$

where r is the microbial carbon contained in soil microsites. The intake rate of microbial grazers was assumed to be proportional to the accessible microbial carbon (Equation 1) and their death rate, d, was assumed to be constant. The dynamics of the carbon pools are given by

$$\frac{dC_s(t)}{dt} = C_{in} - \frac{1}{Y_m}\frac{\mu_m C_s(t)}{(C_s(t)+K_m)}C_m(t) + \frac{\mu_n C_n(t)}{(C_n(t)+K_n)}C_m(t) \tag{2a}$$

$$\frac{dC_m(t)}{dt} = -aC_m(t) - bC_m(t) + \frac{\mu_m C_s(t)}{(C_s(t)+K_m)}C_m(t) - \frac{1}{Y_g}\mu_g R(C_m(t))\, C_g(t) \tag{2b}$$

$$\frac{dC_n(t)}{dt} = bC_m(t) - \frac{\mu_m C_n(t)}{(C_n(t) + K_n)} C_m(t) + dC_g(t) \quad (2c)$$

$$\frac{dC_g(t)}{dt} = \mu_g R\left(C_m(t)\right) C_g(t) - dC_g(t) \quad (2d)$$

where the meaning of the parameters is given in Table 1. Equation (2d) was not included in Model II because in this model C_g was regulated externally and is taken as a constant.

Model calibration

The model was calibrated using data from an experiment by Rutherford and Juma (1992). In this experiment sterile soil was inoculated with bacteria and soluble carbon (glucose). Two treatments were then created: one where microbial-grazing protozoa were added to the prepared soil and one where no grazers were added. The densities of microbes, grazers and the cumulative release of CO_2 were then monitored for over a month. This experiment is particularly well suited for calibrating our model because the data closely correspond to the output of the model and the initial amount of soluble carbon is known (contrary to many other microcosm studies where soluble carbon is uncertain because it is added from plants). Measured data for microbial-carbon and cumulative CO_2 released were log-transformed and used to fit the model parameters and initial conditions by least-squares. Firstly, the model was fitted to the data from the treatment without grazers. Then, keeping these parameters fixed, the grazing parameters and the initial density of grazers were fitted to the remaining data on microbe density, grazer density and CO_2 released when grazers were present. To convert between the number and carbon content of bacteria we used data from Bloem et al. (1995), so that 10^8 bacteria are assumed to contain 5.8 μg of carbon. No such conversion factor could be found between the number and carbon content of protozoa, so we normalised all results to the mean number of grazers. Because this conversion factor was somewhat arbitrary the contribution of the grazing data to the least-squares fit was reduced in importance by multiplying by 0.01.

Parameters

We used the least-squares fit of the model as default model parameters and initial conditions (Table 1). The observed ranges of most parameters (Table 1) were obtained from Toal et al. (2000), with the exception of the grazer's death rate (d), the grazer's production-assimilation ratio (Y_g) and the grazer's feeding rate (μ_g), which were based upon data for nematodes (Ferris et al., 1996; 1997), and protozoa (Zwart and Darbyshire, 1992).

Soluble carbon input rate (C_{in}) could not be parameterised from the fitted model because there was no carbon input in the experiment of Rutherford and Juma (1992). The default value for carbon input rate was set at $C_{in} = 1$ ng C mm^{-3} soil h^{-1}, so that the predicted density of microbial carbon was realistic (i.e. in the order of 100 ng C mm^{-3} soil). This is larger than the value used by Toal et al. (2000) (0.168 ng C mm^{-3} soil, based on Newman (1978)), who noted that 'the equilibrium biomass value predicted by [their] model is considerably lower than biomass figures quoted in the literature'. Our default value for the carbon input rate is still well within the measured range (Table 1; Toal et al., 2000).

To get a system sufficiently simple to analyse, we concentrate on carbon and nitrogen turnover in the rhizosphere. To calculate the turnover of nitrogen we require the carbon to nitrogen ratio for each carbon pool. On average the C:N ratios for both microbes and grazers are approximately five (De Ruiter et al., 1993), which we took as our default. The C:N ratio of the necromass was calculated from the flow of material from the microbial and the grazing carbon pools. For the purposes of this model the soluble carbon pool was assumed to contain no nitrogen, and the source of the nitrogen required for microbial growth was not explicitly specified. The source of nitrogen for microbial growth and the nitrogen released during rhizodeposition are discussed later on, in light of our results. We also looked at the effect of having a lower C:N ratio for microbes compared to grazers by setting their C:N ratios to four and six respectively.

Analysis

The system of Equations (2a-d) is sufficiently simple to allow a mathematical analysis of its dynamics. We started by analysing the equilibrium behaviour of both models I and II using Maple 8 (Waterloo, Canada). A non-trivial, stable equilibrium was found for each model. We calculated the time-scale of the dynamics in the locality of the equilibrium using perturbation methods (Jordan and Smith, 1987) in order to show that in Model I the soluble and the microbial carbon pools approached equilibrium with a time-constant of approximately one day or less, the grazer carbon

Table 1. The default parameters used in the model and their biologically feasible range (based on the references given). The default parameters are found by fitting the model to the data of Rutherford and Juma (1992)

	Parameter	Value range	Default value	Units	Reference
C_{in}	Carbon input rate	0.001–3.5	1.0	ng C mm^{-3}soil h^{-1}	Toal et al. (2000)
μ_m	Maximum microbial growth rate	0.1–0.5	0.33	h^{-1}	Toal et al. (2000)
K_m	Michaelis-Menton constant for microbial growth	1–50	33	ng C mm^{-3} soil	Toal et al. (2000)
a	Microbial maintenance	0.00005–0.005	0.0013	h^{-1}	Toal et al. (2000)
Y_m	Microbial growth yield	0.1–0.8	0.32	–	Toal et al. (2000)
b	Microbial death rate	0.00025–0.05	0.0012	h^{-1}	Toal et al. (2000)
μ_n	Specific necromass decomposition rate	–	0.026	h^{-1}	Toal et al. (2000)
K_n	Michaelis-Menton constant for necromass decay	–	84000	0ng C mm^{-3} soil	Toal et al. (2000)
Y_g	Grazer growth yield	0.58–0.86	0.033	–	Ferris et al., 1997
μ_g	Grazer growth rate	0.0–0.155	0.00077	ng^{-1} C mm^3 soil h^{-1}	Ferris et al., 1997 (nematodes); Zwart and Darbyshire, 1992 (protozoa).
d	Grazer death rate	0.0013–0.0052	0.0020	h^{-1}	Ferris et al., 1996
r	Microbial carbon contained in refuges	–	60	ng C mm^{-3} soil	–
	C:N ratio of microbes	2.8–22.6	5.0	–	Griffiths and Robinson, 1992; De Ruiter et al., 1993
	C:N ratio of grazers	5–10	5.0	–	Griffiths and Robinson, 1992; De Ruiter et al., 1993

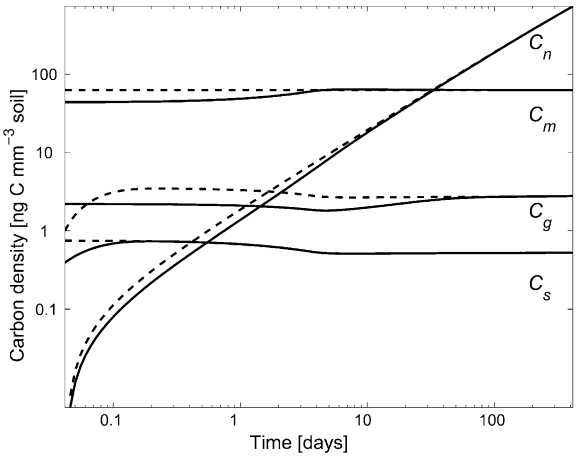

Figure 2. The dynamic behaviour of model I up to 10^3 days after a perturbation where C_s, C_m and C_g start at 70% of their equilibrium values and C_n is set to zero. The solid lines show the exact behaviour of the model (calculated numerically). The dotted lines show the analytical approximation where it is assumed that C_s, C_m, and C_g are at equilibrium with their environment. Default parameter values (Table 1) were used.

pool has a time-constant of several days whilst the necromass carbon pool changed very slowly, with a time-constant of over one year (the same pattern was found for Model II). Although it is difficult to estimate the time-constant of each variable without a quantitative analysis of the system (the time-constant of a variable is the rate at which it returns to equilibrium following a small perturbation away from equilibrium), some idea of the time-constants can be gained by looking at a model's behaviour after a perturbation from equilibrium. Figure 2 shows the effect of a 30% perturbation from equilibrium for Model I, with an initial necromass density of zero. Soluble and microbial carbon return quickly to equilibrium, whilst the grazers take several days to approach equilibrium and the necromass does not reach equilibrium after 1000 days. Based upon this analysis, and the fact that the environment of the rhizosphere will not be constant over a period of weeks, it seems unreasonable to assume that the necromass will be at equilibrium. We therefore concentrated upon the non-equilibrium dynamics of the system, and especially the dynamics

of the necromass. The different time-scales were used to simplify the analysis (Auger and Poggiale, 1998) by treating the necromass as a dynamic variable, whilst the soluble, microbial and grazer carbon pools were always assumed to have reached equilibrium (Figure 2). This allowed the dynamics of the necromass to be explicitly solved from Equation 2c, permitting a full algebraic analysis of the system despite the fact the necromass is not at equilibrium. For model II, Equation 2d was removed from the system and C_g was treated as another parameter.

Carbon (or nitrogen) turnover is defined as the rate at which carbon (nitrogen) is released from the system. The carbon turnover of the system was calculated by adding together all the carbon losses of the system (Figure 1). The nitrogen turnover was approximated by converting the carbon flow into a nitrogen flow, using the C:N ratio of each carbon pool. This approximation of nitrogen turnover assumes that the microbes are responsible for mobilizing nitrogen in the rhizosphere and that they are not nitrogen limited. The effect of adding grazers into the system was measured largely through their effect on carbon and nitrogen turnover. Carbon is acquired into the system through rhizodeposition, whilst nitrogen is mainly acquired during microbial growth (although some of this nitrogen also comes from rhizodeposition). Carbon is released from the system through the maintenance requirements of microbes, and the inefficiencies in microbial growth and grazing. Nitrogen is released from the decomposition of necromass, the maintenance requirements of microbes and the effect of grazing upon the microbes. The sensitivity of carbon and nitrogen turnover to changes in the rate of rhizodeposition (C_{in}) was also calculated. These sensitivities give a conservative estimate of the marginal returns of carbon and nitrogen for each unit of rhizodeposition; sensitivities greater than one imply that the return is greater than the investment. These estimates are conservative because rhizodeposition can involve the release of nitrogen as well as carbon.

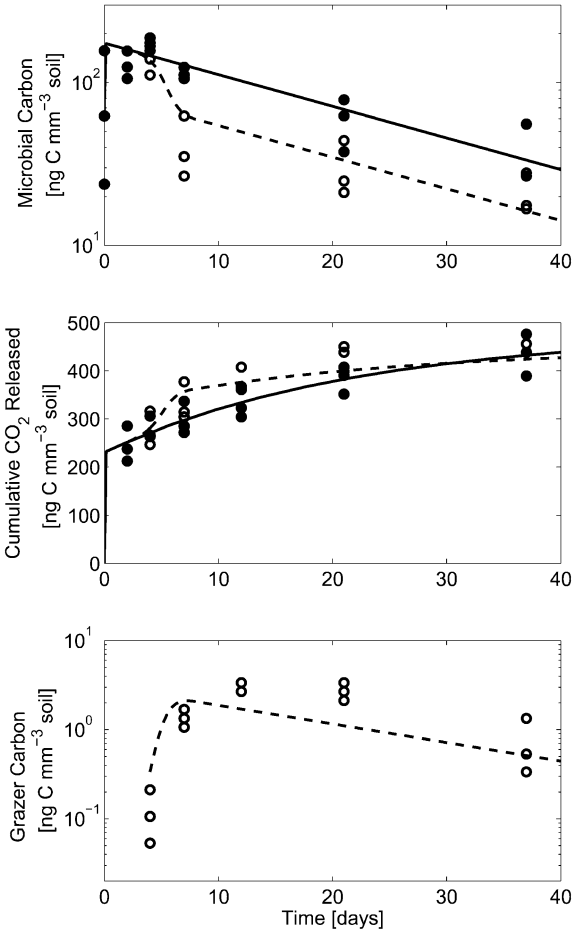

Figure 3. Measured (circles) and simulated (lines) microbial carbon density, cumulative respired CO_2, and grazer density as a function of time after addition of soluble carbon. Solid lines and circles show data in the absence of grazers, whilst open circles and dashed lines show data when grazers are present. Parameters are shown in Table 1 and measured data is from Rutherford and Juma (1992).

Results

Model calibration

The fitted parameters are shown in Table 1 as default parameters, whilst the simulated and measured values for microbial carbon, grazer carbon and released CO_2 are shown in Figure 3. The best fit initial values for the density of soluble carbon, microbes, grazers and necromass were found to be 340, 66, 0.013 and 7000 ng C mm^{-3} soil. The range of realistic initial values of soluble and microbial carbon can be directly calculated from the data in Rutherford and Juma (1992) giving ranges for soluble carbon of 310–370 ng C mm^{-3} soil, and microbial carbon of 24–160 ng C mm^{-3} soil. No range for the initial value of grazers can be given because no conversion factor was found between grazer number and carbon density (see methods section). For necromass it is more difficult to know if the fitted value is realistic (discussed later). The necromass density must be less than the total carbon density of the soil, and the fitted necromass density of 7000 ng C mm^{-3} soil is substantially less than the

carbon content of all the three soils used in the experiment (Rutherford and Juma, 1992). The fit of the model in the absence of grazers explained the density of microbes and the release of CO_2 with an R^2 of 55% and 84%, respectively. When grazers were present the model fit to the density of microbes, grazers and the release of CO_2 gave an R^2 of 74%, 59% and 74%, respectively.

Grazer-microbe dynamics

The dynamical behaviour of model II for the default parameters is shown in Figure 2. This shows the long time-scale of the necromass carbon pool compared to the other carbon pools, and the importance of looking at the non-equilibrium behaviour of the necromass. For the soluble carbon and microbial pools the time-scales are no more than a day, making the equilibrium solution of more biological interest. The non-trivial equilibrium for Model I was calculated to be

$$\hat{C}_s = K_m \left[\frac{\mu_m}{Y_m} \left(\frac{C_{in}}{\hat{C}_m} + \frac{\mu_n C_n}{C_n + K_n} \right)^{-1} - 1 \right]^{-1} \tag{3a}$$

$$\hat{C}_m = r + \frac{d}{\mu_g} \tag{3b}$$

$$\hat{C}_g = \frac{\hat{C}_m Y_g}{d} \left(\frac{\mu_m \hat{C}_s}{K_m + \hat{C}_s} - a - b \right) \tag{3c}$$

and for Model II (assuming $\hat{C}_m > r$)

$$\hat{C}_s = K_m \left[\mu_m \left(a + b + \frac{\mu_g C_g}{Y_g} \left(1 - \frac{r}{\hat{C}_m} \right) \right)^{-1} - 1 \right]^{-1} \tag{4a}$$

$$\hat{C}_m = \left[C_{in} + \frac{\mu_g C_g r}{Y_m Y_g} \right] \left[\frac{a+b}{Y_m} + \frac{\mu_g C_g}{Y_m Y_g} - \frac{\mu_n C_n}{K_n + C_n} \right]^{-1}. \tag{4b}$$

Both models also have a trivial equilibrium where $\hat{C}_s = \hat{C}_m = \hat{C}_g = 0$, and Model I has a third equilibrium when only $\hat{C}_g = 0$, which is given by substituting $C_g = 0$ into Equations (4). Substituting any of these equilibrium solutions into Equation (2c) gives an approximation to the dynamics of C_n. For both models I and II this approximation to the dynamics of C_n can be solved explicitly in terms of a Lambert W function (Corless et al., 1996) such that C_n monotonically increases with time until it reaches its equilibrium density.

For the solutions in Equations (3) and (4) to be feasible a number of constraints must be met. If a population of microbial grazers is to be maintained solely by the local rhizosphere, then we require that $\hat{C}_g > 0$ in Model I. From Equation (3c) this implies that

$$\hat{C}_s > K_m \frac{a+b}{\mu_m - a - b} \tag{5}$$

and substituting Equation (5) into Equation (3a) provides the alternative requirement that

$$\frac{\mu_n C_n}{C_n + K_n} > \frac{a+b}{Y_g} - \frac{C_{in}}{\hat{C}_m} \tag{6}$$

If inequality (5) or (6) are true, then Model I cannot support a population of microbial grazers, and the equilibrium is given by Equations (4) with $C_g = 0$.

Equations (4) give the non-trivial equilibrium for Model II provided that microbes are available for the grazers to feed upon (i.e. $\hat{C}_m > r$), which requires that,

$$\frac{C_{in}}{r} > \frac{a+b}{Y_m} - \frac{\mu_n C_n}{K_n + C_n} \tag{7}$$

and is independent of the grazer density. If microbes are accessible to grazers, then an increase in the density of grazers will always cause a decrease in the density of microbes and an increase in the soluble carbon.

Equation (4b) shows that when grazers are externally regulated (Model II) the density of microbial carbon is positively correlated with the carbon input rate, C_{in}. However, when grazer density is internally regulated (Model I, Equations 3) their population dynamics causes the microbial carbon to be independent of C_{in} (so long as the grazer equilibrium density is positive). In this sense models I and II are extreme scenarios. In model I the grazers completely regulate the microbial carbon density, whilst in model II the grazers have no regulatory effect.

In order to gauge the robustness of the model to changes in the parameters, the proportional change of $\hat{C}_s$, $\hat{C}_m$ and $\hat{C}_g$ to a proportional change in each parameter (i.e. the elasticity) was calculated from Equations (3) and (4), and is presented in Table 2. The elasticities of the variables to changes in necromass (and grazer density for model II) were also calculated.

Effect of grazers and necromass on carbon and nitrogen turnover

The turnover of carbon and nitrogen for model I and II was found to be qualitatively the same. Figure 4

Table 2. The elasticities of the equilibrium state variables with respect to each parameter for models I and II (elasticity is the percentage change in a state variable produced by a percentage change in a parameter). All parameters take their default values (Table 1), the necromass is taken to be $C_n = 1000$, and for model II the density of grazers is assumed to be $C_g = 10$

Parameter	Model I			Model II	
	C_s	C_m	C_g	C_s	C_m
C_{in}	1.00	0.00	1.89	1.00	0.02
μ_m	−1.02	0.00	0.00	−1.02	0.00
K_m	1.00	0.00	0.00	1.00	0.00
a	0.00	0.00	−0.47	0.01	−0.01
Y_m	1.02	0.00	1.91	0.99	0.02
b	0.00	0.00	−0.48	0.01	−0.01
μ_n	0.02	0.00	0.04	0.02	0.00
K_n	−0.02	0.00	−0.04	−0.02	0.00
Y_g	0.00	0.00	1.00	−0.01	0.01
μ_g	0.04	−0.04	0.04	0.01	−0.01
d	−0.04	0.04	−1.04	0.00	0.00
r	0.01	0.96	−0.85	−0.98	0.98
C_n	0.02	0.00	0.04	0.02	0.00
C_g	–	–	–	0.01	−0.01

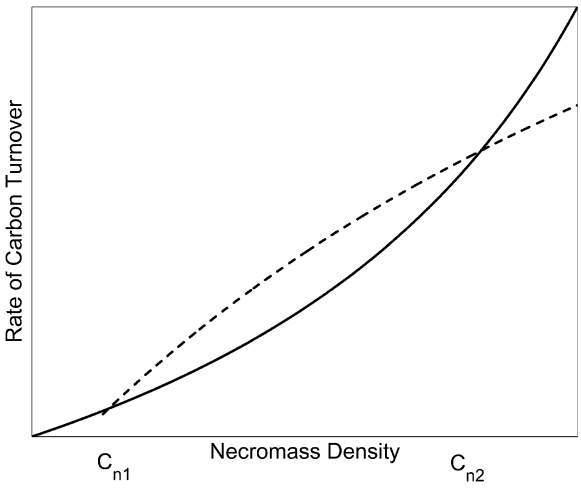

Figure 4. The qualitative behaviour, for both models I and II, of the rate of carbon turnover as a function of necromass carbon density, C_n, when grazers are absent (solid line) and present (dashed line). There are two points where the addition of grazers has no effect on the rate of carbon turnover ($C_n = C_{n1}$ and C_{n2}). If necromass is less than C_{n1} then no grazers are present. Grazers increase the rate of carbon turnover if necromass density lies between C_{n1} and C_{n2}, but they cause a decrease in the rate of carbon turnover if necromass density exceeds C_{n2}. A quantitative example of the model's behaviour is shown in Figure 5.

shows the qualitative behaviour for both Models I and II of the rate of carbon turnover as a function of the necromass density, C_n. The scale of necromass and rate of carbon turnover in Figure 4 depends upon a model's precise parameterisation, so no quantitative information can be drawn. However, Figure 4 demonstrates that both models I and II have several general properties that are independent of the model's precise parameterisation: as necromass increases the rate of carbon turnover increases, above a critical level of necromass additional grazers reduce the rate of carbon turnover, there are always two values of necromass ($C_n = C_{n1}$ and C_{n2}) for which the addition of grazers has no impact upon the rate of carbon turnover (although these values for C_n may be negative for some parameter values, and therefore infeasible). These last two properties imply that microbial grazers will have a positive impact on the rate of carbon turnover only when C_n lies between C_{n1} and C_{n2}. The size of this effect will be discussed when the quantitative results are presented. The first critical level of necromass, C_{n1}, corresponds to the case when $C_g = 0$ or $C_m = r$ for models I and II respectively (inequalities 5–7). The second critical level of necromass can be calculated as

$$C_{n2} = K_n \frac{Y_g(a+b) - b}{Y_g\,(\mu_n Y_m - a - b) + b - \mu_n} \qquad (8)$$

and is the same for both models I and II.

The qualitative result can be understood by considering the relative importance of the loss terms shown in Figure 1. When C_n is high, a large microbial density is the most important factor, as it can break down large amounts of C_n, which in turn can sustain high microbial growth rates. Grazers, therefore, have an overall negative effect on release rate when C_n is high because they decrease C_m. When C_n is low, however, the most important factor is the rapid release of carbon and nitrogen that is bound up in C_m. In this case grazers have a positive overall effect on release rate.

The quantitative effect of the rate of carbon turnover as a function of necromass is shown in Figure 5. With the default parameter set C_{n1} is negative and therefore infeasible, giving only one crossover point at C_{n2}. For necromass densities below this crossover point grazers have a positive effect on the rate of carbon turnover. The mechanisms regulating the grazer population are found to be unimportant for the rate of carbon turnover. In fact the overall presence of grazers does not have a large effect, accounting for a 10% increase in carbon turnover at most. The same qualitative result is seen for nitrogen release, except that the crossover point is at a slightly lower value of C_n (not shown). Using a higher C:N ratio

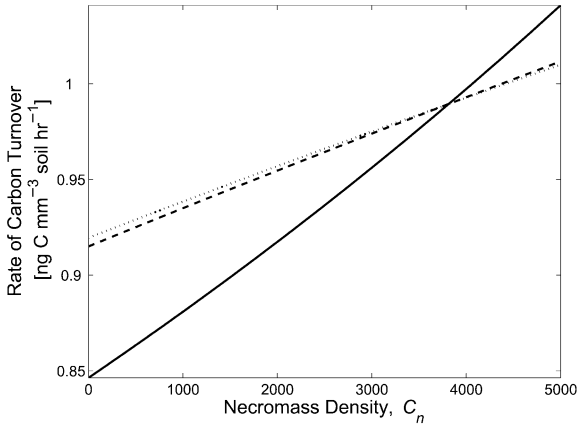

Figure 5. The rate of carbon release as a function of the necromass, C_n, assuming that grazer density, C_g, is internally regulated and at equilibrium (Model I, dotted line) or externally regulated and taking a constant value of either $C_g = 0$ ng C mm^{-3} soil (solid line) or $C_g = 1$ ng C mm^{-3} soil (Model II, dashed line). All other parameters take their default values.

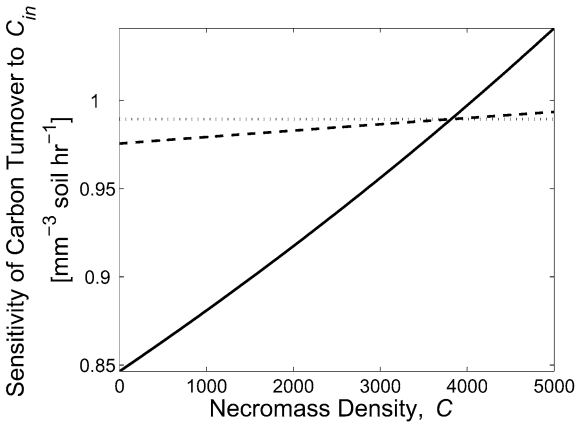

Figure 6. Sensitivity of the carbon release rate (Figure 5) to the carbon input rate, C_{in} as a function of the necromass, C_n. Results are shown assuming that grazer density, C_g, is either internally regulated and at equilibrium (Model I, dotted line) or externally regulated and taking a constant value of either $C_g = 0$ ng C mm^{-3} soil (solid line) or $C_g = 1$ ng C mm^{-3} soil (Model II, dashed line). All other parameters take their default values.

for grazers than microbes increases the rate of nitrogen release, and shifts the crossover point for nitrogen to higher values of C_n. A sensitivity analysis showed that parameters a, b and μ_g had the largest effect on the difference in turnover rates between grazers being present and absent.

Effect of carbon input rate

The importance of the carbon input rate upon the turnover of carbon and nitrogen gives an indication of the importance of rhizodeposition in driving the rate of carbon flow in the system (Figure 6). Equations (3a) and (4b) can be used to show that increasing the carbon input rate increases the equilibrium density of soluble carbon and the equilibrium microbe density for models I and II, respectively. It is therefore no surprise that the carbon input rate has an important effect upon the carbon and nitrogen turnover of the system. When the grazer density is constant (Model II) the sensitivity of the rate of carbon/nitrogen release to the carbon input rate increases with C_n (shown as the dashed line in Figure 6). This means that the return of carbon/nitrogen for each unit of C_{in} increases as the necromass increases. When grazers are internally regulated within the rhizosphere (Model I) the sensitivity of carbon/nitrogen turnover to the carbon input rate is independent of the necromass density (shown as the horizontal dotted line in Figure 6). Models I and II have equivalent sensitivities of carbon turnover when $C_n \sim 4000$. For the sensitivity of nitrogen turnover to C_{in} the models are equivalent at a slightly lower value of necromass, $C_n \sim 3000$. Whilst the effect of grazers in Figure 6 is larger than their effect on carbon turnover (Figure 5), it is still relatively small, implying that the inclusion of grazers is not an important component of the system's dynamics.

Discussion

Model calibration

Despite the simplicity of the model an acceptable fit can be achieved between the model and the data. Confidence in the model fitting is gained by comparing the fitted parameters against their observed ranges, which shows that all but one of the parameters lie within the observed range (Table 1). The one discrepancy is for grazer growth yield, Y_g, whose fitted value is below the observed range, although this range is based on one source (Ferris et al., 1997) where only nematode species were measured (we have not found any value for protozoa). If the grazer growth yield is constrained to lie within the observed range then the best-fit model under predicts the CO_2 production when grazers are present ($R^2 = 54\%$ as opposed to 73% for parameters in Table 1). One possible reason for this is the assumption that microbial growth rate and metabolic rate are independent of the grazing intensity, whilst observations suggest that grazed microbial population increase their growth rate and their metabolic rate (Jurgens and Sala, 2000; Kuikman et al., 1990b; Lebaron

et al., 2001; Pussard et al., 1994). The effect was explicitly included in the model by allowing the parameters μ_m and a to be linearly increasing functions of the number of grazers present, but this was only found to make a small improvement to the model's fit.

Interpretation of C_n

Clearly, one problem in interpreting the model's results is deciding what proportion of soil organic matter should correspond to C_n. Our dynamic model for C_n assumes that the only sources for C_n are the microbe and grazer carbon pools. When considering the dynamics of C_n therefore, the necromass must be interpreted as the fate of the soluble fraction of the rhizodeposits, unless additional carbon sources to the necromass pool are added in to the model (such as sources from plant and animal pools). However, the results presented in this paper are not concerned with the dynamics of C_n, instead they treat the necromass pool as a constant on the time-scale of the other carbon pools and this allows us to broaden our interpretation of C_n. When the model's results are compared to measured values of carbon turnover C_n must correspond to the 'active' part of soil organic carbon (i.e., C_n must account for all the organic matter in the soil that can serve as a source of soluble carbon for microbial consumption). This can be justified if soil organic matter consists mainly of dead microbes and microbial products (although not necessarily only from rhizosphere microbes). This is supported by recent experimental evidence (Kiem and Koegel-Knabner, 2003), although an opposing view proposes that soil organic matter is mainly undecomposed plant residues (largely lignin), because easily decomposable carbon is quickly respired (Elliott and Cambardella, 1991). Analysis of the model shows that the necromass, C_n, takes much longer to come to equilibrium than the other carbon pools. Toal et al. (2000) found this long time-scale unrealistic, but this need not be the case if necromass is interpreted as a component of the soil organic matter, because soil organic matter is known to change on a long time-scale. The slow dynamics of C_n means that the equilibrium is unlikely to be of biological interest, because the environmental conditions (such as the duration of rhizodeposition into the rhizosphere) change on a much shorter time-scale.

Model interpretation

Our simple model can be interpreted in two ways. Firstly, it can be applied to a small homogeneous volume of soil surrounding a root, in which case rhizodeposition must last long enough for our equilibrium approximations to be valid. Secondly, the model can be interpreted as the mean-field approximation over a larger spatial volume (e.g. the whole rhizosphere of a plant).

The expected duration of rhizodeposition from one root tip into a fixed volume of soil is unlikely to exceed a few days. Comparing this time-scale to the time-constants of the model suggests that only the soluble carbon, with a time-constant of less than a day, will be certain of reaching equilibrium. The microbial and grazer carbon pools, which may have a time-constant of up to several days, will be close to equilibrium, and for the purposes of our analysis we have assumed that this is the case. This may not be justified, especially for fast-growing plant species. For example, rhizodeposition of soluble exudates at any one point in the soil will last less than half a day for a fast growing species such as wheat (this is based on the growth rate of wheat root tips being 3.3 cm/day (Zelenev et al., 2000) and exudation of soluble compounds taking place in the first 5 mm of the root tip (Thornton et al., 2004)). We believe that most plants will grow more slowly than the wheat plants measured by Zelenev et al. (2000), although we have been unable to find any published data to support this. Rhizodeposition may be more sustained if there is considerable rhizosphere overlap (discussed by Toal et al., 2000).

This will apply primarily to perennial species with well developed root systems that have explored most of the soil volume (e.g. pasture species). However, as the soluble rhizodeposits are mainly released by the root tip, release of soluble rhizodeposits in any one volume of soil will always show temporal variation. Our analysis of model II is more robust since both C_s and C_m have time-constants less than a day and C_g is considered to be externally regulated, which means that it does not need to go to equilibrium within the time of root exudation.

The second model interpretation, where the model is a mean-field approximation, looks at the average rhizodeposition over a larger spatial scale. This average rhizodeposition is less variable in time (e.g. on the scale of a plant, rhizodeposition will change with plant growth and with the seasons), making the equilibrium assumptions a good approximation. However, the process of averaging over spatial inhomogeneities incurs its own errors because the processes of microbial growth and necromass decay are non-linear (for linear processes the mean-field approximation is exact).

Are microbial grazers important?

The model's results suggest that the addition of grazers is unlikely to change carbon turnover by more than 10%. This is in approximate agreement with the results from a laboratory experiment (Kuikman et al., 1990a). Using the data from this experiment to calculate the plant's nitrogen uptake showed that the plants in the treatment with low and high concentrations of protozoa had respectively taken up only 7% and 15% more nitrogen than the control. Such small effects are unlikely to be observed against the errors associated with field measurements of soil organic matter. It could therefore be argued that microbial grazers can be ignored in larger scale models of carbon and nitrogen turnover (e.g. CENTURY, Parton et al. (1987)). However, the effect of grazer on the soil's carbon and nitrogen turnover should not be completely ignored, because an indirect effect of grazers on plant growth, via increased nitrogen uptake, will be measurable at the 7–15% level. Observations showing that the presence of grazers increases plant growth by much more than 10–20% (Alphei et al., 1996; Clarholm et al., 1985; Kuikman et al., 1990a) suggests that an indirect nutritional effect is not the full picture. It has recently been suggested that this observed growth increase is due to the direct effect of microbial grazers on plants, rather than a purely nutritional effect (Alphei et al., 1996; Bonkowski et al., 2000). Such direct effects are outside the scope of the model considered in this paper.

The effect of rhizodeposition and grazers on N and C turnover

Although the effect is rather small, both models I and II predict that grazers will increase the release rates of carbon and nitrogen when soil organic matter levels (C_n) are low, while decreasing the release rates at high levels of C_n. There is therefore a crossover point, at intermediate values of C_n, where grazers have no effect on carbon and nitrogen release. The experimental evidence suggests that grazers increase release rates of carbon and nitrogen (Alphei et al., 1996; Breland and Hansen, 1996; Clarholm, 1985; Kuikman et al., 1990a). However, these experiments have mainly been performed with agricultural soil, and an experiment testing if there is any correlation between the level of organic matter in the soil and the response of carbon and nitrogen release to grazers would be interesting. If all soil organic carbon can be thought of as C_n (i.e., it is all available for microbial decomposition), then the crossover point predicted by the model would correspond to a soil organic carbon level of about 3–5% (depending on bulk density), which is a fairly high level. However, it is unlikely that all soil organic carbon is readily available to microbes. In this case the crossover point corresponds to a soil with an exceedingly high organic matter content, because C_n accounts for only a fraction of the total organic matter in the soil. This makes it likely that observations will be below the crossover point, and that grazers will generally be found to increase the rate of carbon and nitrogen release. The crossover point does depend upon the parameters of the model (particularly microbial maintenance, a, death rate, b, and grazer growth rate, μ_g, Equation 8), so that for certain parameter combinations (for example low a and high b) the crossover point will occur at lower values of C_n, making it more likely that grazers will be observed to decrease the carbon and nitrogen release rate.

Carbon sequestration can be calculated as the difference between the rate of carbon input and the rate of carbon release. As the available soil organic carbon, C_n, increases the model predicts that carbon accumulation in the soil will slow down, because the rate of carbon release increases. This is as also predicted by large-scale soil organic matter models (e.g. CENTURY) and supported by data (Foereid and Høgh-Jensen, 2004; Parton et al., 1987).

The model's qualitative results are robust to the mechanism of grazer population regulation, so that Figure 4 is identical for both models I and II. Model I assumes that the grazer population is regulated by the local microbial population within the rhizosphere, whilst model II assumes that the grazer population is regulated on a spatial scale which is far larger than the local rhizosphere. These are fairly strong assumptions with the reality likely to be somewhere in between. Since the main results are robust to the selected model, the precise mechanism for the regulation of grazers is unlikely to change our conclusions.

Plant benefits from rhizodeposition

The sensitivity of carbon and nitrogen turnover to carbon input are qualitatively very similar in our model. The sensitivity of nitrogen turnover to carbon input can be interpreted as the return in nitrogen to a plant for each unit of carbon invested in rhizodeposition. The model suggests that without grazers the return of nitrogen to a plant is positively correlated with the level of necromass, but when grazers are present this

correlation is much weaker. This implies that grazers only increase the rate of return of nitrogen to a plant at low levels of necromass.

Rhizodeposition involves a loss of both carbon and nitrogen from the root. If the nitrogen released from the rhizosphere is to be of net benefit to the plant in terms of nitrogen nutrition, then the amount of nitrogen released must exceed the amount of nitrogen lost in rhizodeposition. Measured values for the C:N ratio of rhizodeposits are in the range 9–33 (Griffiths and Robinson, 1992; Robinson et al., 1989). The model's results predict a threshold C:N ratio of rhizodeposits at about 20–25 below which rhizodeposition is not beneficial in terms of nitrogen nutrition. If the C:N ratio of rhizodeposits is below this threshold then rhizodeposition causes a net loss of plant nitrogen. In reality this threshold will be an underestimate. Our model represents very ideal conditions because the microbes are not limited by nitrogen and all nitrogen released from the system is assumed to be available to the plant (Kaye and Hart, 1997). The model therefore predicts that rhizodeposition is neutral or slightly negative for plant nitrogen nutrition. This agrees with the conclusion of a similar calculation based on a more complex model (Griffiths and Robinson, 1992; Robinson et al., 1989), although our model suggests that the level of necromass is an important consideration. On the other hand, a small component of rhizodeposits are of known benefit to the plant (i.e. chelating agents) (Uren, 2001) which suggests that overall, the short-term benefit to the plant of rhizodeposition is approximately neutral. Why has rhizodeposition survived in evolution? There are several possible answers: firstly, rhizodeposition may benefit the plant but not through nitrogen nutrition; secondly rhizodeposition may be a mostly passive process which has not been selected against because it is harmless to the plant: finally, nitrogen nutrition is probably better viewed over a time-scale longer than a couple of days. The nitrogen 'lost' in the model (i.e. the difference between nitrogen input and nitrogen release) mainly represents nitrogen stored in soil organic matter, C_n. This store of nitrogen need not be lost to the plant, and could be of benefit at a later stage. Any long-term benefit of C_n is not included in our model, and would require the inclusion of additional processes.

Conclusions

The model presented here is very simple, and compliments the approach taken by many other workers, who have studied the rhizosphere using multi-trophic level models (e.g. De Ruiter et al., 1993; Zheng et al., 1997) or spatially explicit models (Darrah, 1991a, b). The good fit of our model to experimental data suggests that a simple modelling approach can capture the broad features of the system. The model extends previous models by including microbial grazers in the system, and showing how such a system can be analytically analysed. Microbial grazers are found to have a small effect on the system, suggesting that their inclusion is not a necessary part of a rhizosphere model. The model highlights the different time-scales present within the system and the importance of considering the transient dynamics of the slowest carbon pools (Hastings, 2004). The necromass changes over a long time-scale and, to a good approximation, can be considered constant on the time-scale of rhizodeposition around a root. The model shows that the level of necromass in the soil is important in determining the rate of carbon turnover and the impact of adding microbial grazers; only when necromass is below a threshold level do microbial grazers increase the rate of carbon turnover. The presence of this threshold level of necromass seems insensitive to the processes regulating the population size of microbial grazers. The presence of this threshold is a new hypothesis which is still to be verified. We have also investigated the *short-term* benefits of rhizodeposition for a plant, and the carbon sequestration in the rhizosphere. The general results are relatively insensitive to changes in both model structure and parameter values. In agreement with previous studies using a non-dynamic calculation (Griffiths and Robinson, 1992; Robinson et al., 1989), on the short-term, the net nitrogen benefit to a plant from rhizodeposition seems to be marginal for the mechanisms included in our model. This result, combined with the long time-scale of the necromass carbon pool, suggests that future studies should concentrate upon studying the long-term implications of rhizodeposition.

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References

Alphei J, Bonkowski M and Scheu S 1996 *Protozoa, Nematoda* and *Lumbricidae* in the rhizosphere of *Hordelymus europaeus (Poceae)*: Faunal interactions, response of microorganisms and effects on plant growth. Oecologia 106, 111–126.

Auger P and Poggiale J-C 1998 Aggregation and emergence in systems of ordinary differential equations. Math. Comp. Model 27, 1–22.

Bloem J, Veninga M and Shephers J 1995 Fully-automatic determination of soil bacterium numbers, cell volumes, and frequencies of dividing cells by confocal laser-scanning microscopy and image-analysis. Appl. Environ. Microbiol. 61, 926–936.

Bonkowski M, Cheng W, Griffiths B S, Alphei J and Schau S 2000 Microbial-faunal interactions in the rhizosphere and effects on plant growth. Europ. J. Soil. Biol 36, 135–147.

Breland T A and Hansen S 1996 Nitrogen mineralization and microbial biomass as affected by soil compaction. Soil. Biol. Biochem. 28, 655–663.

Clarholm M 1985 Interactions of bacteria, protozoa and plants leading mineralisation of soil nitrogen. Soil. Biol. Biochem. 17, 181–187.

Curl E A and Truelove B 1986 The Rhizosphere. Springer Verlag, Berlin.

Corless R M, Gonnet G H, Hare D G E, Jeffrey D J and Knuth, DE 1996 On the Lambert W function. Adv. Comput. Math. 5, 329–359.

Darrah P R 1991a Models of the rhizosphere I. Microbial population dynamics around a root releasing soluble and insoluble carbon. Plant Soil 133, 187–199.

Darrah P R 1991b Models of the rhizosphere II. A quasi three-dimensional simulation of microbial population dynamics around a growing root releasing soluble exudates. Plant Soil 138, 147–158.

Darrah P R 1996 Rhizodeposition under ambient and elevated CO_2 levels. Plant Soil 187, 265–275.

De Ruiter P C, Moore J C, Zwart K B, Boouwman L A, Hassink J, Bloem J, De Vos J A, Marinissen J C Y, Didden W A M, Lebbink G and Brussard L 1993 Simulation of nitrogen mineralisation in the below-ground food webs of two winter wheat fields. J. Appl. Ecol. 30, 95–106.

Elliott E T and Cambardella C A 1991 Physical separation of soil organic matter. Agric. Ecosyst. Environ. 34, 407–419.

Ferris H, Eyre M, Venette R C and Lau S S 1996 Population energetics of bacterial-feeding nematodes: stage-specific development and fecundity rates. Soil. Biol. Biochem. 28, 271–280.

Ferris H, Venette R C and Lau S S 1997 Population energetics of bacterial-feeding nematodes: carbon and nitrogen budgets. Soil. Biol. Biochem. 29, 1183–1194.

Foereid B and Høgh-Jensen H 2004 Carbon sequestration potential of organic agriculture in northern Europe - a modelling approach. Nutr. Cycl. Agroecosyst. 68, 13–24.

Fontaine S, Mariotti A and Abbadie L 2003 The priming effect of organic matter: a question of microbial competition? Soil. Biol. Biochem. 35, 837–843.

Griffiths B and Robinson D 1992 Root-induced nitrogen mineralisation: A nitrogen balance model. Plant Soil 139, 235–263.

Hassink J, Bouwman L A, Zwart K B and Brussard L 1993 Relationships between habitable pore space, soil biota and mineralisation rates in grassland soils. Soil. Biol. Biochem. 25, 47–55.

Hastings A 2004 Transients: the key to long-term ecological understanding? Trends in Ecol. Evol. 19, 39–45.

Hiltner L 1904 Uber neuerre erfahrungen und probleme auf dem gebiet der bodenbacteriologie und unter besonderer berucksichtung der grundung und brache. Arbeiten der Deutchen Landwirtshafts Gesellschaft 98, 59–78.

Johansson G 1992 Below-ground carbon distribution in barley (*Hordeum vulgare* L.) with and without nitrogen fertilisation. Plant Soil 144, 93–99.

Jordan D W and Smith P 1987 Nonlinear ordinary differential equations. Oxford University Press, Oxford, 381 pp.

Jurgens K and Sala M M 2000 Predator-mediated shifts in size distribution of microbial biomass and activity during detritius decomposition. Oikos 91, 29–40.

Kaye J P and Hart S C 1997 Competition for nitrogen between plants and soil microorganisms. Trends Ecol. Evol. 12, 139–143.

Kiem R and Koegel-Knabner I 2003 Contribution of lignin and polysaccharides to the refractory carbon pool in C-depleted arable soils. Soil. Biol. Biochem. 35, 101–118.

Kuikman P J, Jansen A G, van Veen J A and Zehnder A J B 1990a Protozoan predation and the turnover of soil organic carbon and nitrogen in the presence of plants. Biol. Fertil. Soils 10, 22–28.

Kuikman P J, van Elsas J D, Jansen A G, Burgers S L G E and van Veen J A 1990b Population dynamics and activity of bacteria and protozoa in relation to their spatial distribution in soil. Soil Biol. Biochem. 22, 1063–1073.

Kuzyakov Y, Kretzchmar A and Stahr K 1999 Contribution of *Lolium perenne* rhizodeposition to carbon turnover of pasture soil. Plant Soil 213, 127–136.

Kuzyakov Y, Friedel K J and Stahr K 2000 Review of mechanisms and quantification of priming effects. Soil Biol. Biochem. 32, 1485–1498.

Lambers H 1987 Does Variation in Photosynthetic Rate Explain Variation in Growth-Rate and Yield. Netherlands J. Agric. Sci. 35, 505–519.

Lebaron P, Servais P, Trousselier M, Courties C, Muyzer G, Bernard L, Schafer H, Pukall R, Stackenbrandt E, Guidulain T and Vives-Rego J 2001 Microbial community dynamics in Mediterranean nutrient-enriched seawater mesocosm: changes in abundances, activity and composition. FEMS Microbiol. Ecol. 34, 255–266.

Lynch J M and Whipps J M 1990 Substrate flow in the rhizosphere. Plant Soil 129, 1–10.

Meharg A A and Killham K 1988 Factors Affecting the Pattern of Carbon Flow in a Grass Soil System. J. Sci. Food Agric. 45, 135–136.

Meharg A A and Killham K 1991 A novel method of quantifying root exudation in the presence of soil microflora. Plant Soil 133, 111–116.

Meharg A A and Killham K 1995 Loss of exudates from roots of perennial rye grass with a range of microorganisms. Plant Soil 170, 345–349.

Newman E I and Watson A 1977 Microbial abundance in the rhizosphere: A computer model. Plant Soil 48, 17–56.

Newman E I 1978 Root microorganisms: their significance in the ecosystem. Biol. Rev. 53, 511–554.

Parton W J, Schimel D S, Cole C V and Ojima D S 1987 Analysis of Factors Controlling Soil Organic Matter Levels in Great Plain Grasslands. Soil Sci. Am. J. 51, 1173–1179.

Paterson E, Rattay E A S and Killham K 1996 Effect of elevated atmospheric CO_2 concentration on C-partitioning and rhizosphere C-flow for three plant species. Soil Biol. Biochem. 28, 195–201.

Paustian K, Cole V C, Sauerback D and Sampson N 1998 CO_2 mitigation by agriculture: An overview. Climatic Change 40, 135–162.

Pussard, M, Alabouvette, C and Levrat, P 1994 Protozoan Interactions with the Soil Microflora and Possibilities for Biocontrol of Plant Pathogen. *In* Soil Protozoa, (Ed.) J F Darbyshire. pp. 123–146. CAB INTERNATIONAL, Wallingford, UK.

Rattray E A S, Paterson E and Killham K 1995 Characterisation of the dynamics of C-partitioning within *Lolium perenne* and to the rhizosphere microbial biomass using ^{14}C pulse chase. Biol. Fertil. Soils 19, 280–286.

Robinson D, Griffiths B, Ritz K and Wheatley R 1989 Root-induced nitrogen mineralisation: A theoretical analysis. Plant Soil 117, 185–193.

Rutherford P M and Juma N G 1992 Influence of texture on habitable pore space and bacterial-protozoan populations in soil. Biol. Fertil. Soils 12, 221–227.

Smith P, Powlson D S, Glendining M J and Smith J 1997 Potential for carbon sequestration in European soils: preliminary estimates for five scenarios using results from long-term experiments. Global Change Biol. 3, 67–79.

Smith P, Powlson D S, Smith J U, Fallon P and Coleman K 2000 Meeting Europe's climate change commitments: quantitative estimates of the potential for carbon mitigation by agriculture. Global Change Biol. 6, 525–539.

Swinnen J, van Veen J A and Merckx R 1995 Root decay and turnover of rhizodeposits in field-grown winter wheat and spring barley estimated by ^{14}C pulse-labelling. Soil Biol. Biochem. 27, 211–217.

Sylvia D M, Fuhrmann J J, Hartel P G and Zuberer D A 1998 Principles and Applications of Soil Microbiology. Prentice Hall, New Jersey

Thornton B, Paterson E, Midwood A J, Sim A and Pratt S M 2004 Contribution of current assimilation in supplying root exudates of *Lolium Perenne* L. measured using steady-state ^{13}C labelling. Physiol. Plant 120, 434–441.

Toal M E, Yeomans C, Killham K and Meharg A A 2000 A review of rhizosphere carbon flow modelling. Plant Soil 222, 263–281.

Uren N C 2001 Types, Amounts, and Possible Functions of Compounds Released into the Rhizosphere by Soil-Grown Plants. Eds. Pinton, R, Varanini, Z, Nannipieri, P The Rhizosphere Biochemistry and Organic Substances at the Soil-Plant Interface, pp. 19–40. Marcel Dekker, New York, USA.

Wardle D 1999 How soil food webs make plants grow. Trends Ecol. Evol. 14, 418–420.

Zelenev V V van Bruggen A H C and Semenov A M 2000 'BACWAWE', a Spatial-Temporal Model for Travelling Waves of Bacterial Populations in Response to a Moving Carbon Source in Soil. Microb. Ecol. 40, 260–272.

Zheng D W, Bengtsson J and Ågren G I 1997 Soil food webs and ecosystem processes: decomposition in donor-control and Lotka-Volterra systems. Am. Nat. 149, 125–148.

Zwart K B and Brussard L 1991 Soil fauna and cereal crops. *In* The Ecology of Temperate Cereal Fields (Eds) L G Furbank N Carter J F Darbyshire and G R Potts. pp. 139–167. 32th Symposium of the British Ecological Society, Blackwell Scientific Publications, Oxford, 469 pp.

Zwart K B and Darbyshire J F 1992 Growth and nitrogenous excretion of a common soil flagellate *Spumella sp.* – A laboratory experiment. J. Soil Sci. 43, 145–157.