Modeling rhizosphere carbon and nitrogen cycling in *Eucalyptus* plantation soil

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Abstract. Vigorous *Eucalyptus* plantations produce 10^5 to 10^6 km ha^{-1} of fine roots that probably increase carbon (C) and nitrogen (N) cycling in rhizosphere soil. However, the quantitative importance of rhizosphere priming is still unknown for most ecosystems, including these plantations. Therefore, the objective of this work was to propose and evaluate a mechanistic model for the prediction of rhizosphere C and N cycling in *Eucalyptus* plantations. The potential importance of the priming effect was estimated for a typical *Eucalyptus* plantation in Brazil. The process-based model (ForPRAN - Forest Plantation Rhizosphere Available Nitrogen) predicts the change in rhizosphere C and N cycling resulting from root growth and consists of two modules: (1) fine root growth, and (2) C and N rhizosphere cycling. The model describes a series of soil biological processes: root growth, rhizodeposition, microbial uptake, enzymatic synthesis, depolymerization of soil organic matter, microbial respiration, N mineralization, N immobilization, microbial death, microbial emigration and immigration, SOM formation. Model performance was quantitatively and qualitatively satisfactory when compared to observed data in the literature. Input variables with most influence on rhizosphere N mineralization were (in order of decreasing importance): root diameter > rhizosphere thickness > soil temperature > clay concentration. The priming effect in a typical *Eucalyptus* plantation producing 42 $m^3\,ha^{-1}\,year^{-1}$ of shoot biomass, with assumed losses of 40 % of the total N mineralized, was estimated to be 24.6 % of plantation N demand (shoot + roots + litter). The rhizosphere cycling model should be considered for adaptation to other forestry and agricultural production models where the inclusion of such processes offer the potential for improved model performance.

1 Introduction

Nitrogen is a nutrient essential for plant growth and sustainability of natural and managed ecosystems, including *Eucalyptus* plantations (Barros and Novais, 1990; Jesus et al., 2012; Pulito et al., 2015; Smethurst et al., 2015). Low N availability commonly limits plantation growth, and plantations on soils with low organic matter concentrations are most severely affected (Barros and Novais, 1990; Pulito et al., 2015; Smethurst et al., 2015) as most N taken up by trees comes from decomposition of soil organic matter (i.e. N mineralization) (Barros and Novais, 1990; Pulito et al., 2015; Smethurst et al., 2015).

Measurements of *in situ* net N mineralization are laborious, but can be predicted to some degree using models. Smethurst et al. (2015) evaluated a process-based model (SNAP) for estimating net N mineralization in *Eucalyptus* plantations in southeastern Brazil. The authors estimated annual rates of net N mineralization ranging from 148 to 340 kg ha^{-1} per year of N in the 0-20 cm soil depth, with additional available N expected in deeper soil layers. These rates of N supply were similar to or higher than the N demand of young plantations in the region, and therefore consistent with the observation that growth responses to N fertilization were minor or absent. An extension of the *in situ* core measurement used can estimate N uptake by plantations and has been independently validated (Smethurst and Nambiar, 1989). However, spatial and other methodological errors in this core technique are high. One source of error relates to severing of roots at the start of *in situ* field incubations, which may lead to a disturbance of rhizosphere processes (i.e. N turnover) associated with root exudation and decomposition. Therefore, understanding and quantifying rhizosphere processes could lead to reduced errors in estimates of N supply in Brazilian *Eucalyptus* plantations.

There is speculation that rhizosphere processes might be a significant source of N supply for some trees (Grayston et al., 1997), as the roots and litter from the trees create environments more favorable to microbial activity than occur in bulk soil. This effect is mainly due to the release of C to soil in the form of dead roots or rhizodepositions (secretions, lysates, gases, mucilages, etc). Therefore, the effect of the plant on biological activity in the rhizosphere may be important for the prediction and measurement of biological phenomena like net N mineralization in a range of ecosystems. Finzi et al. (2015) estimated that the mineralization in rhizosphere soil of temperate forests can represent 1/4 of all mineralized N in the ecosystem. This high rate of N supply from rhizosphere processes is explained by exudates released by tree roots that include carbohydrates, amino acids, organic acids, fatty acids, phenolic acids, vitamins, volatile compounds, and growth factors (Grayston et al., 1997), which serve as substrates for the growth of soil microbes and their production of enzymes (Drake et al., 2013). This effect of C addition on microbial behavior and, consequently, on SOM mineralization, is popularly known in the scientific literature as the priming effect, which is described in detail for soil under *Eucalyptus* by Derrien et al. (2014).

Hurtarte (2017), in a study under greenhouse conditions, observed that in the rhizosphere of *Eucalyptus* seedlings contains significant amounts of citric, malic and oxalic acids, as well as sucrose, alose, fructose, glutamine, inositol and asparagine. The author found that the release of these organic compounds was associated with decreased total N concentration in the rhizosphere, suggesting a nutritional benefit for the *Eucalyptus* seedlings. Also in a native *Eucalyptus* forest after fire,

Eucalyptus roots enhanced microbial activity and N mineralisation (Dijkstra et al., 2017). Despite these advances, there are no quantitative studies examining the importance of the priming effect in *Eucalyptus* plantations.

In relation to plant systems in general, and based on Schimel and Weintraub (2003) and Allison et al. (2010), Drake et al. (2013) developed the Microbial C and N Physiology general model (abbreviated as MCNiP by Davidson et al., 2014) to estimate C and N rhizosphere cycling. In this model, mineralization rates depend on system stoichiometry and soil temperature. However, to improve the application of this model, it needed to be linked to plant growth and root development, as well as microbial population dynamics as affected by water, nutrients and other soil properties.

The objectives of this work were to (1) propose a model for estimating rhizosphere C and N cycling in *Eucalyptus* plantation soil, (2) evaluate model performance and input sensitivity, and (3) estimate the potential importance of rhizosphere priming on N supply in a typical *Eucalyptus* plantation in Brazil.

2 Methods

2.1 ForPRAN theoretical model

The Forest Plantation Rhizosphere Available N model (ForPRAN) is based on the laws of conservation of matter and energy and on the principle that systems seek self-organization as a strategy of self-preservation. One of these strategies is cooperation between organisms for mutual benefit (mutualism). In this case, trees release organic compounds that modulate the rhizosphere microbial processes. The release of organic compounds into the rhizosphere provides energy and labile nutrients - factors in greater abundance for it and scarce for microbiota - and receives in return a higher supply of N and other nutrients mineralized from soil organic matter. This symbiosis involves shoots, roots, soil microbes, and other soil properties, the biological components of which may have co-evolved to sustain N and energy fluxes in the forest ecosystem. The application presented is for *Eucalyptus*, but the principles and model could be adapted to other plant-soil systems where data are available to guide parameterization. The process is schematically summarized in Figure 1.

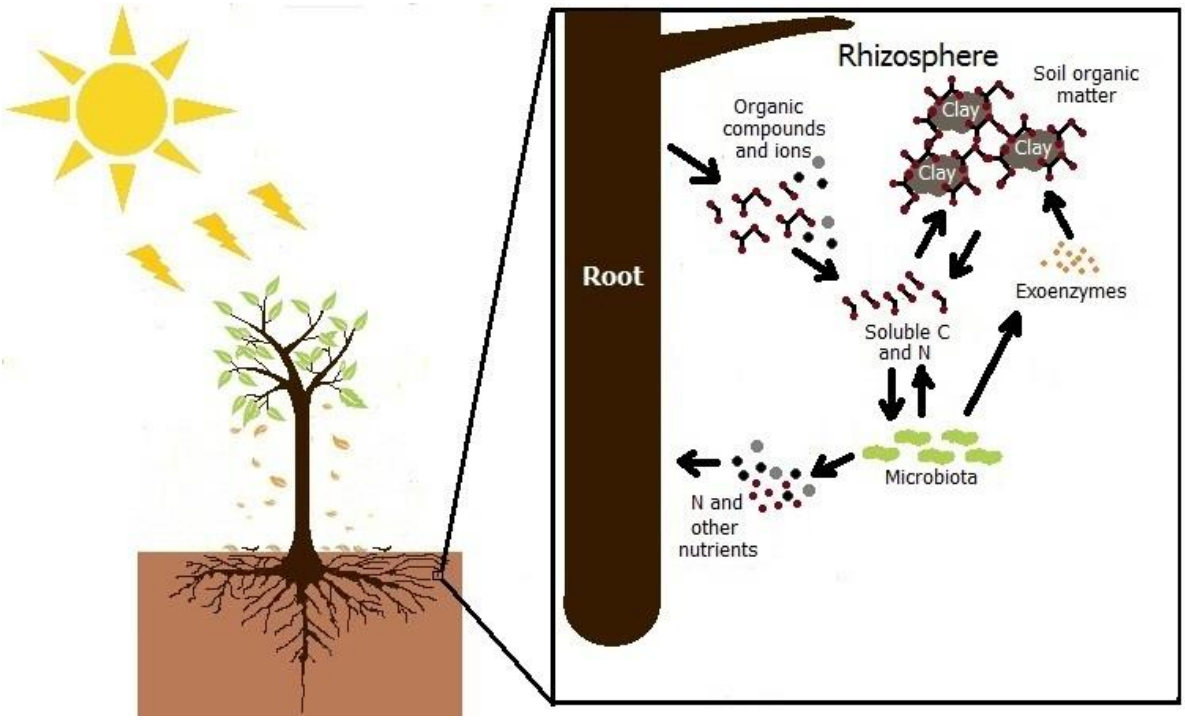

Figure 1. Illustration of rhizosphere C and N cycling processes in the ForPRAN model

Rhizosphere N supply is described as a function of key variables that reflect the complexity of the N cycle in the rhizosphere. These variables can be grouped into three categories, which are related to: 1- rhizosphere dimensions (root diameter; rhizosphere thickness; clay concentration; soil layer considered; dry matter of aerial part); 2- C and N availability and microbial demand and metabolism (C radicular efflux rate; soil organic matter concentration; rhizodeposition C/N ratio; soil C/N ratio; enzymes C/N ratio; microbiota C/N ratio; soil protection capacity); 3- conditions that affect microbial turnover (total porosity; moisture; temperature).

2.1.1 Rhizosphere dimensions

Rhizosphere volume is one of the most important factors influencing the priming effect. In the logic of ForPRAN, rhizosphere volume is related to the length of fine roots and their diameter and also to the thickness of the rhizosphere. Root length is strongly related to shoot biomass as the source of stored and newly fixed C (Mello et al., 1998; Neves, 2000; Leles, 2001; Teixeira et al., 2002; Gatto et al., 2003; Maquere, 2008). Root length is also related to soil clay concentration in association with its effects on available water and nutrients. Rooting depth also affects N priming, as roots are usually concentrated in the top 30 cm of soil (Mello et al., 1998). The thickness of the rhizosphere depends on the nature and amount of rhizodeposited compounds (Finzi et al., 2015) and soil properties, but for simplicity ForPRAN uses a constant user-specified value of thickness based on observations by Jones (1998), Barber (1995), Sauer et al. (2006) and Hurtarte (2017).

2.1.2 C and N availability and microbial demand

The model follows the logic of stoichiometric balance between substrate supply and microbial demand, and the 'Law of the Minimum' applied to the microbial processes, as presented by Schimel and Weintraub (2003), Allison et al. (2010), Drake et al. (2013), and Finzi et al. (2015). In general, the model assumes that an increase in the availability of organic substrates increases microbial biomass and enzyme production, and therefore the processes related to soil organic matter mineralization. Microbial processes are affected in different ways according to the availability of organic C and N. For instance, when the availability of N exceeds microbial demand, C becomes a limiting factor leading to an increase in net N mineralization and C immobilization. On the other hand, when C availability exceeds microbial demand, N becomes the limiting factor leading to an increase in respiration and net N immobilization. Substrate availability for these processes is modulated by soil protection that in turn depends mainly on the amount of clay, mineralogy, a and soil C content (degree of saturation of clays by organic C). Protection of C by the soil matrix prevents microbes accessing such C to satisfy nutritional demands and thereby limits microbial growth (Silva et al., 2011). On the other hand, if soil has minimal C and N protection, these resources are more readily available to microbial attack (Silva et al., 2011).

2.1.3 Factors affecting microbial turnover

Soil moisture affects microbial metabolism because of its role as a universal solvent (i.e. all microbial reactions depend on water) (Brock and Madigan, 1991; Abramoff et al., 2017). The positive effect of moisture increase on microbial processes is very important in tropical environments where it varies greatly. In conditions of low water availability, microorganisms expend more energy adapting to their electrochemical environment, often by synthesizing proline and glutamine or by taking up K^+ (Brock and Madigan, 1991). However, such mechanisms do not always compensate for water deficit, leading to reduce microbial biomass under dry conditions (Sato et al., 2000). This effect is presented in ForPRAN model by means of a modifier (Ku) in the microbial death rate (Kmf), the value of which is inversely proportional to water availability.

Temperature is another important factor affecting microbial metabolism, that operates in two opposing ways. Rising temperatures are responsible for elevated rates of chemical and enzymatic reactions (Brock and Madigan, 1991). Such increases have a positive impact on microbial biomass and therefore are related to increases in CO_2 evolution and N mineralization rates (Brock and Madigan, 1991). On the other hand, above a certain temperature microbial cellular components are denatured (like exo-enzymes), causing microbial process rates to fall sharply (Brock and Madigan, 1991). We assumed that temperature influences enzymatic kinetics by being optimal in the range 25 °C to 40 °C and decreasing rapidly at higher

and lower values. This effect was implemented in the ForPRAN model through the KappaD variable that influences the rate of SOM enzymatic depolymerization and, consequently, the rate of microbial growth.

In ForPRAN, soil physical conditions affect microbial communities via porosity. Extremes of porosity reduce microbial biomass and consequently C and N mineralization (Silva et al., 2011). This change occurs because soil porosity affects the concentration and transport of O_2 (Torbert and Wood, 1992), as well as the liquid and solute movement, and C and N protection by the soil matrix (Silva et al., 2011). This effect is presented in ForPRAN by means of a modifier (Kpt) of the microbial death rate (Kmf), for which extreme values raise the Kmf rate in accordance with data present by Silva et al. (2011).

2.2 Mathematical model overview

ForPRAN model processes are based on previously developed functions, and also on functions developed in the present work. We used data from literature to parameterize the model. The model has two sequential parts: (1) a module of fine root growth and rhizodeposition, and (2) a module of C and N turnover in the rhizosphere (Figure 2).

In the first part we used the 3-PG model (Landsberg and Waring, 1997) to represent the conversion of light energy to dry vegetable matter. The 3-PG model is used widely for this purpose by researchers and managers in the forest plantation industry (Almeida and Sands, 2016). Root biomass and depth are estimated in 3-PG, but not root length density of fine roots. To represent the growth of fine roots (including root length density), we used a non-linear model fitted to the data of Mello et al. (1998), Neves (2000), Leles et al. (2001), Teixeira et al. (2002), Gatto et al. (2003), and Maquere (2008). Then the rate of C and N release processes from roots are calculated according to Personeni et al. (2007) and Farrar et al. (2003).

In the second part of the model, we described the rhizosphere C and N cycling system. To do so, we modified the MCNiP model (Drake et al., 2013; Davidson et al., 2014) to include the effects on microbes of soil moisture, physical conditions, temperature (effect on exo-enzymes kinetics), and microbial immigration and emigration (Figure 2).

The model simulates the effect of *Eucalyptus* roots on C and N cycling in rhizosphere soil, with particular focus on N availability and C balance. The model does not simulate N availability or C balance in bulk soil, and changes in rhizosphere C and N do not feedback to affect plant growth. For the latter, a more complex plantation production model than 3-PG is required as 3-PG does not explicitly consider N cycling. Further details of the model are presented in the Supplementary Material section.

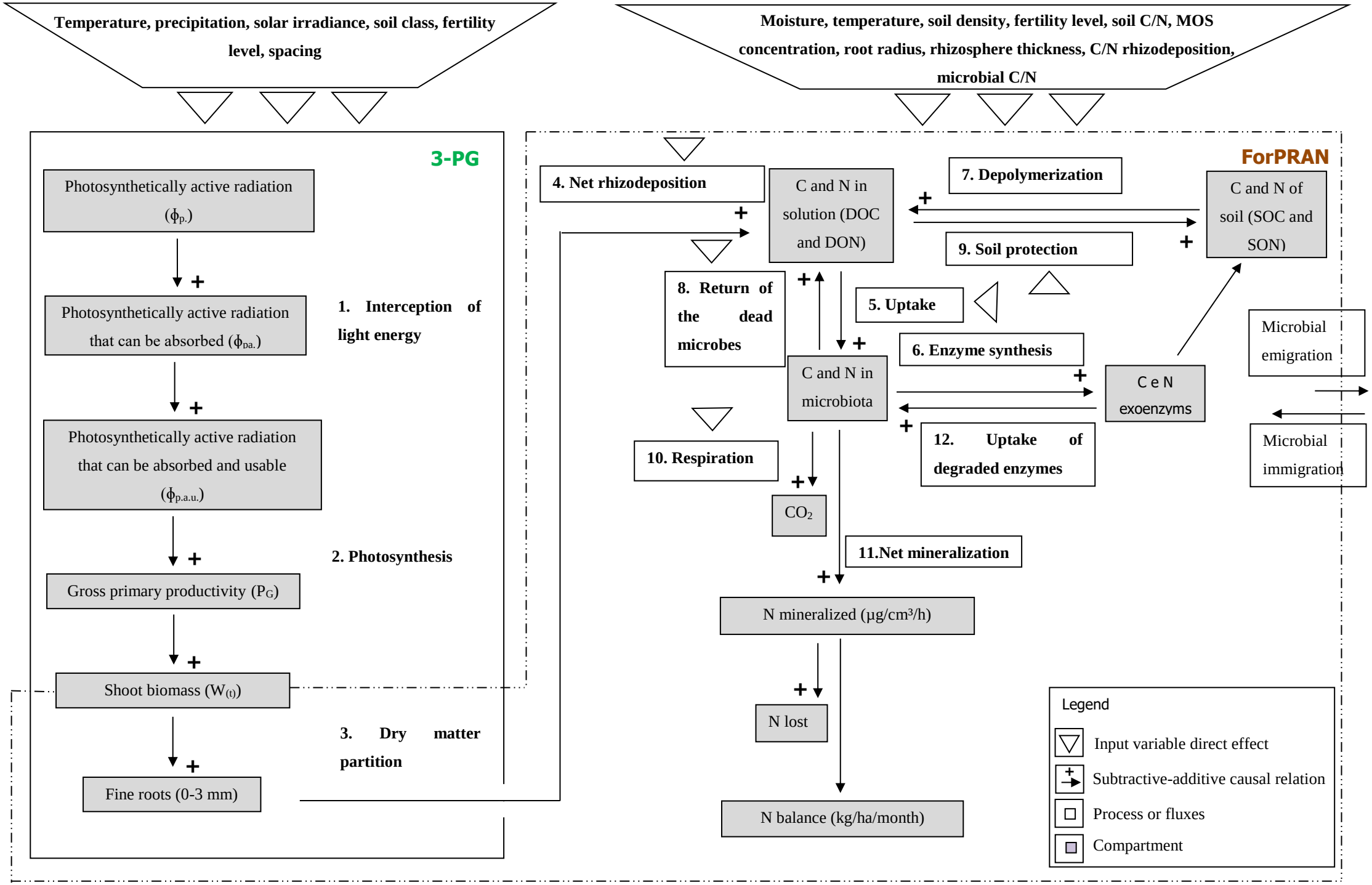

Figure 2. Flow chart of processes represented in the ForPRAN model

2.3 Parameter estimation

Most of the parameters present in ForPRAN were based on values observed in previous studies. For instance, parameters used for modelling fine root growth and rhizodeposition were based in several studies: Mello et al. (1998), Neves (2000), Leles et al. (2001), Teixeira et al. (2002), Gatto et al. (2003), Maquere (2008), and Personeni et al. (2007). Other parameters used for simulating C and N cycling in rhizosphere soil were based mainly on the studies of Schimel and Weintraub (2003), Allison et al. (2010), and Drake et al. (2013). In addition, data were used from Sato et al. (2000), Neergaarda and Magid (2001), Silva et al. (2011) to estimate the modifying coefficients of population dynamic in relation to the effects of water, soil organic matter and soil physical conditions. A detailed presentation of the parameters used and their respective data sources is presented as Supplementary Material.

2.4 Evaluation of the rhizosphere model

During model development, substrate use efficiency was assumed to be 0.3 μg μg^{-1} (SUE, Table S2 of Supplementary Materials) for conditions of low availability of C and N. For higher N availability, we assumed more efficient use of C (SUE = 0.35 μg μg^{-1}). We also assumed a low rate of enzyme production of 0.0075 μg C μg^{-1} h^{-1} (Kep) in the absence of C and N, while in the presence of both C and N this value was assumed intermediate (0.0125 μg C μg^{-1} h^{-1}), and 0.02 μg C μg^{-1} h^{-1} in the presence of C only (in the absence of N). This range was used to reflect more investment in enzymes to try to meet the microbial demand for N when C is not the most limiting nutrient.

The following are the main statistics used to describe the performance of the model in predicting microbial behavior under different treatments presented in Drake et al. (2013). The experiment of Drake et al. (2013) measured microbial biomass inclueded after daily pulse of water, water+C and water+C+N during early summer.

1- A linear model of the type $O = \boldsymbol{\beta}_1 P + \boldsymbol{\beta}_0$ was fitted, where P is the value predicted by the model, and O is the value observed in field experiments. Model performance was evaluated through the coefficient of determination (R^2). In addition, coefficient $\boldsymbol{\beta}_1$ was tested for significant difference from 1, and coefficient $\boldsymbol{\beta}_0$ for significant difference from 0 using t-tests.

2- Nash Sutcliffe efficiency (NSE), which describes the relative magnitude of the residual variance compared to the measured data variance (Moriasi et al., 2007).

$$NSE = 1 - \frac{\sum_{i=1}^{n}(P_i - O_i)^2}{\sum_{i=1}^{n}(O_i - \bar{O})^2} \quad \text{Eq. 1}$$

3- Mean Error (ME), which indicates any bias in the predictions.

$$ME = \frac{1}{n}\sum_{i=1}^{n}(P_i - O_i) \quad \text{Eq. 2}$$

4- Mean Absolute Error (MAE), which provides a simple description of the magnitude of estimation errors.

$$MAE = \frac{1}{n}\sum_{i=1}^{n}|P_i - O_i| \quad \text{Eq. 3}$$

5- Root Mean Square Error to Standard Deviation Ratio (RSR), which provides a standardized value of the root mean square error.

$$RSR = \frac{\sqrt{\sum_{i=1}^{n}(O_i - P_i)^2}}{\sqrt{\sum_{i=1}^{n}(O_i - \bar{O})^2}} \quad \text{Eq. 4}$$

6- A qualitative evaluation was presented considering the relationship between the increases on root exudation effect on microbial biomass vs the exo-enzymes production, respiration and total N of soil.

2.5 Sensitivity analysis

In the sensitivity analysis, each variable was increased and decreased in comparison to a base value, while keeping other inputs constant. In this way, the effect of each input variable on the response variable (e.g. N availability) was estimated. The ranges of values tested for each variable were based on natural variability. The sensitivity analysis was standardized using Equation 5 (Allison et al., 2010).

$$Sensitivity\ (S) = \frac{|\log|higher\ output| - \log|lower\ output||}{|\log|higher\ input| - \log|lower\ input||} \quad \text{Eq.5}$$

3 Results and Discussion

3.1 Statistical parametrization and evaluation of the model

3.1.1 Fine root biomass

Predicted fine root biomass had a satisfactory fit with observations (R^2 = 0.75; Figure 3). The intercept was not significantly different from 0 and the slope of 1.01 was not significantly different from 1. These results are satisfactory considering the difficulty in obtaining root data and the simplicity of the equation ($MSfr = aClay^b\ TSL^c\ MDAP^d$).

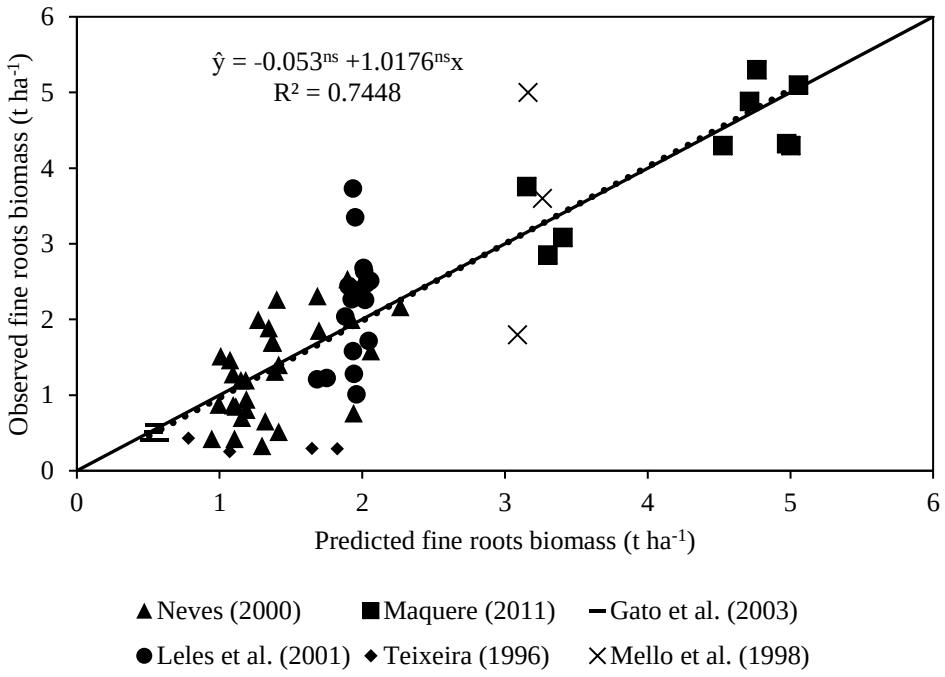

Figure 3. Regression of fine root biomass reported in literature against values predicted using the ForPRAN model. The dotted line is the mean regression, with neither intercept nor slope significantly different from 0 or 1, respectively. Solid line: 1:1 relationship.

3.1.2 Rhizosphere processes

The model satisfactorily simulated microbial biomass across the range of observed data (Figure 4); the intercept was not significantly different from 0 and the slope of 0.89 was not significantly different to 1, with $R^2 = 0.91$ and NSE = 0.90. Mean Error (ME) (0.02) and Mean Absolute Error (MAE) (1.77) indicate that the error associated with predictions was low considering the range of the observed values (19.7-38.2 µg C g^{-1}). The value of RSR was 0.32, which is low according to Moriasi et al. (2007). Simulation of the experiment performed by Drake et al. (2013) indicated daily fluctuations in microbial biomass, and the expected longer-term differences between treatments where maximum microbial biomass occurred with +C+N, intermediate with +C-N, and least with only water (-C-N) added (Figure 5).

Qualitatively, microbial behaviour predicted by ForPRAN when microorganisms received C were as expected (Figure 6). As C availability increased, biomass increased, which is in response to increased exo-enzyme production and respiration. Conversely, when microbial biomass increased there was a tendency for reduced total organic N – a condition in which the decomposition of native soil organic matter can surpass the formation of new SOM in the rhizosphere.

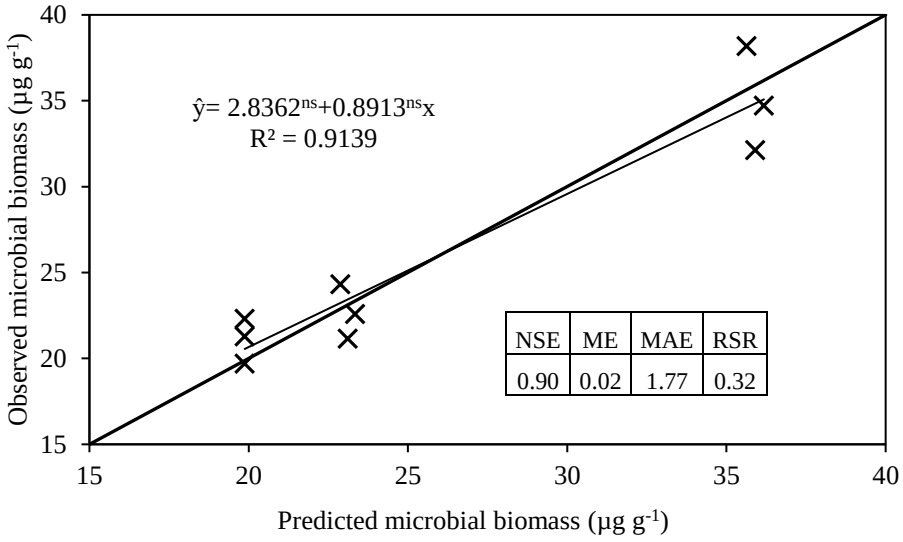

Figure 4. Regression of microbial biomass observed by Drake et al. (2013) against ForPRAN results. Regression parameters were not significantly different from 1 (slope) and 0 (intercept), respectively. Nash Sutcliffe Efficiency (NSE), Mean Error (ME), Mean Absolute Error (MAE), and Root Mean Square Error to Standard Deviation Ratio (RSR) are indicators of model efficiency and bias.

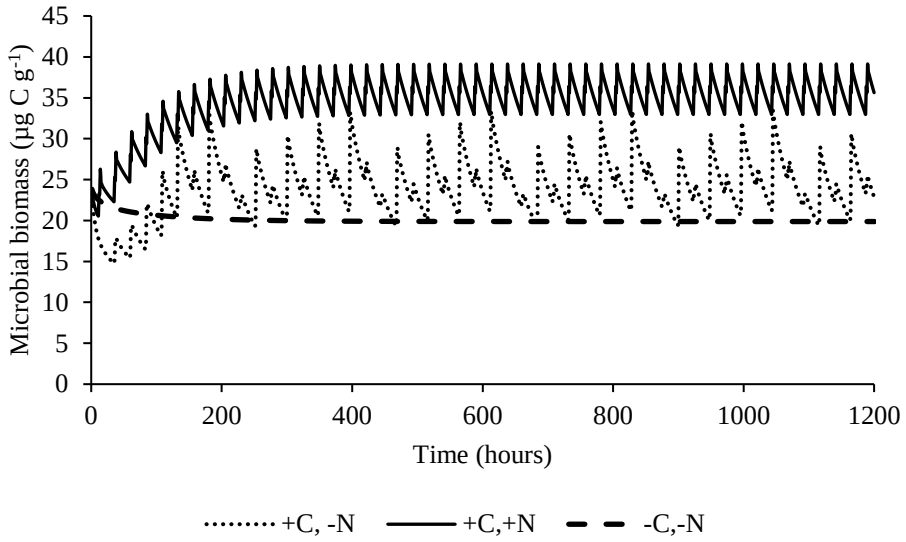

Figure 5. Predicted effect of daily pulses of substrates containing water, water+C or water+C+N (as occurred in Drake et al., 2013) on microbial biomass during 50 days of treatment.

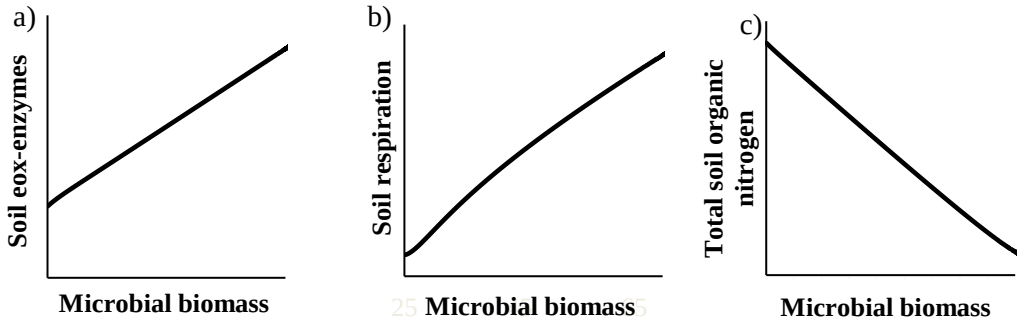

Figure 6. General trends predicted by the ForPRAN model of a) soil exo-enzymes b) soil respiration and c) total soil organic N as a function of microbial biomass under conditions of increasing availability of C and N

3.2 Sensitivity analysis

3.2.1 Modeling fine root growth and rhizodeposition

The length of fine roots is of high importance for rhizosphere processes, because it partially defines the volume of the rhizosphere, and root length is an output of the model, not an input. Hence, for a given amount of C allocation to fine roots and an assumed constant carbon concentration in roots, an increase in the upper limit of root diameter classes considered as fine roots leads to a commensurate increase in root length, and it is one of the parameters to which the model is most sensitive (Table 1). Comparatively, model outputs were less sensitive to soil clay concentrations, layer depth, and shoot mass (Table 1). Volume of the rhizosphere had similar sensitivity as root diameter, and the thickness of the rhizosphere was the second variable that most influenced total volume (Table 4).

For a given root system, the larger the diameter considered to have a rhizosphere effect in the range 0-3 mm, the greater the estimated total root length and the larger the rhizosphere volume. On the other hand, when clay concentration was varied, an inverse relationship was observed with root length. For soils with lower clay concentrations, the model estimated higher values of fine root length and, consequently, rhizosphere volume, and vice versa (Table 1). According to Reis et al. (1985), *E. grandis* sites in soils of poorer quality (chemical and water characteristics) tend to present higher investment in

roots compared to those of better quality, which explains the lower shoot-to-fine root ratio in sites with higher clay concentration (soils which have greater capacity to retain water and nutrients). In the case of the input variable thickness of the soil layer within a given soil profile, there is a direct relation such that increasing soil layer thickness also increases the total length of fine roots and the volume of rhizosphere. In such a case though, there would be less soil depth (and rhizosphere volume) remaining in the rest of the profile. Finally, when shoot mass was varied, there was also a direct relation with root length and rhizosphere volume. Although these qualitative changes to rhizosphere volume in the sensitivity analysis were therefore logical, this analysis provides an indication of the relative quantitative importance of each of the inputs analyzed.

Root length in the base condition was 17,308 km ha^{-1}, for a stand with 140 t ha^{-1} of aboveground biomass, soil with 30 % clay, soil depth of 0-25 cm and roots up to 1 mm in diameter (Table 1). Minimum root length observed in the sensitivity analysis was associated with root diameter of 0.25 mm (1,069 km ha^{-1}), and maximum length occurred with clay of 10 % (47,555 km ha^{-1}). Melo et al. (1998) found values ranging from 40,880 to 497,844 km ha^{-1} for the 0-30 cm soil depth, which varied with genetic material and the type of propagation. In the case of rhizosphere volume, for our base condition of a rhizosphere thickness of 0.5 mm, the volume of soil was 135,937.5 dm^3, which was approximately 5.4 % of total soil volume. Similarly, the lowest value of rhizosphere volume occurred when root diameter was less than 0.25 mm (<1 % of soil volume). The highest value observed was at the upper limit of diameter for fine roots (3 mm), with a value of 461,767 dm^3 (18.5 % of soil volume).

The value of the rhizosphere soil volume simulated by ForPRAN does not deviate from the estimates of Finzi et al. (2015), according to which the volume occupied by the rhizosphere of temperate forests is between 5 and 25 % of the total soil volume. The volume of rhizosphere soil is determined by root length and rhizosphere thickness (Finzi et al., 2015). As root length here was based on field measurements (Mello et al., 1998; Neves, 2000; Leles, 2001; Teixeira et al., 2002; Gatto et al., 2003; Maquere, 2008), greater remaining uncertainty about the volume of rhizosphere would be related to its thickness. This, in turn, depends on the amount and nature of rhizosphere deposits, and on the physical, chemical and biological properties of the soil that limit the distribution of those deposits beyond the root surface (Finzi et al., 2015). Default rhizosphere thickness in ForPRAN was 5 mm, which is somewhat conservative as literature values are 0.2-1 mm (Jones, 1998), 2-12 mm (Sauer et al., 2006) and up to 20 mm (Barber, 1995). A better understanding of this aspect might be important for future improvements in ForPRAN, whereby C transport models from the root surface towards bulk soil could be based on soil properties.

During release of rhizodeposits, using the model of Personeni et al. (2007), it was noted that there were certain simplifications of the process. After 8 hours of C and N rhizodeposition, it was assumed that the model reaches maximum values of 7.5 and 0.75 μg cm^{-3} h^{-1}, respectively, with no change thereafter. In nature, this value can be altered as a function of the source-sink relations in the plant, root development (Finzi et al., 2015), and of physical and chemical soil properties such as P availability and the presence of Al (Farrar et al., 2003).

In order of decreasing importance, the variables that most influenced the total amount of C rhizodeposition were: root diameter > rhizosphere thickness = root efflux rate > clay content > soil layer thickness considered > aboveground biomass (table 2). After 10,000 hours for a stand of 140 t ha^{-1} of shoot (70.42 t ha^{-1} of C), about 1,274.4 kg ha^{-1} of C in rhizodeposits was estimated to have been produced, which was 1.8 % of shoot net primary production. The minimum value of rhizodeposition observed in the sensitivity analysis occurred when roots with a diameter equal to or less than 0.25 mm were assumed (19.7 kg ha^{-1} of C, or 0.02 % of the net primary productivity). The highest value observed was when all roots with diameter up to 3 mm (4,329 kg ha^{-1} of C, or 6.15 % of the net primary productivity of the shoot) were considered, which demonstrates the influence of root length on the calculation of the rhizodeposition.

As far as a typical *Eucalyptus* plantation is concerned, the only approximation we have at an ecosystem scale is the study of Aoki et al. (2012), who studied soils with low levels of P supporting several species of the Myrtaceae family to which *Eucalyptus* belongs. The estimates above are in general agreement with Aoki et al. (2012), who showed that species of Myrtaceae, represented by the genera *Syzygium* and *Tristaniopsis* had exuded large amounts of C in the form of organic acids.

The above authors attributed this remarkable exudation capacity to high specific root surface root, high number of root apices, and also to the ability of the plant to up-regulate exudation in low P soils.

3.2.2 Modeling C and N cycling in rhizosphere soil

According to our model, the variables that most influenced the population dynamics of rhizosphere microbiota were the following (in order of decreasing importance): soil porosity > soil temperature > soil organic matter > radicular efflux rate (Table 2). The maximum observed value was 142 μg g^{-1}, when soil temperature was 35 °C. The main effect of temperature was on exo-enzymes kinetics, as described by the KappaD variable in figure 7, which is based on Brock and Madigan (1991). Enzymatic activity in ForPRAN is maximized between 25 and 40 °C (Figure 7).

We used data presented by Silva et al. (2011) for Oxisol soils to establish a relationship between porosity and ideal conditions for microbial growth (Figure 8). This empirical relationship led us to conclude that porosity values close to 0.53 cm^3 cm^{-3} were most favorable for the survival of microorganisms (using soil particle density of 2.60 g cm^{-3}). The effect of soil moisture on microbial biomass was based on the work of Sato et al. (2000), where more pronounced limitations on microbial biomass were observed under soil moisture conditions below 40 % of field capacity (Figure 9).

Increasing the supply of C and N in the rhizosphere led to growth of the rhizosphere microbial population in ForPRAN simulations. The model simulated values with a mean of 53 μg g^{-1} (or μg cm^{-3} for 1 g cm^{-3} soil bulk density), which corresponds to the values presented in the second quartile of 206 field observations of *Eucalyptus* plantations of southeastern Brazil (Figure 10). When temperature and the amount rhizodeposited C was reduced, the population decreased (Table 2) and became more similar to the populations represented by the first and second quartiles of Figure 10. Silva et al. (2010) reported mean values of 358 μg microbial biomass per g soil, for the 0-20 cm depth of a soil planted with *Eucalyptus* in Minas Gerais State, Brazil, which was higher than the maximum values observed under the sensitivity analysis conditions (153 μg g^{-1}). Gama-Rodrigues et al. (2008) observed microbial biomass (C) of 80.6 μg g^{-1} (Aracruz/ES), 310.2 μg g^{-1} (Guanhães/MG), 95.3 μg g^{-1} (Luís Antônio/SP), 62.4 μg g^{-1} (Lençóis Paulista/SP). Therefore, values of microbial biomass vary significantly with forest site, some of the complexity of which may be represented in the ForPRAN model.

As a result of biological activity in the rhizosphere, average values of mineralized N (accumulated for the 10,000 h period) of about 87.8 kg ha^{-1} were simulated (Table 2) and a maximum of 300 kg ha^{-1} summing the contribution referring to mineralization influenced by the roots with diameters between 0 to 3 mm. A minimum value of 1.4 kg occurred with root diameter up to 0.25 mm. The variables that most influenced this process were (in descending order of importance): root diameter > rhizosphere thickness > soil temperature > clay content (Table 2). Finzi et al. (2015) estimated that N mineralization in rhizosphere soil of temperate forests can represent 1/4 of all mineralized N in the ecosystem. Our work supports the hypothesis that rhizosphere processes are quantitatively important, which might also explain why in some soils supporting *Eucalyptus* plantations there is a trend of decrease in organic matter content (Pulito et al., 2015). However, the mobilization of C and N through the rhizosphere can be counterbalanced by other processes related to the cycle of these nutrients in the forest soil, leading to conditions of greater stability of SOM stocks in well managed forests and in better quality sites. In complex systems, changes in factors could act individually or in combination, e.g. soil or climatic factors, and result in changes in soil organic matter. Such changes could potentially be simulated through further improvements to the ForPRAN model, e.g. by combining it with a more complex plant production and soil model such as APSIM (Holzworth et al., 2014).

The balance of inorganic N in the system expresses potential N gain by the plant as a result of interaction with the soil microbes (Table 2). The actual gain of N by the plant (assimilated) is lower than the mineralized values presented previously because the plant has to release some N to induce the priming effect. The balance for standard conditions for a 10,000 h simulation was of 24.15 kg N ha^{-1}, and the maximum value reached in the sensitivity analysis at a temperature of 35 °C (228.15 kg ha^{-1}) (Table 2). The minimum value observed was when rhizodeposition occurred at a C/N ratio 5, which led to

a negative balance of about -26 kg ha^{-1} for the *Eucalyptus* plant (Table 2). In this case, the plant released more N than it took up as a result of rhizosphere priming effect. Input variables that most influenced N balance were (in descending order of importance): soil temperature > soil C/N ratio > soil protection capacity > rhizodeposition C/N ratio.

3.2.3 Rhizosphere priming in a typical *Eucalyptus* plantation

A typical *Eucalyptus* plantation was simulated for scenarios with soils of two C protection capacities (15 and 30 %), and otherwise standard conditions of the sensitivity analysis were assumed (Table 1 and 2): a rhizosphere thickness of 3 mm (Hurtarte, 2017), and root of 0 to 3 mm in diameter. With high soil C and N protection there was a low or negative potential for rhizosphere N supply (or N gain to the plant). Under these conditions, *Eucalyptus* plants would be expected to be more responsive to N fertilization. However, under conditions of lower C and N protection (15 %) and 4 % SOM, rhizosphere supply was estimated to contribute significantly to the N balance. For these conditions, which are speculative, the process had a positive balance for the plant equal to 24.6 % of N demand by the ecosystem (root + shoot + litter) or 38.4 % of tree (root + shoot) demand, which also assumed losses of 40 % due to leaching, denitrification and volatilization. This is a *Eucalyptus* plantation situation in which it is probably important to consider rhizosphere priming when simulating plant production. Likewise, the model should be considered for adaptation to other forestry and agricultural production models where the inclusion of such processes offers the potential for improved model performance.

This result supports the understanding of how *Eucalyptus* trees are able to take up high amounts of N, even under conditions of reduced nitrogen fertilization (Melo et al., 2016; Pulito et al., 2015; Smethurst et al., 2015). This effect may be related to the observation that many woody species have a higher positive priming effect compared with grasses and crops (Huo et al., 2017). *Eucalyptus regnans* forests are able to take up adequate amounts of N even in nutrient-poor soils (Dijkstra et al., 2017). According to these authors, the roots of these trees stimulate soil microbiological activity, respiration and N mineralization (Dijkstra et al., 2017). In greenhouse experiments, growth of seedlings of a hybrid clone of *E. grandis* x *E. urophylla* on an Oxisol were observed to reduce C stocks associated with mineral fractions in the rhizosphere, especially when the plants were under nutritional stress by N (Hurtarte, 2017).

Table 1. Values of input variables used in the model in relation to estimates of fine root length, rhizosphere volume, and C rhizodeposition

	Input			Length (x10^3 km ha^{-1})				Rhizosphere volume (x 10^3 dm^3)				C rhizodeposition (x 10^3 kg ha^{-1})			
Name	Mean	Lower	Higher	Mean	Lower	Higher	S(1)	Mean	Lower	Higher	S(1)	Mean	Lower	Higher	S(1)
Clay concentration in soil (%)	30	10	50	17.3	47.6	10.8	0.90	135.9	373.5	85.0	0.90	1.3	3.5	0.8	0.92
Soil layer considered (cm)	25	5	50	17.3	6.4	26.6	0.60	135.9	50.1	208.9	0.60	1.3	0.5	2.0	0.62
Rhizodeposition C/N ratio (µg $µg^{-1}$)	20	5	60	17.3	17.3	17.3	0.00	135.9	135.9	135.9	0.00	1.3	1.3	1.3	0.00
Root diameter maximum for the fine roots (mm)	1	0.25	3	17.3	1.1	19.6	1.20	135.9	2.1	461.8	2.20	1.3	0.02	4.3	2.17
Shoot dry matter (t ha^{-1})	140	40	280	17.3	13.6	19.7	0.20	135.9	107.1	155.1	0.20	1.3	1.0	1.5	0.19
Soil moisture (%)	50	5	100	17.3	17.3	17.3	0.00	135.9	135.9	135.9	0.00	1.3	0.1	2.6	0.00
Enzymes C/N ratio (µg $µg^{-1}$)	5	3	7	17.3	17.3	17.3	0.00	135.9	135.9	135.9	0.00	1.3	1.3	1.3	0.00
Microbiota C/N ratio (µg $µg^{-1}$)	7	3.5	14	17.3	17.3	17.3	0.00	135.9	135.9	135.9	0.00	1.3	1.3	1.3	0.00
Soil C/N ratio (µg $µg^{-1}$)	12	6	30	17.3	17.3	17.3	0.00	135.9	135.9	135.9	0.00	1.3	1.3	1.3	0.00
Rhizosphere thickness (cm)	0.5	0.1	1	17.3	17.3	17.3	0.00	135.9	27.2	271.9	1.00	1.3	0.3	2.6	1.00
Soil organic matter concentration (g dm^{-3})	40	12	80	17.3	17.3	17.3	0.00	135.9	135.9	135.9	0.00	1.3	1.3	1.3	0.00
C radicular efflux rate (µg cm^{-2} h^{-1})	1.5	0.25	4.5	17.3	17.3	17.3	0.00	135.9	135.9	135.9	0.00	1.3	0.2	3.8	1.00
Total soil porosity (dm^3 dm^{-3})	0.53	0.45	0.59	17.3	17.3	17.3	0.00	135.9	135.9	135.9	0.00	1.3	1.3	1.3	0.00
Soil protection (%)	15	5	30	17.3	17.3	17.3	0.00	135.9	135.9	135.9	0.00	1.3	1.3	1.3	0.00
Microbial immigration (µg $µg^{-1}$ h^{-1})	0.01	0.001	0.1	17.3	17.3	17.3	0.00	135.9	135.9	135.9	0.00	1.3	1.3	1.3	0.00

(1) Sensitivity index

Table 2. Values of the input variables used in the model in relation to estimates of fine root length, rhizosphere volume, and C rhizodeposition

	Value			BCm (µg/g soil)				N mineralized (kg ha^{-1})				N balance (kg ha^{-1}) [2]			
Name	Mean	Lower	Higher	Mean	Lower	Higher	S [1]	Mean	Lower	Higher	S [1]	Mean	Lower	Higher	S [1,3]
Clay content in soil (%)	30	10	50	52.84	52.84	52.83	0.00	87.87	241.44	87.87	0.63	24.15	66.36	24.15	0.63
Soil layer considered (cm)	25	5	50	52.84	52.84	52.84	0.00	87.87	32.40	135.05	0.62	24.15	8.90	37.12	0.62
Rhizodeposition C/N ratio (µg µg^{-1})	20	5	60	52.84	52.84	52.84	0.00	87.87	229.17	56.48	0.56	24.15	-25.71	35.23	1.66
Root diameter maximum for fine roots (mm)	1	0.25	3	52.84	52.84	52.84	0.00	87.87	1.36	298.50	2.17	24.15	0.37	82.04	2.17
Shoot dry matter (t ha^{-1})	140	40	280	52.84	52.84	52.84	0.00	87.87	69.26	100.24	0.19	24.15	19.04	27.55	0.19
Soil moisture (%)	50	5	100	52.84	24.12	52.97	0.26	87.87	69.66	87.94	0.08	24.15	5.94	24.21	0.47
Enzymes C/N ratio (µg µg^{-1})	5	3	7	52.84	52.84	52.84	0.00	87.87	86.62	88.41	0.02	24.15	22.90	24.69	0.09
Microbiota C/N ratio (µg µg^{-1})	7	3.5	14	52.84	52.84	52.84	0.00	87.87	77.04	93.29	0.14	24.15	13.32	29.57	0.58
Soil C/N ratio (µg µg^{-1})	12	6	30	52.84	52.84	52.84	0.00	87.87	141.36	55.78	0.58	24.15	77.63	-7.94	2.70
Rhizosphere thickness (cm)	0.5	0.1	1	52.84	52.84	52.83	0.00	87.87	17.58	175.75	1.00	24.15	4.83	48.30	0.68
Soil organic matter content (g dm^{-3})	40	12	80	52.84	23.58	84.77	0.67	87.87	69.17	100.26	0.20	24.15	5.45	36.54	1.00
C radicular efflux rate (µg cm^{-2} h^{-1})	1.5	0.25	4.5	52.84	19.00	119.66	0.64	87.87	36.79	177.65	0.54	24.15	26.17	-13.51	1.28
Total soil porosity (dm^3 dm^{-3})	0.53	0.45	0.59	52.84	47.71	43.17	0.75	87.87	85.35	82.92	0.21	24.15	21.63	19.19	0.85
Soil temperature (ºC)	15.5	5	35	52.84	35.66	142.19	0.71	87.87	48.65	291.89	0.92	24.15	-15.06	228.15	2.83
Soil protection (%)	15	5	30	52.84	69.20	34.95	0.38	87.87	123.01	52.64	0.47	24.15	59.28	-11.08	2.38
Microbial immigration (µg µg^{-1} h^{-1})	0.01	0.001	0.1	52.84	52.05	60.50	0.03	87.87	86.92	97.12	0.02	24.15	23.20	33.39	0.08

(1) Sensitivity index; (2) ΔN = (Inorganic-N Vrhizo) - (N rhizodeposited Vrhizodeposition); (3) When in the presence of negative values (N balance), we sum the module of the negative value (y) plus in the lowest output (log (y + |y| + 1)) and in the higher output (z) (z + |y| + 1), being the equation represented in the following way: $Sensitivity\ (S) = \frac{|\log|z+|y|+1|-\log|y+|y|+1||}{|\log|higher\ input|-\log|lower\ input||}$

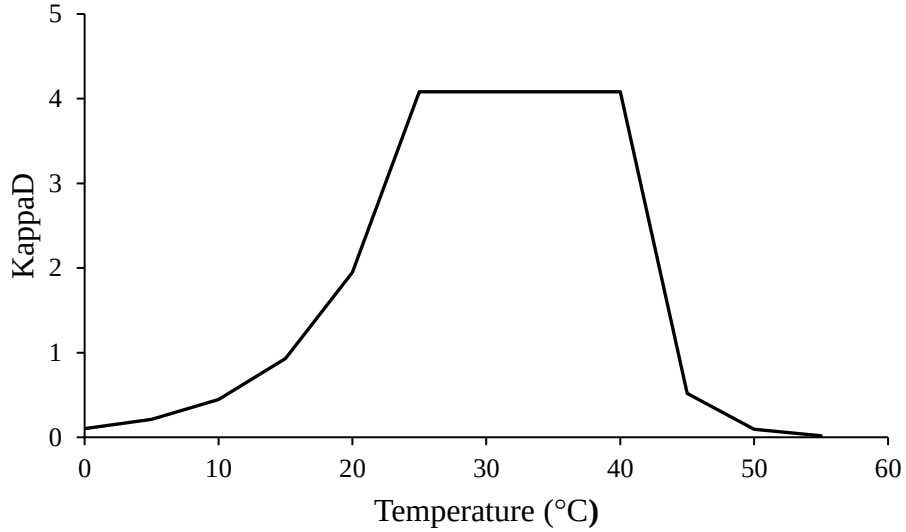

Figure 7. Temperature dependence the kinetic enzyme variable KappaD used in ForPRAN model simulations.
(Based on theoretical representation of Brock and Madigan, 1991).

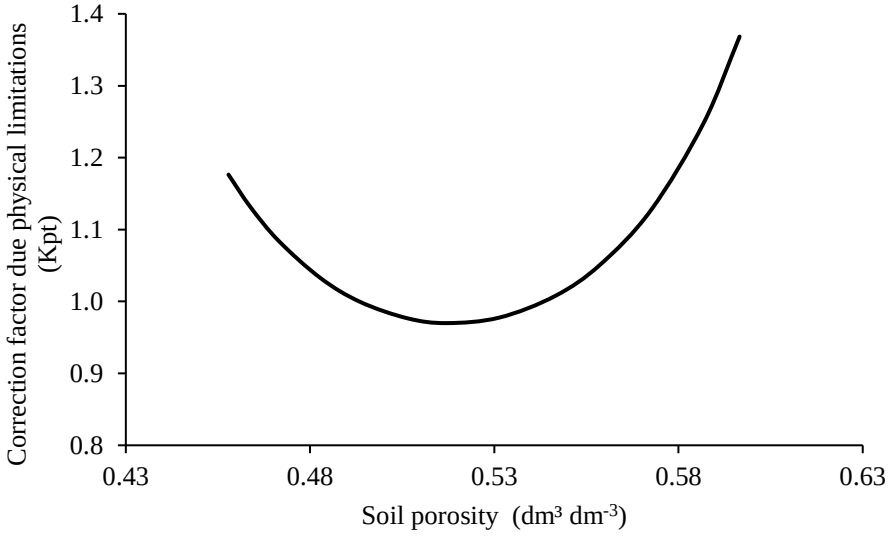

Figure 8. Soil porosity dependence of the modifier of microbial death rate due to limitations of physical conditions (Kpt) used in ForPRAN model simulations.
(Source: The equation used in the Kpt modifier was parameterized with data presented in Silva et al., 2011).

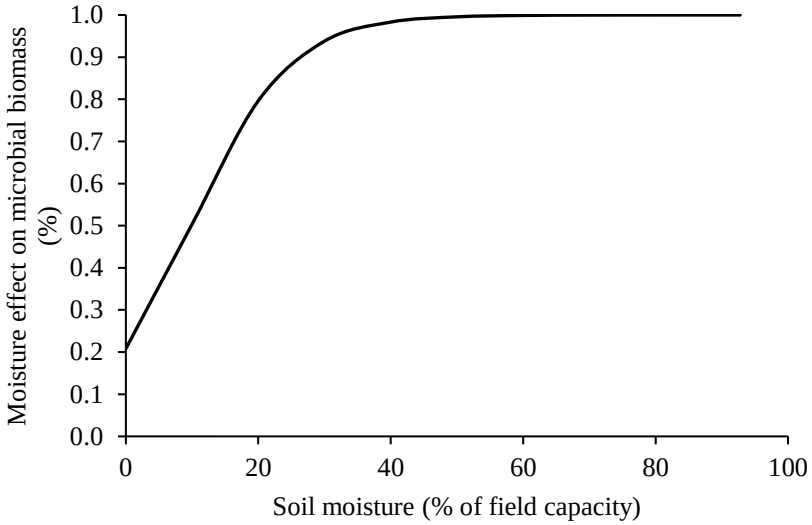

Figure 9. Soil moisture dependence of the modifier of microbial death rate due to water limitation (Ku) used in ForPRAN model simulations. (Source: The equation used in the Ku modifier was parameterized with data presented in Sato et al., 2000)

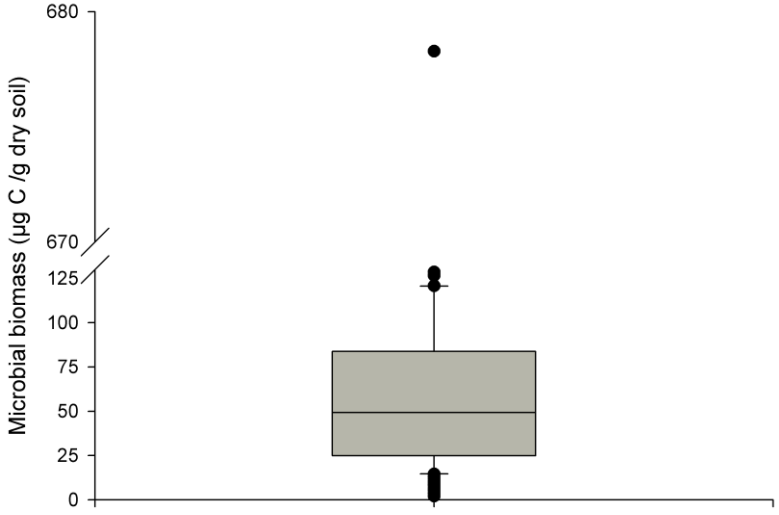

Figure 10. Boxplot of 206 observations of microbial biomass of soils under *Eucalyptus* growing in southeast Brazil (0-10 cm depth) (M. R. Tótola pers. comm.)

Table 3. Simulation of N balance (kg N ha^{-1}) due to the priming effect in *Eucalyptus* plantations with two levels of soil protection of C and N

		C and N protection by soil (%)	
Stand age (year)	Root length (km ha^{-1})	15	30
0.25	5191	13	-7
1.39	10793	28	-14
2.53	13971	36	-18
3.67	15553	40	-20
4.81	16502	42	-21
5.95	16981	43	-21
7.10	17321	44	-22
Cumulative rhizosphere supply		247	-121
Eucalyptus demand (root+shoot)		383	383
Rhizosphere supply - Demand[1]		-136	-504

[1]Based on the equation of nutritional efficiency coefficient (CUB) proposed by Valadares (2015) and plant biomass.

4 Conclusion

This research is the first to demonstrate how a previously described model operating at the root scale for calculating C-N dynamics in rhizosphere soil could be linked with an ecosystem scale model. In this case, a commonly used forest plantation production model was used to predict the effects of rhizosphere priming on N supply for wood production. Simulation of a *Eucalyptus* plantation suggested that rhizosphere processes could be an important supplement to N supplied from bulk soil. This result therefore provides a template for including rhizosphere C-N dynamics in other plant production models where that might be needed, e.g. in the APSIM or DSSAT suite of crop models (Holzworth et al., 2014) or models of native ecosystems.

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SUPPLEMENTARY MATERIAL

Part 1 – Modeling fine root growth and rhizodeposition

1.1 Converting light energy in *Eucalyptus* dry matter

We used the 3-PG ecophysiological process model (Landsberg; Waring, 1997) to estimate the conversion of light energy to mass of dry matter for a mono-cultural *Eucalyptus* plantation. The role of this module is to simulate C directed to root growth and exudation in a forest plantation. To better represent the growth of plantations under tropical conditions, we used the version parameterized by Borges et al. (2012), due to its greater degree of universality in relation to the other model parameterizations (Borges, 2012). We used shoot mass estimated by the 3-PG model as input to the next step. Thus, it was possible to estimate the root length and rhizosphere volume by the ForPRAN model. For a better understanding of the equations used in the ForPRAN model, we summarized the main variables, constants and compartments in the Table 1. The 3-PG and ForPRAN models are implemented as spreadsheets in Microsoft Excel.

Table S1. Variables, constants and compartments of the fine root growth and rhizodeposition model

Name	Symbol	Unit	Default
Parameter a[1]	a	$\%^{-1}$ cm^{-1}	0.97
Soil clay content[3]	Clay	%	-
Parameter b[1]	b	unl*	-0.92
Parameter c[1]	c	unl*	0.62
C released at time zero[2]	C_0	µg cm^{-3}	2.1
Thickness of the soil layer considered[3]	TSL	cm	-
Concentration of organic carbon in soil solution regulated by fine root[4]	Ce	µg cm^{-3}	-
C/N ratio of root rhizodeposition[3]	CNrizo	µg μg^{-1}	-
Root length per diameter class[2]	RLdc	cm	-
Specific root length[2]	SRL	km kg^{-1}	24.54
Specific root length per diameter[2]	CREd	cm g^{-1}	-
Parameter d[1]	d	unl*	0.19
Root diameter[3]	Droot	mm	-
Parameter of the intercept f[1]	f	unl*	88
Parameter ɣ[2]	ɣ	unl*	0
Exponential decay coefficient h[1]	h	mm^{-1}	6.5
Parameter of the intercept i[1]	i	unl*	20
Exponential decay coefficient j[1]	j	mm^{-1}	1.6
Mass of dry matter of aerial part[3]	MDAP	t ha^{-1}	-
Mass of dry matter of fine roots[4]	MSfr	t ha^{-1}	-
Mass of fine roots per diameter class[4]	MSfrcd	t ha^{-1}	-
Percentage of root length ratio per diameter[4]	PAC	unl*	-
Percentage of root mass ratio per diameter[4]	PAM	unl*	-
Mean root radius[3,5]	r	cm	-
Volume of solution involving the root[4]	V	cm^3	-
Rate of efflux at the root apex[2]	α	µg C cm^{-2} h^{-1}	1.5
Relative influx of C[2]	β	µg C cm^{-1} h^{-1}	0.2

[1]Parameterization based on data from the studies of Mello et al. (1998), Neves (2000), Leles et al. (2001), Teixeira et al. (2002), Gatto et al. (2003) and Maquere (2008); [2]Personeni et al. (2007); [3]user-defined input data; [4]model output data; [5]Root mean radius = ((radius of the lower limit of the diameter class) + (radius of the upper limit of the diameter class))/2; *unitless.

1.2 Estimation of carbon partitioning to fine roots (MSfr, t ha^{-1})

An empirical model was used for partitioning of the dry matter mass to fine roots (<= 3 mm), with independent variables of clay content of the soil, thickness of the soil layer of interest, and shoot mass of the trees. The function was based on data presented in Mello et al. (1998), Neves (2000), Leles (2001), Teixeira et al. (2002), Gatto et al. (2003) and Maquere (2008). We considered fine roots to be less than 2 or 3 mm, as presented by the authors. As there was no statistical difference of dry matter partition between these two diameter limits, we proposed a general model for fine roots based on 3 mm diameter.

$$MSfr = aClay^{b}TSL^{c}\mathrm{MDAP}^{d} \quad \text{Eq. 1}$$

1.3 Estimation of the length of fine roots

To estimate the proportion of the root length in different diameters (equation 2), we assumed a sigmoidal distribution of the percentage of the total length as a function of the diameter of the fine roots, following the original proposition of Finzi et al. (2015). For example, the model for *Eucalyptus* calculated an average of 88 % of the total length of fine roots had a diameter less than 1 mm (Table 1), as observed by Baldwin and Stewart (1987) and Mello et al. (1998).

$$PAC = \frac{1}{1+fe^{-hDroot}} \quad \text{Eq. 2}$$

1.4 Estimating mass partitioning to fine roots of different diameter

According to Baldwin and Stewart (1987), roots with a diameter less than or equal to 1 mm contribute more than 85 % of the total length of fine roots, but there percentage of total dry matter of fine roots was much less (approximately 20 %) (Table S1). Thus, we parameterized a sigmoidal model to represent the proportion of dry matter (PAM) in relation to total root mass according to the maximum diameter considered (Droot, Equation 3). Root mass per diameter (MSfrd, in kg ha^{-1}) was estimated using the Equation 4.

$$PAM = \frac{1}{0{,}8354+ie^{-jDroot}} \quad \text{Eq. 3}$$

$$MSfrd = MSfr\,PAM \quad \text{Eq. 4}$$

1.5 Root growth per diameter class

We used total root length in Mello et al. (1998) and equations 4 and 5 to calculate specific root length (SRL, km kg^{-1}) for a root diameter class of interest (SRLd, km kg^{-1}) (equation 5). Root length per diameter class (RLdc, km ha^{-1}) was estimated by multiplying the root mass per diameter (MSfrd, kg ha^{-1}) by the specific root length of the lower (i) and upper diameter (n) (Equation 6). After that, the value is multiplied by 10^5 to find the result in centimeter for entry into the rhizodeposition model.

$$\mathrm{SRLd} = \mathrm{SRL}\frac{(\mathrm{PAC})}{(\mathrm{PAM})} \quad \text{Eq. 5}$$

$$\mathrm{RLdc} = (MSrfd_n\,SRLd_n) - (MSrfd_i\,SRLd_i) \quad \text{Eq. 6}$$

1.6 Estimation of the rizodeposition process

We used equation 7 to describe net rhizodeposition of carbon by the root, using a model proposed by Farrar et al. (2003) and optimized and parameterized by Personeni et al. (2007). The estimation of rhizodeposition of organic N was carried out by dividing the carbon value by the C/N ratio of the rhizodeposited material (Ne, µg cm^{-3}) (equation 8).

$$Ce = \frac{\alpha}{\beta(1-\gamma)\mathrm{RLdc}}\left[(\mathrm{RLdc}+1)^{1-\gamma}-1\right]\left(1-e^{-\frac{\beta 2\pi r \mathrm{RLdc}}{V}t}\right)+\frac{C_0}{V}e^{-\frac{\beta 2\pi r \mathrm{RLdc}}{V}t} \quad \text{Eq. 7}$$

$$Ne = \frac{Ce}{CN_{rizo}} \quad \text{Eq. 8}$$

Part 2 – Modeling C and N cycling in the rhizosphere soil (bacteria + fungi)

To estimate N rhizosphere cycling, we used the model of fine root growth and rhizosphere C flux described above coupled to the equations of Schimel and Weintraub (2003) and Allison et al. (2010), and modified and parameterized by Drake et al. (2013) in the MCNiP model. In this model, the mineralization rates depend on stoichiometry and soil temperature. To improve the temporal and spatial resolution, we considered the plant component, as previously mentioned in the module 1, and also the population dynamics module as affected by water, nutrients, temperature, and soil properties. In a very simplified way, we attribute constants to the effect of soil on the protection of the released compounds in solution, and also to the processes of microbial immigration and emigration, the effect of temperature on the enzymatic kinetics, and the organic matter effect on the rate of microbial death. Table S2 lists the variables, parameters, units, and reference values used in this part of the model.

Table S2. Variables, constants and compartments of the microbial rhizosphere model

Name	Symbol	Unit	Default
C in microbial biomass in one hour[2]	BCm	$\mu g\ g^{-1}\ h^{-1}$	-
N in microbial biomass in one hour[2]	BNm	$\mu g\ g^{-1}\ h^{-1}$	-
Soil moisture[3]	CAD	%	-
Enzyme C/N ratio[2,3]	CNenz	$\mu g\ \mu g^{-1}$	3
Microbiota C/N ratio[2,3]	CNm	$\mu g\ \mu g^{-1}$	7
Soil C/N ratio[2,3]	CNs	$\mu g\ \mu g^{-1}$	12
Rate of C release from dead microbes that return to DOC[4]	CYc	$\mu g\ g^{-1}\ h^{-1}$	-
Rate of N release from dead microbes that return to DON[4]	CYn	$\mu g\ g^{-1}\ h^{-1}$	-
Depolymerization rate of soil organic C[4]	Dc	$\mu g\ g^{-1}\ h^{-1}$	-
Depolymerization rate of soil organic N[4]	Dn	$\mu g\ g^{-1}\ h^{-1}$	-
Organic C in solution in one hour[4]	DOC	$\mu g\ g^{-1}\ h^{-1}$	-
Organic N in solution in one hour[4]	DON	$\mu g\ g^{-1}\ h^{-1}$	-
Density of particules[3]	Dp	$g\ cm^{-3}$	-
Density of the soil[3]	Ds	$g\ cm^{-3}$	-
Activation energy for absorption of DOC[1]	Eauptake	$kJ\ mol^{-1}\ °C^{-1}$	47
Enzyme C in one hour[4]	EC	$\mu g\ g^{-1}\ h^{-1}$	-
Enzyme N in one hour[4]	EM	$\mu g\ g^{-1}\ h^{-1}$	-
Enzyme decay constant[4]	K_1	$\mu g\ \mu g^{-1}\ h^{-1}$	0.05
Rate of enzymatic degradation of C[4]	ELc	$\mu g\ g^{-1}\ h^{-1}$	-
Rate of enzymatic degradation of N[4]	ELn	$\mu g\ g^{-1}\ h^{-1}$	-
Rate of enzyme production of C[4]	EPc	$\mu g\ g^{-1}\ h^{-1}$	-
Rate of enzyme production of N[4]	EPn	$\mu g\ g^{-1}\ h^{-1}$	-
Universal gas constant[1]	Gasconstant	$kJ\ mol^{-1}\ K^{-1}$	0.008314
Microbial immobilization rate[4]	Jn	$\mu g\ g^{-1}\ h^{-1}$	-
Temperature-dependent SOC decomposition factor[4]	kappaD	$\mu g\ g^{-1}\ h^{-1}$	-
Rate of enzymatic production per unit of biomass[1]	Kep	$\mu g\ \mu g^{-1}\ h^{-1}$	0.0005
Half-saturation Michaelis-Menten constant[1]	Kes	unl*	0.3
Microbial maintenance respiration rate[1]	Km	$\mu g\ \mu g^{-1}\ h^{-1}$	0.01
Temperature-dependent Michaelis constant[4]	Kmuptake	$\mu g\ C\ g^{-1}$	-
km of DOC uptake at 0 °C[1]	Kmuptake0	$\mu g\ C\ g^{-1}$	0.154
Rate of increase of km uptake with temperature[1]	Kmuptakeslope	$\mu g\ C\ g^{-1}\ °C^{-1}$	0.015
Basic proportion of microbiota death[1]	Kb	unl*	0.012

(To be continued...) [1]Based on studies of Schimel e Weintraub (2003), Allison et al. (2010), Drake et al. (2013), Sato et al. (2000), Neergaarda and Magid (2001) and Silva et al. (2011); [2]suggested initial values; [3]user-defined input data; [4]model output data; *unitless.

Table S2. Variables, constants and compartments of the microbial rhizosphere model

Name	Symbol	Unit	Default
Immigration constant flow[2]	Ki	$\mu g\ g^{-1}\ h^{-1}$	0.01
Emigration constant flow[2]	Ke	$\mu g\ g^{-1}\ h^{-1}$	0.005
Proportion of biomass dying due to water deficiency[4]	K_U	unl*	-
Proportion of DOC and DON that is protected by soil[4]	Kpr	unl*	0.15
Rate of death by limitation by level of fertility[4]	Kft	unl*	-
Death by limitation for physical reasons[4]	Kpt	unl*	-
Final rate of microbial death[4]	Kmf	unl*	-
Root length[4]	L	cm	-
Microbial rate of mineralization[4]	Mn	$\mu g\ g^{-1}\ h^{-1}$	-
N loss[2]	Nloss	unl*	0.4
Inorganic N in one hour[4]	Nin	$\mu g\ g^{-1}\ h^{-1}$	-
Microbial respiration rate for enzymatic production	Re	$\mu g\ g^{-1}\ h^{-1}$	-
Rate of microbial respiration for growth	Rg	$\mu g\ g^{-1}\ h^{-1}$	-
Maintenance respiration rate	Rm	$\mu g\ g^{-1}\ h^{-1}$	-
Overflow respiration rate	Ro	$\mu g\ g^{-1}\ h^{-1}$	-
Substrate use efficiency	SUE	$\mu g\ \mu g^{-1}$	0.3
Soil temperature	Ts	°C	-
Rate of C uptake by microbes	Uc	$\mu g\ g^{-1}\ h^{-1}$	-
Rate of N uptake by microbes	Un	$\mu g\ g^{-1}\ h^{-1}$	-
Maximum inflow of C and N by microbiota	Vmaxuptake	$\mu g\ C\ \mu g^{-1}\ h^{-1}$	-
Pre-exponential rate of C uptake	Vmaxuptake0	$\mu g\ C\ g^{-1}\ h^{-1}$	$1.5\ 10^{8}$
Rhizosphere volume (or mass)	Vrhizo	cm^3 (or g)	-
Rhizodeposition volume factor	frhizo	$cm^3\ cm^{-3}$	0.21
N concentration in the rhizodeposition	Nrhizo	$\mu g\ cm^{-3}$	-
Rhizodeposition volume	Vrhizodep	cm^3	-
Root mean radius	r	cm	-
Rhizosphere thickness	Z	cm	-
Parameter p_1[2]	p_1	unl*	1
Parameter p_2[2]	p_2	unl*	-12.206
Parameter p_3[2]	p_3	$(cm^3\ cm^{-3})^{-1}$	51.060
Parameter p_4[2]	p_4	$(cm^3\ cm^{-3})^{-2}$	-49.239
Parameter z_1	z1	unl*	1
Parameter z_2	z2	unl*	3.805
Parameter z_3	z3	$\%^{-1}$	0.135

[1]Based on studies of Schimel e Weintraub (2003), Allison et al. (2010), Drake et al. (2013), Sato et al. (2000), Neergaarda and Magid (2001) and Silva et al. (2011); [2]suggested initial values (or default values); [3]user-defined input data; [4]model output data; [5]Root mean radius = ((radius of the lower limit of the diameter class) + (radius of the upper limit of the diameter class))/2; *unitless.

2. 1 Soil organic matter (SOM) depolymerization by microbes

The rate of depolymerization of C (SOC) and soil organic N (SON) to produce C (DOC) and N (DON) forms in soil solution was described as a Michaelis-Menten kinetic model, related to the concentration of enzymes in soil (EC) (equation 9) (Schimel; Weintraub, 2003; Drake et al., 2013). According to these authors, the depolymerization fluxes of SOC and SON (Dc and Dn) are linked by the C/N ratio of the soil (equation 9). Depolymerization would theoretically be limited by the stocks of SOC and SON, but we assumed on average that roots do not have sufficient longevity to exhaust the entire stocks of SOC and SON. Nevertheless, we consider that once the entire stock of organic matter in the soil is depleted, the microorganisms will be supplied solely by the rhizodeposition flux.

$$Dc = kappa_D \frac{EC}{Kes+EC} \quad \text{Eq. 9}$$

$$Dn = \frac{Dc}{CN_S} \quad \text{Eq. 10}$$

We assumed that temperature influences enzymatic kinetics by being optimal in the range 25°C to 40°C and decreasing rapidly at higher and lower values, which is consistent with Brock and Madigan (1991) and Drake et al. (2013).

$$\begin{cases} if\ T \leq 25\ °C, kappaD\ =\ 0.1014e^{0.1478T} \\ if\ 25 < T \leq 40\ °C, kappaD = 4.0809 \\ if\ T > 40\ °C, kappaD\ =\ 2 * 10^6 e^{-0.337T} \end{cases} \quad \text{Eq. 11}$$

2.2 Flow of carbon and nitrogen uptake from the soil by the microbiota

The uptake of DOC and DON by the microbes presented in Drake et al. (2013) followed the original proposal of Allison et al. (2010). The maximum velocity (Vmax) and the half-saturation constant of uptake (Km) was calculated as a function of soil temperature, according to equations 12 and 13. To estimate the soil temperature (to the depth of up to 20 cm) from air temperature, we used the daily time-step model proposed by Paul et al. (2004) for ecosystems with trees. The uptake of DOC (Uc) and DON (Un) is estimated according to the Michaelis-Menten model presented in equations 14 e 15. Uptake rates are limited by substrate availability, which means that Uc and Un cannot exceed DOC and DON, respectively (equations 16 and 17).

$$Vmaxuptake = Vmaxuptake0\ e^{-1(Eauptake \div Gasconst \cdot (T + 273.15))} \quad \text{Eq. 12}$$

$$\text{Kmuptake} = \text{kmuptakeslope T} + \text{Kmuptake0} \quad \text{Eq. 13}$$

$$Uc = \frac{Vmaxuptake\ BCm\ DOC}{Kmuptake + DOC} \quad \text{Eq. 14}$$

$$Un = \frac{Vmaxuptake\ BNm\ DON}{Kmuptake + DON} \quad \text{Eq. 15}$$

$$\text{Uc} = \begin{cases} \text{Uc}, & \text{se Uc} < DOC \\ \text{DOC}, & \text{se Uc} > DOC \end{cases} \quad \text{Eq. 16}$$

$$\text{Un} = \begin{cases} \text{Un}, & \text{se Un} < DON \\ \text{DON}, & \text{se Un} > DON \end{cases} \quad \text{Eq. 17}$$

2.3 Microbial metabolism

In the model, microbial demand considers the fact that microorganisms use C and N to synthesize exoenzymes and for the maintenance of the biomass via respiration (Schimel; Weintraub, 2003; Allison et al. 2010; Drake et al., 2013). The calculation of demand aims to determine which of the two nutrients is more limiting to the growth of the microbiota, according to equation 18. Therefore, in each step of the model, if DOC uptake does not reach a value that meets microbial demand (Uc), microorganisms are considered limited by C (Schimel; Weintraub, 2003; Allison et al. 2010; Drake et al., 2013). Otherwise, when Uc exceeds or equals microbial demand for C, microorganisms are assumed to be limited by N (Schimel; Weintraub, 2003; Drake et al., 2013).

$$\begin{cases} Uc < Rm + \frac{EP_c}{SUE} + (Un - EP_n)\frac{CN_m}{SUE}, \text{therefore, it is limited by C} \\ Uc \geq Rm + \frac{EP_c}{SUE} + (Un - EP_n)\frac{CN_m}{SUE}, \text{therefore, it is limited by N} \end{cases} \quad \text{Eq. 18}$$

2.4 Mineralization and immobilization

The immobilization rate of N (Jn) is zero with C limitation, or immobilization occurs under N limitation (equation 19) (Schimel; Weintraub, 2003; Allison et al. 2010; Drake et al., 2013). Microorganisms mineralize N during C limitation, but N mineralization is zero when limited by N (equation 20) (Schimel; Weintraub, 2003; Allison et al. 2010; Drake et al., 2013).

$$Jn = \begin{cases} 0, & \text{if is limited by C} \\ \left(Uc - Rm - \frac{EPc}{SUE}\right)\left(\frac{SUE}{CN_m}\right) - EPn - Un, & \text{if is limited by N} \end{cases} \quad \text{Eq. 19}$$

$$Mn = \begin{cases} Un - EPn - \left(Uc - Rm - \frac{EPc}{SUE}\right)\left(\frac{SUE}{CN_m}\right), & \text{if is limited by C} \\ 0, & \text{if is limited by N} \end{cases} \quad \text{Eq. 20}$$

2.5 Production and degradation of enzymes

It was assumed that the rate of enzyme production by the microbiota is directly proportional to microbial biomass (equation 21) and that the degradation of the enzymes was described by a constant that is multiplied by the amount of enzymes in rhizosphere soil (equation 22), as presented Allison et al. (2010) and Drake et al. (2013). Similarly, N transferred during enzymatic (EPn) and degradation (ELn) production was represented by equations 23 and 24, respectively.

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$$EPc = Kep\ BCm \quad \text{Eq. 21}$$

$$ELc = K_1 EC \quad \text{Eq. 22}$$

$$EPn = \frac{EPc}{CN_{enz}} \quad \text{Eq. 23}$$

$$ELn = \frac{ELc}{CN_{enz}} \quad \text{Eq. 24}$$

2.6 Respiration process

Microorganisms use C in the respiratory process to support the maintenance of biomass (Rm) (equation 25), enzyme production (Re) (equation 26), growth (Rg) (equation 27) and "overflow" metabolism (equation 28) (Schimel; Weintraub, 2003; Allison et al. 2010; Drake et al., 2013). At this point in particular, the 'Law of the Minimum' in the respiratory process for growth is applied, so whether C or N is missing determines the magnitude of respiration.

$$Rm = Km\ BCm \quad \text{Eq. 25}$$

$$Re = \frac{EPc\ (1-SUE)}{SUE} \quad \text{Eq. 26}$$

$$Rg = \begin{cases} \left(Uc - \frac{EPc}{SUE} - Rm\right)(1 - SUE), & \text{if limited by C} \\ (Un - J_n - EP_n)CN_m \frac{(1-SUE)}{SUE}, & \text{if limited by N} \end{cases} \quad \text{Eq. 27}$$

$$Ro = \begin{cases} 0, & \text{if limited by C} \\ \left(Uc - Rm - \frac{EP_c}{SUE}\right) - (Un + Jn - EPn)\frac{CN_m}{SUE}, & \text{if limited by N} \end{cases} \quad \text{Eq. 28}$$

2.7 Population dynamics

In addition to the MCNiP model, the processes of microbial immigration and emigration, are represented by constant inputs to and outputs from the rhizosphere. As for Schimel e Weintraub (2003), Allison et al. (2010) and Drake et al. (2013), there is an assumed rate (kb) of death of microorganisms each hour. However, differently from the above authors, we consider this rate for standard conditions for the survival of the rhizosphere microorganisms to be increased by a multiplicative factor (K_U) under inadequate water conditions, as previously commented. For this purpose, we used a logistic model based on data presented in Sato et al. (2000). We also consider important that soil physical conditions affected the death of the microbiota by changes in the availability of O_2, water retention and access to substrates. Thus, we adjusted an equation that aims to correct the rate of death of microbial biomass as a function of changes in total soil porosity (K_{pt}), according to data presented in Silva et al. (2011). The standard particle density was 2.6 g cm^{-3}, but can be changed as needed.

We also considered the effect of fertility on microbial death (K_{ft}), based on data presented about of the difference in microbial biomass between fertile and infertile soils (Neergaarda; Magid, 2001). These modifications were the main improvements made in the MCNiP model.

Immigration and emigration

$$Im = Ki \quad \text{Eq. 29}$$

$$Em = Ke \quad \text{Eq. 30}$$

Death by water limitation

$$K_U = \left(\frac{z1}{z1+z2e^{(-z3CAD)}}\right)^{-1} \quad \text{Eq. 31}$$

Death by physical conditions limitations

$$K_{Pt} = \frac{p1}{p2+ p3\ Pt +p4\ Pt^2} \quad \text{Eq. 32}$$

$$Pt = 1 - \frac{Ds}{Dp}$$

Death by soil fertility limitations

$$K_{tf} = \frac{Kb}{level\ n} \quad \text{Eq. 33}$$

Level 1 (low fertility) = 1 (SOM ≤ 1.2 dag kg^{-1})

Level 5 (medium fertility) = 3 (1.2 dag kg^{-1} < SOM ≤ 4 dag kg^{-1})

Level 10 (high fertility) = 10 (4 dag kg^{-1} < SOM ≤ 8 dag kg^{-1})

Final rate of microbial death

$$Kmf = K_b K_U K_{pt} K_{ft} \quad \text{Eq. 34}$$

2.8 Internal cycling of the dead microbiota

The ratio (Kmf) of the C and N contained in microbes that due death process returns to the DOC (CY_c) and DON (CY_n) compartments is described in equations 35 and 36.

$$CY_c = KmfBC \quad \text{Eq. 35}$$

$$CY_n = \frac{CY_c}{CN} \quad \text{Eq. 36}$$

2.9 Module of changes in the compartments of rhizosphere C and N

This module integrates C and N cycling in relation to rhizosphere microbes and soil, constituting the main outputs of the ForPRAN model. Changes in the different compartments are simulated over time at an hourly time-step, using equations 37-48. Another modification in relation to the MCNiP was to consider that only one proportion (1-Kpr) of the DOC and DON compartment as able to be absorbed by microbes, so that a value (Kpr DOC and Kpr DON) is protected by soil from microbial attack returning to the compartment C and N of the soil (SOC and SON).

Table S3. Equations used to calculate compartment changes

N°	Compartiment	Equation
37	Microbial biomass (carbon, µg cm^{-3})	$BCm\ (i+1) = BCm\ (i) + Uc - CYc - EPc - Ro - Re - Rm - Rg + Imc - Emc$
38	Microbial biomass (nitrogen, µg cm^{-3})	$BNm\ (i+1) = BN\ (i) + Un - CYn - EPn - Mn + Jn + Imn - Emn$
39	Enzymes (carbon, µg cm^{-3})	$EC(i+1) = EC(i) + EPc - ELc$
40	Enzymes (nitrogen, µg cm^{-3})	$EN\ (i+1) = EN(i) + EPn - ELn$
41	Carbon in solution (DOC, µg cm^{-3})	$DOC\ (i+1) = (1 - Kpr)(DOC(i) + Ce + Dc + CYc + ELc) - Uc$
42	Nitrogen in solution (DON, µg cm^{-3})	$DON\ (i+1) = (1 - Kpr)(DON(i) + Ne + Dn + CYn + ELn) - Un$
43	Soil organic carbon (SOC, µg cm^{-3})	$SOC\ (i+1) = SOC\ (i) - Dc_{i+1} + Kpr\ (DOC(i) + Dc_i + Ce + CYc + ELc)$
44	Soil organic nitrogen (SON, µg cm^{-3})	$SON\ (i+1) = SON(i) - Dn_{i+1} + Kpr\ (DON(i) + Dn_i + Ne + CYn + ELn)$
45	Inorganic nitrogen (µg cm^{-3})	$N\ (i+1) = (1\text{-loss})[N\ (i) + Mn - Jn]$
46	Vrhizosphere	$Vrhizosphere = 2\pi r\ RLdc\ Z$
47	Vrhizodeposition	$Vrhizodeposition = f_{rhizo} Vrhizosphere$
48	N balance (kg ha^{-1})	ΔN = (N inorgânico Vrhizosphere)– (Ne Vrhizodeposition)

References

Abramoff, R.Z., Davidson, E.A., Finzi, A.C. A parsimonious modular approach to building a mechanistic belowground carbon and nitrogen model. J. Geophys. Res. Biogeosci., 122, 9, 2418-2434, doi:10.1002/. 2017JG003796, 2017

Allison, S. D., Wallenstein, M. D., Bradford, M. A. Soil-carbon response to warming dependent on microbial physiology. Nat. Geosci., 3, 336–340, doi: 10.1038/ngeo846, 2010.

Almeida, A.C., Sands, P.J. Improving the ability of 3-PG to model the water balance of forest plantations in contrasting environments. Ecohydrology, 9(4), 610-630, 2016.

Aoki, M., Fujii, K., Kitayama, K. Environmental control of root exudation of low-molecular weight organic acids in tropical rainforests. Ecosystems, 15, 1194–1203, doi:10.1007/s10021-012-9575-6, 2012.

Baldwin, P. J., Stewart, H. T. L. Distribution, length and weight of roots in young plantations of *Eucalyptus grandis* W. Hill ex Maiden irrigated with recycled water. Plant Soil, 97, 243–252, doi:10.1007/BF02374947, 1987.

Barber, S. A. Soil Nutrient Bioavailability: A Mechanistic Approach. 2ª ed., p.414, 1995. New York: Wiley.

Barros, N. F., Novais, R. F. Relação solo-eucalipto. 1ª ed. Viçosa: Folha de Viçosa, 1990.

Borges, J. S., Neves, J.C.L., Lourenço, H.M., Barros, N.F. de, Dias, S.C.M. Parameterization of the 3-PG model for eucalypt in the region of cerrado in Minas Gerais state. Ci. Fl., 22(3), 567-578. https://dx.doi.org/10.5902/198050986623, 2012.

Borges, J. S. Modulador edáfico para uso em modelo ecofisiológico e produtividade potencial de povoamentos de eucalipto, Universidade Federal de Viçosa. 2012.

Brock, T. D., Madigan, M. T. Biology of microorganisms**.** 6th ed. New Jersey: Englewood Cliffs, 1991.

Davidson, E.A., Savage, K.E., Finzi, A.C. A big-microsite framework for soil carbon modeling. Glob. Change. Biol., 20: 3610-3620. doi:10.1111/gcb.12718, 2014.

Derrien, D., Plain, C., Courty, P., Gelhaye, L., Moerdijk-Poortvliet, T.C.W., Thomas, F., Versini, A. Zeller, B. Does the addition of labile substrate destabilise old soil organic matter? Soil Biol. Biochem., 76: 149-160, doi: 10.1016/j.soilbio.2014.04.030, 2014.

Dijkstra, F.A., Jenkins, M., Courcelles, V. de R. de, Keitel, C., Barbour, M.M., Kayler, Z.E., Adams, M.A. Enhanced decomposition and nitrogen mineralization sustain rapid growth of *Eucalyptus regnans* after wildfire. J. Ecol, 105, 229–236, doi: 10.1111/1365-2745.12663, 2017.

Drake, J. E., Darby, B. A., Giasson, M. A. et al. Stoichiometry constrains microbial response to root exudation-insights from a model and a field experiment in a temperate forest. Biogeosciences, 10, 821–838, doi: 10.5194/bg-10-821-2013, 2013.

Farrar, J., Hawes, M., Jones, D., Lindow, S. How roots control the flux of carbon to the rhizosphere. Ecology, 84, 827–837, doi: 10.1890/0012-9658(2003)084[0827:HRCTFO]2.0.CO;2, 2003.

Finzi, A. C., Abramoff, R. Z., Spiller, K. S., Brzostek, E.R., Darby, B.A., Kramer, M.A., Philips, R.P. Rhizosphere processes are quantitatively important components of terrestrial carbon and nutrient cycles. Glob. Chang. Biol., 21, 2082–2094, doi: 10.1111/gcb.12816, 2015.

Gama-Rodrigues, E. F. DA, Barros, N. F., Viana, A. P., Santos, G. de A. Alterações na biomassa e na atividade microbiana da serrapilheira e do solo, em decorrência da substituição de cobertura florestal nativa por plantações de eucalipto, em diferentes sítios da região sudeste do Brasil. Rev. Bras. Ciênc. Solo, 32, 1489–1499, doi: 10.1590/S0100-06832008000400013, 2008.

Gatto, A., Barros, N.F. DE, Novais, R.F. DE, Costa, L. M. DA, Neves, J. C. DE L. Efeito do método de preparo do solo, em área de reforma, nas suas características, na composição mineral e na produtividade de plantações de *Eucalyptus grandis*. Rev. Árvore, 27, 635–646, doi: 10.1590/S0100-67622003000500006, 2003.

Grayston, S. J., Vaughan, D., Jones, D. Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. Appl. Soil Ecol., 5, 29–56, doi: 10.1016/S0929-1393(96)00126-6, 1997.

Holzworth et al. APSIM - Evolution towards a new generation of agricultural systems simulation. Environ. Model. Softw., 62, 327-350, doi: 10.1016/j.envsoft.2014.07.009, 2014.

Hurtarte, L. C. Carbon mineralization in the rhizosphere of *Eucalyptus* spp. depends on its nitrogen status, Federal University of Viçosa. 2017.

Huo, C., Luo, Y., Cheng, W. Rhizosphere priming effect: A meta-analysis. Soil Biol. Biochem., 111: 78-84, doi: 10.1016/j.soilbio.2017.04.003, 2017.

Jesus, G. L. DE, Barros, N. F. DE, Silva, I. R. DA, Neves, J.C.L., Heriques, E.P., Lima, V.C., Fernandes, L.V., Soares, E.M.B. Doses e fontes de nitrogênio na produtividade do eucalipto e nas frações da matéria orgânica em solo da região do cerrado de Minas Gerais. Rev. Bras. Ciênc. Solo, 36, 201–214, doi: 10.1590/S0100-06832012000100021, 2012.

Jones, D. L. Organic acids in the rhizosphere - A critical review. Plant Soil, 205, 25–44, doi: 10.1023/A:1004356007312, 1998.

Landsberg, J. J., Waring, R. H. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For. Ecol. Manage. 95, 209–228, doi:10.1016/S0378-1127(97)00026-1, 1997.

Leles, P. S. dos S., Reis , G. G., Reis, M. das G. F., Morais, E.J. Crescimento, produção e alocação de matéria seca de *Eucalyptus camaldulensis* e *E. pellita* sob diferentes espaçamentos na região de cerrado, MG . Scientia Forestalis, 77–87, 2001.

Maquere, V. Dynamics of mineral elements under a fast-growing *Eucalyptus* plantation in Brazil . Implications for soil to cite this version, AgroParisTech. 2008.

Mello, S. L. DE M., Gonçalves, J. L. DE M., Oliveira, L. E. G. Característica do sistema radicular em povoamentos de eucaliptos propagados por sementes e estacas. Scientia Forestalis, 54, 17–28, 1998.

Melo, E.A.S.C. et al. Responses of clonal eucalypt plantations to N, P and K fertilizer application in different edaphoclimatic conditions. Forests, 7: 1–15, doi: 10.3390/f7010002, 2016.

Moriasi, D.N., Arnold, J.G., Van Liew, M.W., Bingner, R.L. Model evaluation guidelines for systematic quantification of accuracy in watershed simulations. Transactions of the ASABE, 50, 885-900. doi: 10.13031/2013.23153, 2007.

Neergaarda, A. de, Magid, J. Influence of the rhizosphere on microbial biomass and recently formed organic matter. Eur. J. Soil Sci., 52, 377–384, doi: 10.1046/j.1365-2389.2001.00393.x, 2001.

Neves, J. C. L. Produção e partição de biomassa, aspectos nutricionais e hídricos em plantios clonais de eucalipto na região litorânea do Espírito Santo. 2000.

Paul, K. I., Polglase, P. J., Smethurst, P. J., O´Connell, A.M., Carlyle, C.J., Khanna, P.K. Soil temperature under forests: a simple model for predicting soil temperature under a range of forest types. Agric. For. Meteorol., 121, 167–182, doi: 10.1016/j.agrformet.2003.08.030. 2004.

Personeni, E., Nguyen, C., Marchal, P., Pagès, L. Experimental evaluation of an efflux-influx model of C exudation by individual apical root segments. J Exp Bot., 58, 2091–2099, doi: 10.1093/jxb/erm065, 2007.

Pulito, A. P., Gonçalves, J. L. DE M., Smethurst, P. J.; et al. Available nitrogen and responses to nitrogen fertilizer in brazilian eucalypt plantations on soils of contrasting texture. Forests, 6, 973–991, doi:10.3390/f6040973, 2015.

Reis, M. das G.F.; Barros, N.F., Kimmins, J.P. Acúmulo de biomassa em uma seqüência de idade de *Eucalyptus grandis* plantado no cerrado em duas áreas com diferentes produtividades. Rev. Árvore, 9: 149–162, 1985.

Sato, A., Tsuyuzaki, T., Seto, M. Effect of soil agitation, temperature or moisture on microbial biomass carbon of a forest and an arable soil. Microb. Environ., 15, 23–30, doi: 10.1264/jsme2.2000.23, 2000.

Sauer, D., Kuzyakov, Y., Stahr, K. Spatial distribution of root exudates of five plant species as assessed by 14C labeling. J. Plant Nutr. Soil Sci.. 169, 360–362, doi: 10.1002/jpln.200621974, 2006.

Schimel, J. P., Weintraub, M. N. The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: A theoretical model. Soil Biol. Biochem., 35, 549–563, doi: 10.1016/S0038-0717(03)00015-4, 2003.

Silva, R. R., Silva, M. L. L. N., Cardoso, E. L., Moreira, F.M.S., Curi, N., Alovisi, A.M.T. Biomassa e atividade microbiana em solo sob diferentes sistemas de manejo na região fisiográfica de campos das vertentes -MG. Rev. Bras. Ciênc. Solo, 34, 1585–1592, 2010.

Silva, S. R., Silva, I. R. DA, Barros, N. F. DE, SÁ Mendonça, E. DE. Effect of compaction on microbial activity and carbon and nitrogen transformations in two oxisols with different mineralogy. Rev. Bras. Ciênc. Solo, 35: 1141–1149, doi: 10.1590/S0100-06832011000400007, 2011.

Smethurst, P. J., Gonçalves, J. L. DE M., Pulito, A. P., Gomes, S. Paul, K., Alvares, C.A.. Appraisal of the snap model for predicting nitrogen mineralization in tropical soils under *Eucalyptus*. Rev. Bras. Ciênc. Solo, 39, 523–532, doi: 10.1590/01000683rbcs20140379. 2015.

Smethurst, P.J., Nambiar, E.K.S. An appraisal of the *in situ* soil core technique for measuring nitrogen uptake by a young *Pinus radiata* plantation. Soil Biol. Biochem.. 7, 939- 942, doi: 10.1016/0038-0717(89)90084-9, 1989.

Teixeira, P. C., Novais, R. F., Barros, N. F., Neves, J. C. L., Teixeira, J. L. *Eucalyptus urophylla* root growth, stem sprouting and nutrient supply from the roots and soil. For. Ecol. Manage.. 160, 263–271, doi: 10.1016/S0378-1127(01)00469-8, 2002.

Torbert, H. A., Wood, C. W. Efffects of soil compactation and water-filled pore space on soil microbial activity and N losses. Commun. Soil Sci. Plant Anal., 23, 1321-1331, 1992.

Valadares, S. V. Modelagem da aquisição de fósforo e da eficiência nutricional de eucalipto, 2015. Universidade Federal de Viçosa.