RAFAEL VASCONCELOS VALADARES

MODELING RHIZOSPHERE CARBON AND NITROGEN CYCLING IN EUCALYPTS

Thesis submitted to the Soil Science and Plant Nutrition Graduate Program of the Universidade Federal de Viçosa in partial fulfillment of the requirements for the degree of *Doctor Scientiae*.

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APPROVED: February 19th, 2018.

Fernando Palha Leite

Ivo Ribeiro da Silva

Marcos Rogério Tótola

Maurício Dutra Costa

Júlio César Lima Neves
(Advisor)

I dedicate this thesis to Laura, Tânia, Samuel, and Alonso (*in memoriam*).

"Mestre, qual é o maior mandamento da Lei?

Respondeu Jesus: Ame o Senhor, o seu Deus de todo o seu coração, de toda a sua alma e de todo o seu entendimento.

Este é o primeiro e maior mandamento.

E o segundo é semelhante a ele: Ame o seu próximo como a si mesmo.

Destes dois mandamentos dependem toda a Lei e os Profetas." — Mestre Jesus Cristo

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AUTHOR'S BIOGRAPHY

Rafael Vasconcelos Valadares, son of Tânia Mara Vasconcelos and Alonso Cordeiro Valadares, was born in Pará de Minas, state of Minas Gerais, Brazil, on June 5, 1989. Rafael began his studies about agriculture in the agricultural technical course of the Universidade Federal de Viçosa (UFV) Campus de Florestal. In 2007, he joined the Agronomy course of the Universidade Federal dos Vales do Jequitinhonha e Mucuri (UFVJM), where he received basic scientific background. In 2008, he transferred to the Universidade Federal de Minas Gerais (UFMG), completing most of his formal training as Agronomist in 2011. Later, between 2012 and 2014, he did his master's degree in Soils and Plant Nutrition (UFV). In 2014, he joined the Ph.D. course at the same institution under the guidance of Professors Júlio César Lima Neves, Maurício Dutra Costa (the mentor of the research project hypothesis), and Dr. Philip J. Smethurst, to whom Rafael is very grateful for his knowledge in soils, microbiology, and modeling.

SUMMARY

GENERAL ABSTRACT

VALADARES, Rafael Vasconcelos, D.Sc., Universidade Federal de Viçosa, February, 2018. **Modeling rhizosphere carbon and nitrogen cycling in eucalypts.** Adviser: Júlio César Lima Neves

Eucalypts as well as other trees allocate large amounts of fixed carbon to produce roots and rhizodepositions, which include exudates, secretions, lysates and gases. The role of these compounds has been studied to elucidate the benefits for the trees of the transfer of matter/energy to the rhizosphere microorganisms. It is currently well known that the results of the interaction between the trees and the microbiota can be positive, neutral or negative, depending on the plant species, associated microbial population, and environmental conditions. This can ultimately determine the growth rate, planting stand, and even whether or not a given tree species will survive in the environment. Numerous studies have been carried out to investigate the effect of the activation of rhizosphere microbial communities previously in a state of oligotrophy or quasi-dormancy by the rhizodepositions, in the so-called rhizosphere priming effect. This process triggers changes in the structure and activity of rhizosphere communities that affect the dynamics of soil organic matter (SOM) decomposition and formation. In the particular case of the soil under eucalypts, this process predominantly accelerates the decomposition of the SOM inside the rhizosphere and, therefore, may present a positive return to the trees by the increase of the nitrogen supply (M.D. Costa, personal information[1]). Despite this, there are still no models to measure the quantitative importance of this process for forest plantations of the *Eucalyptus* genus. Thus, the present thesis aimed to develop a mechanistic model to estimate the carbon (C) and nitrogen (N) cycling in the rhizosphere soil under eucalypts. Before this, for the elaboration of this mathematical representation, it was necessary to take into account that the rhizosphere system is entirely dependent on the activity of the roots and, therefore, it does not make sense its modeling without the prediction of the plant root growth and estimation of the rhizodeposition process. For this reason, the objective of the thesis was also to present and improve a growth model for *Eucalyptus* in the APSIM (next generation) agricultural models platform. This model has, among other advantages, greater sensitivity to the soil factor, which includes the effect of the N supply by processes of SOM mineralization and litter decomposition. Thus, in Chapter I, it was reviewed the main processes and factors involved in the subsequent chapters, which are more related to the mathematical representation of key processes for rhizosphere mineralization. In Chapter II, the APSIM model was presented and validated for 12 forest sites; out of those 12 sites, nine are geographically located in Brazil and the

other three are located in Australia. The APSIM model presented a satisfactory treatment of the growth processes, considering the diverse climatic and edaphic conditions and the different forest managements. However, in order to improve its performance, adjustments were suggested regarding carbon partitioning for the roots, as well as considering other nutritional limitations besides N; and other nutrient flows such as those occurring in the rhizosphere environment. Chapter III, on the other hand, was devoted to the conceptual elaboration, presentation, evaluation and sensitivity analysis of the Forest Plantation Rhizosphere Available Nitrogen model (ForPRAN) for estimates of the C and N mineralization fluxes in the rhizosphere soil. The performance of the model was quantitatively and qualitatively satisfactory when compared to the data observed in the literature. The input variables that most influenced the increase of N by rhizosphere mineralization were (in order of decreasing importance): root diameter> rhizosphere thickness> soil temperature> clay concentration. The rhizosphere mineralization in a typical eucalypt plantation producing 42 m^3 ha^{-1} a^{-1} of shoot biomass, with assumed N losses of 40 % by different processes, was estimated in 24.6 % of the amount of N accumulated in the plantations (shoot+root+litter). From this point of view, it was concluded that the rhizosphere cycling model should be considered for adaptation of other models of forest and agricultural production, such as APSIM *Eucalyptus*, where the inclusion of such processes offers the potential to improve the growth predictions. Finally, in Chapter IV, it was tested the mathematical modeling hypothesis that the rhizosphere priming effect (RPE) is quantitatively important for nitrogen nutrition of eucalypts in different climatic and soil conditions. To test this hypothesis, the eucalypts growth was simulated using the general APSIM *Eucalyptus* model and the rhizosphere processes using the ForPRAN model. *Eucalyptus* growth was projected at four sites, two in Brazil - Aracruz/ES and Curvelo/MG - and the other two in Australia - Wagga Wagga/NSW and Coffs Harbour/NSW. At the end of the 7-year rotation, considering the cycling in the 0-20 cm depth layer, it was estimated that 12, 11, 10 and 5 % of the total soil was occupied by the rhizosphere at Aracruz, Coffs Harbour, Wagga Wagga and Curvelo, respectively. Because of the rhizodeposition and of the different pedoenvironments, the ForPRAN model suggested an increase in the rhizosphere microbial biomass in the four sites, whose average values were between 70.3 μg cm^{-3} and 246.1 μg cm^{-3} of C. In general, the RPE has the potential to explain between 15 and 38 % of the N demand of the forest ecosystem (shoot+root+litter), considering the studied cases. Higher temperatures and rainfall volumes cause increase in the N rhizosphere supply, in absolute values, in Brazilian sites

as compared with the Australian ones, which also explains part of the observed smaller N limitation in eucalypts plantations in Brazil.

RESUMO GERAL

VALADARES, Rafael Vasconcelos, D.Sc., Universidade Federal de Viçosa, fevereiro de 2018. **Modelagem da ciclagem rizosférica de carbono e nitrogênio em eucalipto.** Orientador: Júlio César Lima Neves

Árvores, como as de eucalipto, investem grandes quantidades de carbono fixado para a produção de raízes e rizodeposições, as quais incluem exsudados, secreções, lisados e gases. O papel destes compostos tem sido estudado visando elucidar os benefícios da transferência de matéria/energia das árvores para os microrganismos da rizosfera. Atualmente, sabe-se que os resultados da interação entre as árvores e a microbiota podem ser positivos, neutros ou negativos, a depender da espécie vegetal, população microbiana associada e do ambiente. Em última instância, o saldo dessas interações pode determinar a taxa de crescimento dos povoamentos e, até mesmo, a permanência ou não de uma dada espécie no ambiente. Nesse particular, o efeito da ativação de populações microbianas rizosféricas pelas rizosdeposições, o chamado efeito *priming* rizosférico, tem sido o foco de muitas pesquisas. Esse processo desencadeia mudanças na estrutura e na atividade das comunidades rizosféricas que repercutem na dinâmica de decomposição e formação da matéria orgânica do solo (MOS). No caso específico dos solos sob eucalipto, esse processo ocorre predominantemente no sentido de acelerar a decomposição da MOS e, por conseguinte, tem um retorno positivo para a planta, aumentando o suprimento de nitrogênio para as árvores (M. D. Costa, informação pessoal[1]). A despeito disso, ainda não existem modelos matemáticos que quantifiquem esse processo para as plantações florestais do gênero *Eucalyptus.* Dessa forma, a presente tese teve por objetivo desenvolver um modelo mecanístico para estimar a ciclagem de carbono (C) e nitrogênio (N) no solo rizosférico de agroecossistemas com essas árvores. Para a elaboração dessa representação matemática, levou-se em conta que o sistema rizosférico é inteiramente dependente da atividade das raízes. Por isso, não faria sentido sua modelagem sem a predição do crescimento das mesmas e a estimativa do processo de rizodeposição. Sendo assim, teve-se também como objetivo do presente trabalho a apresentação e o aprimoramento de um modelo de crescimento para o eucalipto na plataforma de modelos agrícolas APSIM (*next generation*). Tal modelo tem, entre outras vantagens, a maior sensibilidade ao fator solo, o que inclui o efeito do suprimento de N por processos de mineralização e de decomposição do *litter*. No capítulo I, procurou-se apresentar uma revisão de literatura sobre os principais assuntos da temática em estudo, de forma que o leitor pudesse entender os processos e os fatores que estão relacionados à representação

matemática da ciclagem de C e N na rizosfera. Na sequência, no capítulo II, realizou-se a apresentação e a validação do modelo APSIM *Eucalyptus* para 12 sítios florestais, sendo que nove deles apresentam localização geográfica no Brasil e os outros três estão localizados na Austrália. O modelo APSIM apresentou tratamento satisfatório dos processos de crescimento, considerando as diversas condições climáticas e edáficas e os diferentes manejos culturais. Todavia, visando aprimorar a sua performance, sugeriram-se ajustes com relação à partição de carbono para as raízes, bem como a inserção de outras limitações nutricionais além do N, e outros fluxos de nutrientes, a exemplo daqueles que ocorrem no ambiente da rizosfera. O capítulo III foi dedicado à elaboração conceitual, apresentação, avaliação e análise de sensibilidade do modelo Forest Plantation Rhizosphere Available Nitrogen (ForPRAN) para estimativas dos fluxos de mineralização de C e N no solo rizosférico. Como resultado, observou-se que o desempenho do modelo foi satisfatório quantitativamente e qualitativamente quando comparado aos dados observados na literatura. As variáveis de entrada que mais influenciaram a mineralização rizosférica do N foram (em ordem de importância decrescente): diâmetro da raiz > espessura da rizosfera > temperatura do solo > teor de argila. A mineralização rizosférica de N em plantação típica de eucalipto produzindo 42 m^3 ha^{-1} a^{-1} de massa de parte aérea, com perdas de N assumidas de 40 % por processos diversos, foi estimada em 24,6 % da demanda de N do plantio (parte aérea+raiz+*litter*). A partir disso, concluiu-se que o modelo de ciclagem de rizosfera deve ser considerado para adaptação de outros modelos de produção florestal e agrícola, como o APSIM *Eucalyptus*, onde a inclusão de tais processos oferece o potencial de melhorar o desempenho das estimativas. Por fim, o capítulo IV foi elaborado com o objetivo de testar, por meio da modelagem matemática, a hipótese de que o efeito *priming* da rizosfera (RPE) é quantitativamente importante para a nutrição nitrogenada do eucalipto. Para testar essa hipótese, foi simulado o crescimento do eucalipto utilizando o modelo geral de APSIM *Eucalyptus* e os processos de rizosfera utilizando o modelo ForPRAN. Foi projetado o crescimento do eucalipto em quatro locais, sendo dois no Brasil - Aracruz/ES e Curvelo/MG - e outros dois na Austrália - Wagga Wagga/NSW e Coffs Harbour/NSW. No final de sete anos de rotação simulada, considerando a ciclagem na camada de 0-20 cm de profundidade, estimou-se que 12, 11, 10 e 5 % do volume de solo total foi ocupado pela rizosfera nos sítios de Aracruz, Coffs Harbour, Wagga Wagga e Curvelo, respectivamente. Como resultado da rizodeposição, o modelo ForPRAN sugere nos quatro locais aumento na biomassa microbiana (BM) rizosférica, cujos valores BM médios estiveram entre 70,3 μg cm^{-3} e 246,1 μg cm^{-3} de C. Em geral, o RPE tem potencial para explicar de 15 a 38 % do N acumulado no ecossistema

florestal (parte aérea+raiz+*litter*), considerando as situações estudadas. Temperaturas e volumes de precipitação mais elevados contribuem para maior suprimento de N por meio da mineralização rizosférica, em valores absolutos, nos sítios brasileiros do que nos australianos, o que também explica parte da menor limitação por N nas plantações de eucalipto no Brasil.

GENERAL INTRODUCTION

Eucalyptus trees are able to uptake nitrogen (N) enough to attend their nutritional demand, even in soils with low natural fertility. Many experiments indicate that nitrogen is one of the most accumulated nutrients in these trees. Nevertheless, this nutrient does not represent the main nutritional limitation of the Brazilian forest plantations. Thus, a central issue for the adequate N fertilization and others managements is the estimation of the N supply in the forest soil.

In this regard, numerous studies have been developed to elucidate the N cycling in the soil under *Eucalyptus*, including the processes that occur inside the rhizosphere. The rhizosphere is the part of the forest soil under the roots influence, being important in ecosystem-scale due to the extensive root system and the high capacity to release rhizodeposition of the *Eucalyptus* trees. The higher availability of rich-energy organic compounds in the rhizosphere soil activates microbial populations previously in a state of dormancy or oligotrophy, which impacts the N supply for these trees. This process of microbial activation, so-called rhizosphere priming effect (RPE), is related to the reduction of the rhizosphere SOM stocks and to the increase of the N availability for the trees.

The N mineralization in the *Eucalyptus* rhizosphere may aid to explain the lower frequency of nutritional limitation of the plantations by N when compared with other nutrients, such as phosphorus, potassium, calcium, and boron (M. D. Costa, personal information). Furthermore, the interest on rhizosphere processes was intensified by the observations that, under increased CO_2 concentrations and progressive nutrient limitation, rhizosphere priming effect is prioritized by increased rhizodeposition along with other rhizosphere processes conducted by numerous plants, including trees.

However, the missing link in this research field is the lack of an integrative view on the quantitative importance of C and N cycling in the rhizosphere, through the mechanistic modeling. To measure its quantitative importance, it has been a challenge to consider plant growth dynamics coupled with nutrient cycling modeling, since the rhizosphere represents the soil-plant interface. Another point that prevents more realistic estimates of C and N cycling in the rhizosphere is that the cycling models do not always consider the interactions of the soil microbiota with biotic and abiotic factors, hindering, for example, the understanding of nutrient flows in many environments with distinct primary productivity and with different patterns of soil temperature and moisture.

Therefore, the present research aimed at presenting a growth model for *Eucalyptus* stands and to develop a mechanistic model for rhizosphere C and N cycling, allowing simulations of plant growth and nutrient cycling under different scenarios.

CHAPTER I

Eucalyptus rhizosphere importance for C and N cycle: from basic concepts to modeling perspectives

1.1. Importance of rhizosphere for nutrient cycling in *Eucalyptus* forests

The term rhizosphere was used for the first time by Hiltner in 1904 to refer to the soil zone under the influence of legume roots. The word has its composition based on the Greek "rhiza", which means root, and "sphaira", meaning literally sphere. The definitions of rhizosphere found in the literature are generally similar to that of Hiltner, with only minor modifications, e.g.: i) soil zone immediately adjacent to the plant roots, where the quantities or activities of microorganisms differ from those of the rest of the soil; ii) soil volume influenced by root activity; iii) soil adjacent to the roots, with different physical, chemical, and biological properties compared to the rest of the soil (FAGERIA; STONE, 2006). The rhizosphere contains a microbiome that is totally influenced by the roots and corresponds to a region in the soil that is constantly altered by organic compounds and ions. The rhizosphere is generally associated to a microbial community with unique diversity and metabolic activity.

According to Mcnear Jr. (2013), the understanding on the rhizosphere has evolved, being recognized three of its compartments. The first one is represented by the endorhizosphere and comprises the apoplasmic space between the endoderm and the epidermis (MCNEAR JR., 2013). The second one is represented by the rhizoplane, which refers to the root epidermis surface (MCNEAR JR., 2013). And the last one is the ectorhizosfere, that is, the soil zone chemically, physically, and biologically altered by the root activity, with particular longitudinal and radial characteristics (MCNEAR JR., 2013).

There is some controversy about these compartments, especially in relation to the first compartment. The prefix *endo* refers to the inner part of the rhizosphere. Such terminology would not find logical meaning in the original rhizosphere definition presented by Hiltner (1904), which is clearly linked to the soil niche. In addition, the term would also present some redundancy when considering endophytic microorganisms (KLOEPPER; SCHIPPERS; BAKKER, 1992). However, it is undeniable that root endophytes are related to the rhizosphere, since they migrate from the ectorhizosphere to the rhizoplane, and then to the root cortex (KLOEPPER; SCHIPPERS; BAKKER, 1992).

According to Grayston et al. (1997), *Eucalyptus* trees can alter the rhizosphere mainly by the release of rhizodepositions, which include secretions, lysates, gases, and mucilages. Whipps and Lynch (1985) defined, for the first time, the term rhizodeposition as the material lost from plant roots, including water-soluble exudates, secretions of insoluble materials, lysates, dead fine roots, as well gases, such as CO_2 and ethylene.

These materials can be divided into four groups: (1) water-soluble exudates, such as sugars, amino acids, organic acids, hormones and vitamins, for which there is no direct energy expenditure for their release; (2) secretions, including polymeric carbohydrates and enzymes, that are dependent on energy-driven metabolic processes for being released; (3) lysates, including products of cellular autolysis; (4) and gases, such as ethylene and CO_2 (CHENG; GERSHENSON, 2007).

In the *Eucalyptus* rhizosphere, significant amounts of citric, malic, and oxalic acids (SILVA et al., 2004), as well as sucrose, alose, fructose, glutamine, inositol, and asparagine are found (HURTARTE, 2017). These compounds provide a unique nutritional basis for the growth of many bacterial and fungal species in the rhizosphere (FAGERIA; STONE, 2006).

Rhizodeposition and root C can represent approximately 40 to 73 % of the C assimilated through photosynthesis (SANTANTONIO; HERMANN; OVERTON, 1977; VAN VEEN et al., 1991). Newman (1985) estimated that soluble exudates and insoluble materials range from 10-100 and 100-250 mg g^{-1} of dry root, respectively. According to Newman (1985) and Whipps (1990) several factors affect the rhizodeposition process, such as soil texture, anoxia, water stress, cultivar, nutrient source, environmental variables, and microorganisms. These authors calculated that the upper limit for the rhizodeposition should not exceed 600 mg g^{-1} of dry root. Trees can shuttle large amounts of carbon to their roots and may have rhizodeposition rates of 5.8 to 7.5 t ha^{-1} a^{-1} of C (LYNCH; WHIPPS, 1990). Such large investment may be related to the relatively greater exposure of roots to prolonged periods of stress, which trigger the release of the excess of carbohydrate and reduction power by the "overflow metabolism" (LYNCH; WHIPPS, 1990).

Soil microorganisms, under oligotrophic conditions, can be maintained viable for long periods in a state of “arrested metabolism" (similar to dormancy) and oligotrophy (LYNCH; WHIPPS, 1990). As a result, rhizodeposition attract and also activate organisms with different types of interaction with trees, which may have a positive, neutral or negative effect on their growth (KLOEPPER; SCHIPPERS; BAKKER, 1992). For instance, the presence of phosphate solubilizing bacteria in the *Eucalyptus* rhizosphere, such as *Enterococcus avium*, *Burkholderia cepacea*, and *Burkholderia pyrrocinia* can favor tree growth under limiting P availability (MASSENSSINI et al., 2016). Some fungal genera present in the *Eucalyptus* rhizosphere (eg.: *Penicillium* sp. and *Aspergillus niger*) also act as growth-promoting microorganisms through many

mechanisms, including the production of indole-acetic acid, siderophores, gibberellins, ACC deaminase, volatile compounds, and organic acids (SANTOS, 2011).

The role of organic acids, such as oxalic acid, produced by plant growth promoting fungi, on the solubilization of calcium compounds or the mitigation of the toxic effect of aluminum has been reported (GONZALEZ et al., 2009). Knowledge on the activities of organic acids may improve the understanding on how calcium uptake in environments with a virtual absence of labile Ca forms can be accomplished and, also, how these compounds may participate in the mechanism of Al-tolerance (GONZALEZ et al., 2009; SILVA et al., 2004).

Some rhizosphere fungi are capable of forming mutualistic mycorrhizal symbioses aiding compatible trees in the uptake of water, phosphorus, zinc, and copper. It is noteworthy the importance of mycorrizhal fungi for our study since these microorganisms may affect C and N cycle in the soil through the synthesis of enzymes, such as amylase, cellulase, pectinase (SANTOS, 2011), laccase, and Mn-peroxidase (DELVAUX, 2014).

A dramatic example of negative interactions between plant roots and microorganisms is exemplified by the invasion of the root rot pathogen, *Phytophthora*, into *Eucalyptus* spp. habitats. Weste (1986) reported that the invasion of the Australian open forests by *Phytophthora cinnamoni* caused the death of more than 40 % of the dominant eucalypt species as well as the complete destruction of the dominant sclerophyllous understory shrub, *Xanthorrhoea australis*. According to Weste and Ashton (1994), community composition was not able to recover even after thirty years after the invasion. Therefore, the predominance of positive or negative interactions with microbes in a given environment can be determinant for the ecosystem primary productivity. Primary productivity can vary with time due to changes in species composition, to the death of individuals, or to decreases or increases in plant growth, all influenced by rhizosphere microorganisms. The activation of rhizosphere processes that increase the availability of nutrients, such as N, in the short term, involves positive feedback relations with plants and may help to explain the ecological success of *Eucalyptus* trees in countries such as Brazil.

1.2. Factors controlling priming effect and N supply for *Eucalyptus* plants

The majority of soil microorganisms present heterotrophic metabolism and play an important role in the carbon cycle through the respiratory process and also by cycling of nutrientes (e.g., nitrogen) (WOLF; WAGNER, 2005). Therefore, most of the soil microorganisms are entirely dependent on the energy and reduced carbon supplied by primary producers (e.g., plants and photosynthetic and chemoautotrophic bacteria), so that they can grow, multiply, and survive in the soil (WOLF; WAGNER, 2005).

Different microbial populations may coexist or mutually succeed each other when a mix of compounds is added to the soil. This is, in part, due to the initial and final chemical composition of that mix (e.g., rhizodeposition) (WOLF; WAGNER, 2005). Simpler compounds are generally used for the growth of rapidly growing and short-lived microbial populations, also called copiotrophic or r-strategists (WOLF; WAGNER, 2005). More complex materials are decomposed by the action of microorganisms called oligotrophic or k-strategists that break down organic matter more slowly (WOLF; WAGNER, 2005). Between these two groups of organisms, there are bacteria, actinobacteria, and fungi. The performance of each microbial group is essential for the decomposition process because each one produces a particular set of degradative enzymes (WOLF; WAGNER, 2005).

In favorable environments, simple carbon compounds such as those released in the rhizosphere, can be fully utilized to produce cellular structures, carbon dioxide and/or inorganic nitrogen (WOLF; WAGNER, 2005). Monomeric units of sugars or amino acids can be completely metabolized by microbial communities (WOLF; WAGNER, 2005). Then, a succession may occur in which, first, r-strategists and, then, k-strategists grow. The reverse may also occur in the case of the degradation of more complex compounds present in the mucilage. The break-down of polymers into simpler components by k-strategists would occur first, followed by the growth of r-strategists that would consume the unitary compounds (WOLF; WAGNER, 2005).

Theoretically, when any compound is added to the soil, it undergoes decomposition and its original amount decreases with time (Figure 1). At the same time, microbial biomass increases with the supply of energy and nutrients and so does respiration. But after a peak of growth, microbial biomass undergoes a decline returning to the same level as before the addition of the residue. The soil returns to the same state of biological activity and organic matter content, characterizing a steady-state condition (Figure 1). Under steady-state, the extra amount of carbon and nitrogen loss from the soil has the same equivalent of formation.

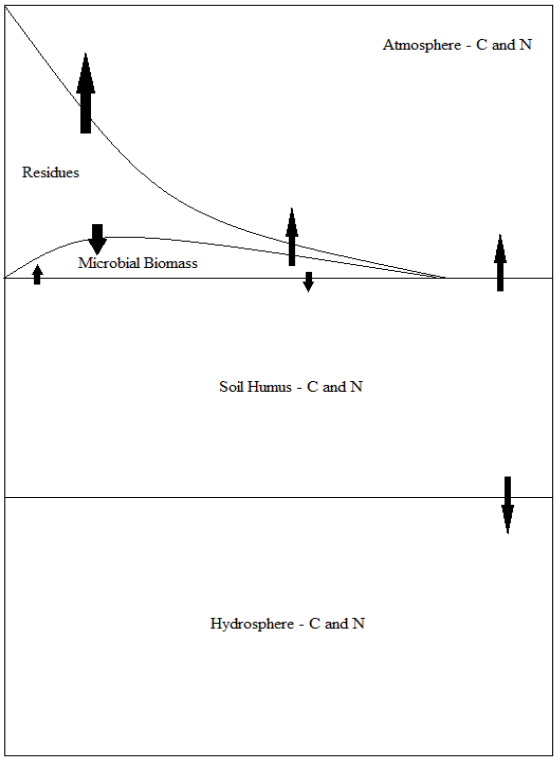

Figure 1. A condition in which the formation of organic matter is equivalent to decomposition over the time. At first, microbial biomass and respiration increase with the addition of residues (left side of the figure). But over the time, there is no real increase in the content of soil organic matter (right side of the figure). That is, the rate of formation of new organic matter is equal to the rate of decomposition of the old organic matter. (Source: adpated from Brady and Weil (2002), cited by Wolf and Wagner (2005).

$$(C,N)_t - (C,N)_{t-1} = 0, for\ all\ time\ (t)$$

However, considering the fact that the soil is an open system, clime and soil conditions, plant productivity, and cropping systems do not always contribute to the stability of soil organic mattern (SOM) stocks (steady-state condition) (SANTOS et al., 2008). The conversion of a stable natural ecosystem to an agricultural system may lead to a net loss of C and N, which may exceed the formation of new organic matter in amounts that reach 40 % in a few years (WEI et al., 2015). These losses are closely associated with the microbial dynamics, which in tropical conditions of higher temperatures and rainfall tend to be more active than in temperate regions, besides the fact that important losses occur due to erosion, leaching, and volatilization (in the case of N) (SANTOS et al., 2008). The inverse may also occur, with the increase in C and N stocks, being appropriate the study of both the decomposition and formation of SOM mechanisms (COOK et al. 2016). The present work is more associated to the mechanisms of decomposition, which are related to the availability of N for the plants.

Nutrient fluxes from organic matter to the soil tend to be higher in tropical regions, which helps to understand part of the ecological success of the *Eucalyptus* forests

plantations in these areas, even when relatively small amounts of nutrients are supplied, especially nitrogen (NAIRAM; NEVES; NOVAIS, 2005; SOARES; GOMES, 2010). On the other hand, such faster cycling may be in some cases a source of environmental degradation and environmental pollution due to the sharp decreases of SOM stocks (PULITO et al., 2015) and CO_2 release (WOLF; WAGNER, 2005). Thus, a highly productive forest can face negative feedbacks in the long term as a result of the interactions between plant-microbes-soil-climate, especially with regard to the exhaustion of SOM stocks (PULITO et al., 2015). However, it is imperative to point out that the Brazilian forestry sector is currently highly developed from a technical point of view, so that the use of diverse technological resources has allowed planted forests to reach a considerable degree of sustainability and productivity.

However, the net loss of organic matter (organic C and N) is a relatively common phenomenon in some agricultural systems in the tropics and, therefore, requires more attention managing N fertilization as well as for achieving a more sustainable system. In Australia, for example, Dalal and Mayer (1986), reported that fast SOM cycling can lead to a net decline in organic C and N corresponding to 19-67 %, in the six major soil classes of the Southern Queensland cereal belt, for cultivation periods ranging from 20 to 70 years. As expected, the decreases in SOM negatively affected N uptake by the plants in the long term (DALAL; MAYER, 1986).

In Brazil, the annual loss coefficient of SOM can reach 10 % per year, or 0.1 a^{-1} (BAYER; MIELNICZUK; MARTIN-NETO, 2000). Lower SOM losses estimated as, approximately, 0.014 a^{-1} was found for an Oxisol (62 % of clay with 21 % Fe_2O_3) in conventional tillage systems, while the same soil under no-tillage presented lower SOM losses (0.012 a^{-1}). Meanwhile, the loss rates for an Ultisol were high, varying from 0.054 to 0.029 a^{-1} (22 % of clay with 10.3 % Fe_2O_3) in conventional and no-tillage systems, respectively (BAYER; MIELNICZUK; MARTIN-NETO, 2000). Therefore, predicting SOM dynamics, which include N mineralization, is difficult due to its dependence on factors such as crop/forest type, climate, cultivation system, and soil properties (SANTOS et al., 2008).

The rhizosphere effect is influenced by the forest type, climate, and soil properties and can affect SOM dynamics and the N supply as a consequence of an intensified microbial activity. In this context, it has been recently demonstrated that the rhizosphere microbial populations of *Eucalyptus* genus are able to mineralize nitrogen from SOM surrounding the fine roots much faster, via the so-called process of positive priming effect

(PPE), than the bulk soil populations (DERRIEN et al., 2014; DIJKSTRA et al., 2017; HURTARTE, 2017).

To understand the priming process, one must go back to its origins. The priming effect (PE) was suggested by Löhnis (1926), who studied the decomposition of green manure of legume plants in the soil. He found intensified humus mineralization after the addition of fresh organic residues. Nowadays, it is well known that PE takes place in the rhizosphere of most plant species and may be caused by other compounds besides plant residues, such as dead microorganisms, high- and low-molecular organic substances, or even mineral N (KUZYAKOV, 2002; BLAGODATSKAYA; KUZYAKOV, 2008; CHENG et al., 2014; DIJKSTRA et al., 2013; ZHU et al., 2014).

The PE is defined as a short-term change in SOM turnover caused by the addition of plant residues, dead microorganisms, high and low-molecular organic substances or mineral N (KUZYAKOV; FRIEDEL; STAHR, 2000). However, the addition of such substances does not always lead to a real change in SOM turnover (i.e., net SOM loss or formation). When the accelerated release of CO_2 and N is not be related to SOM turnover, the so-called apparent priming effect (APE) is under operation (C-added <C-respirated (SOM) <C-microbial biomass) – it is caused by the increased microbial biomass turnover (BLAGODATSKAYA; KUZYAKOV, 2008).

The mechanism of priming effect can be seen in the following way: 1- after the addition of a C source, a microbial succession begins, when the activation of several previously inactive microorganisms occurs - many of them respond to specific substrates (BLAGODATSKAYA; KUZYAKOV, 2008); 2- the increased activity of these microorganism increases SOM degradation as a result of co-metabolism and increased enzyme production (i.e., real priming effect (RPE)) (C-added <C-respirated (SOM) >C-microbial biomass) (BLAGODATSKAYA; KUZYAKOV, 2008). Therefore, the main difference between the apparent and the real priming effect is that in APE only increased microbial turnover takes place, while in RPE increased SOM turnover is central (BLAGODATSKAYA; KUZYAKOV, 2008).

Additions of C corresponding to less than 15 % of the amount of C in the microbial biomass (MB) C are associated with the so-called positive priming effect (PPE), through which net loss of SOM occurs (BLAGODATSKAYA; KUZYAKOV, 2008). Such observation indicates that PPE is substrate/energy limited. At C addition above 50 % of the MB, decreases in the priming effect occurs. Values from 200 to 500 % of the MB lead to neutral to negative priming effect (NPE) (BLAGODATSKAYA; KUZYAKOV,

2008). The NPE would result from a preferential use of the highly available and accessible substrate rather than the more recalcitrant and protected material represented by more stabilized SOM. According to these authors, it is important to notice that PPE could happen even under conditions of greater availability of carbon/energy in the case of nutritional limitation, for example, for N. It is also possible that APE is followed by RPE.

The C source quantity and quality play an important role in RPE, provoking changes in the structure of the rhizosphere microbial community. The addition of glucose and glutamic and oxalic acids to the soil led to different patterns of SOM mineralization and bacterial community structure in an experiment mimicking rhizosphere exudation (FALCHINI et al., 2003). Native SOM mineralization was stimulated in the presence of all compounds and marked co-metabolism was observed at the initial stages after glucose and glutamic acid application, followed by greater decomposition of the native SOM when the concentration of the most labile sources decreased (FALCHINI et al., 2003). In the case of oxalic acid, a longer lag phase was observed, which was attributed to the activation process of specific bacterial populations. The authors hypothesized that the lower positive priming effect when oxalic acid was used was due to the low energy content of this compound and the possibility of its reaction with Ca^{+2} and formation of insoluble complexes, especially in $CaCO_3$-rich soils (FALCHINI et al., 2003). The activation of specific bacterial populations was observed when oxalic and glutamic acids were available in the soil, but not with glucose addition (FALCHINI et al., 2003). This was probably due to the fact that glucose is the most abundant monomeric carbohydrate in ecosystems and the basis for the production of energy via catabolic processes, so that all microorganisms in the soil theoretically have the capacity to metabolize this compound (FALCHINI et al., 2003).

Oxidation state of the C source can affect microbial uptake and utilization. Lower oxidation state is related to lower uptake and mineralization rates, which implies higher C incorporation into structural cellular compounds (GUNINA et al., 2017). These authors, studying the effect of C oxidation state, number of -COOH groups, and C atoms, verified that the half-life ($T_{1/2}$) of low molecular weight organic compounds (LMWOCs) decreased with increasing C oxidation states. On the other hand, the number of C atoms of the LMWOCs was related to higher $T_{1/2}$, probably due to a lower soil diffusion rate. At the same time, the proportion of mineralized C-LMWOCs increased with C oxidation state (GUNINA et al., 2017). Therefore, there is a trend for higher incorporation of C-

LMWOCs into the structural cellular compounds and, consequently, to SOC of C-LMWOCs with lower oxidation states, reflecting a higher anabolism/catabolism ratio (GUNINA et al., 2017).

The degree of the recalcitrance of the compounds released in the forest soil is also of paramount importance for the understanding of the cycling process (GOLDFARB et al., 2011). A study of more than 2,200 bacterial taxa showed greater abundance (> 500 of 2,200) when labile substrates (glycine, sucrose) were added to the soil, with a predominance of Proteobacteria and Actinobacteria, such as Actinomycetales, Enterobacteriales, Burkholderiales, Rhodocyclales, Alteromonadales, and Pseudomonadales (GOLDFARB et al., 2011). Lower taxon abundance (<168) was found when more recalcitrant chemical compounds (cellulose, lignin or tannin-proteins) were added. Main taxa included Clostridiales, Sphingomonadales, and Desulfovibrionales (GOLDFARB et al., 2011). Only 6 % of the taxa presented growth with the simultaneous presence of labile and recalcitrant compounds. In such case, the abundance of Burkholderiales was noteworthy. These results suggest that the degradation of more recalcitrant compounds is also a phenomenon dependent on microbial population specialization/preference (GOLDFARB et al., 2011).

With respect to rhizosphere phenomena, the addition of labile C induced increases in rRNA/genome in fast-growing, copiotrophic microorganisms, while this variable decreased for slow-growing microorganisms (oligotrophic) (GOLDFARB et al., 2011). These results led the authors to propose that, in complex communities, newly released labile compounds are primarily used by fast-growing microorganisms that were later succeeded by slow-growing organisms when labile C sources were already depleted (GOLDFARB et al., 2011). In this particular case, an important message is sent regarding the presence of *Burkholderia* in the *Eucalyptus* rhizosphere. This taxon shows greater metabolic plasticity and greater adaptability to the intra-population rhizosphere competition conditions, and, consequently, co-metabolize SOM as an adaptive advantage.

Furthermore, the quality of the compounds added to the soil may influence the structure of the microbial community due to the fact that microbial populations exhibit specific food specialization/preference patterns (WANG et al., 2015). For example, fresh organic material with high C/N ratio and lignin concentration, tend to increase the abundance of fungi and actinomycetes, clearly more adapted to oligotrophic environments (WANG et al., 2015). On the other hand, the addition of fresh organic material of better quality (lower C/N ratio and lignin content) seems to facilitate the

growth of gram-negative bacteria (WANG et al., 2015). The study of the fatty acid profile of soil microbial communities after the addition of residues with different qualities indicates that the priming effect happens primarily because of an unsatisfied demand for C/energy and/or nutrients (WANG et al., 2015). In both cases, a NPE may occur at the beginning, as explained by the hypothesis of preferential substrate use, followed by a PPE when the depletion of the energy and/or nutrients source occurs (N mining hypothesis – see details below) (WANG et al., 2015). PPE tends to take place faster when the good quality material is added to the soil, although this is not determinant for the final, accumulated priming effect (WANG et al., 2015).

Energy-rich compounds can be used for microbial growth and growth-supporting functions, such as the production of extracellular enzymes, that in some environments may constrain decomposers to break down more complex compounds from SOM (DI LONARDO et al., 2017). Fungi, Gram-positive and Gram-negative bacteria are involved in PE (DI LONARDO et al., 2017). In general, bacteria present a wider metabolic diversity and an opportunistic strategy that allows them to uptake soluble substrate fastly (DI LONARDO et al., 2017). In contrast, fungi are better explorers of solid substrates, being able to keep connected to the source of easily-available substrates (tree) and with stable SOM by hyphal growth; they are also able to produce a suite of enzymes that act on recalcitrant compounds, such as lignin-degrading peroxidases (AUDET, 2012; BOBERG et al., 2011). For this reason, it has been hypothesized that fungi may be more important for PE than bacteria (FONTAINE, et al., 2011). *Eucalyptus* may be associated to several fungal groups. Some are biotrophic (e.g., arbuscular mycorrhizal fungi), while others may play a role as saprophytes (e.g., some ectomycorrhizae and associative fungi) (JOHNSON; GEHRING, 2007). The saprophytes are more likely to perform SOM mineralization, being favored by acid environments and low mineral N availability (JOHNSON; GEHRING, 2007).

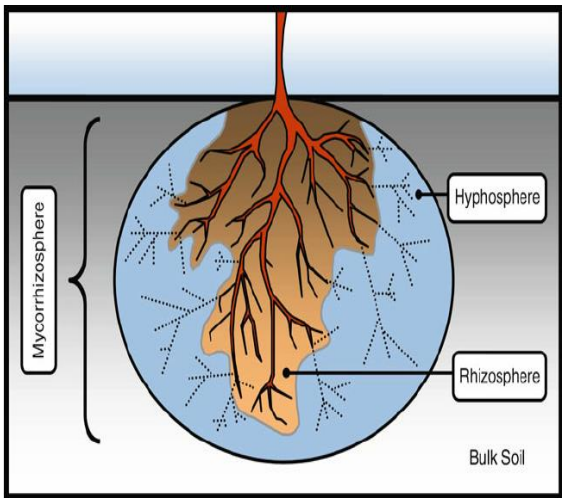

Figure 2. Higher soil volume explored by fungi associated to roots. Brown and blue are the rhizosphere and mycorhizosphere volume, respectively. Source: extracted from Audet (2012), adapted from Beare et al. (1995).

Besides the direct effect of rhizodeposition on C and N mineralization, Keiluweit *et al.* (2015) reported that oxalic acid, a common root exudate produced by fungi in the eucalypt rhizosphere, is responsible for the destabilization of organo-mineral complexes, what facilitates microbial access to compounds previously protected by minerals. This mechanism helps to understand the biotic-abiotic mechanisms that precede the PE. This mechanism defies the assumption that SOM fractions would be protected from degradation on millennial time scales (KEILUWEIT et al., 2015).

1.3. General hypothesis to explain the priming effect

Chen *et al.* (2014) highlight that there are some hypotheses explaining the different aspects of PE, being the most notable: co-metabolism (KUZYAKOV; FRIEDEL; STAHR, 2000), shifts in the composition of microbial communities (FONTAINE, SÉBASTIEN; MARIOTTI; ABBADIE, 2003), microbial activation (DRAKE et al., 2013), preferential substrate utilization (CHENG, 1999), competition for mineral nutrients in the rhizosphere (CHENG, KUZYAKOV, 2005), and microbial mining (DIJKSTRA et al., 2013). Some of these hypotheses are contradictory or overlap each other so that the interpretation of PE can become a hard task without a good domain of this knowledge. For this reason, we have decided to summarize each of these hypotheses bellow.

Co-metabolism

According to Kuzyakov et al. (2000), rhizodepositions are easily accessible to rhizosphere microorganisms, stimulating microbial growth. As an effect of microbial growth, an increased co-metabolic decomposition of SOM may occur, resulting in positive priming effect.

Shift in microbial communities composition

According to this hypothesis, after fresh organic matter input into the soil, many specialized microorganisms grow fastly and decompose the fresh organic matter (FONTAINE, SÉBASTIEN; MARIOTTI; ABBADIE, 2003). Priming effect is a result of the competition for energy and nutrient acquisition between the microorganisms specialized in the decomposition of fresh organic matter and microorganism that attack polymerized SOM (FONTAINE, SÉBASTIEN; MARIOTTI; ABBADIE, 2003).

Microbial activation

According to the hypothesis of microbial activation, microbial biomass increases in response to energy-rich organic compounds, but are limited by the low N availability. In the presence of C and N, microorganisms are able to increase biomass and synthesize enzymes for SOM degradation (DRAKE et al., 2013).

Preferential substrate utilization

If there is a high mineral nutrient supply, rhizosphere microorganisms prefer labile root-derived C, instead of soil-derived carbon (CHENG, 1999). Therefore, there is a reduction of SOM decomposition when the availability of C increases (CHENG, 1999). However, if nutrients are limited, rhizosphere microorganisms use nutrient-rich SOM instead of root-derived C, causing an increase in SOM decomposition when more root-derived C is released (CHENG, 1999) (Figure 3). This hypothesis has as a basic premise that the C/N ratio of the SOM is much narrower than that of the rhizodeposition.

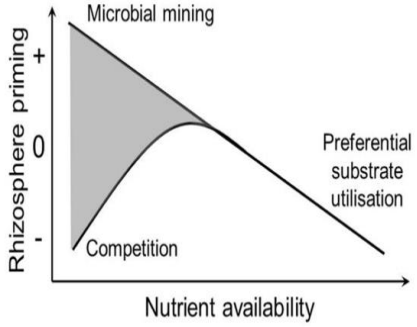

Figure 3. Hypothetical relationship between soil nutrient availability and rhizosphere priming. In conditions of low soil fertility, both positive and negative priming effects may occur. Source: Extracted from Dijkstra et al. (2013a).

Competition for mineral nutrients in the rhizosphere

According to this hypothesis, during plant growth in soils with low nutrient availability (e.g., nitrogen), root uptake intensifies the competition for nutrients in the rhizosphere and reduces microbial growth and metabolism, and, as an effect, limits SOM decomposition (CHENG, KUZYAKOV, 2005). Therefore, under nutrient limiting conditions, SOM decomposition decreases due to the competition between roots and soil microorganisms by nutrients; on the other hand, roots increase SOM decomposition under higher nutrient availability by providing energy-rich organic compounds (CHENG, KUZYAKOV, 2005).

Microbial mining for N and P

This hypothesis was postulated for the first time by Craine et al. (2007) and later improved by Dijkstra et al. (2013a). It was hypothesized that rhizosphere priming is influenced by nutrient availability, but also can affect nutrient supply to plants. The authors postulated that rhizosphere priming effect may enhance N supply to plants in systems that are limited by this nutrient, but not in systems that are phosphorus (P) limited (DIJKSTRA et al., 2013). The so-called "nitrogen mining" is consistently suppressed by N supply (CRAINE; MORROW; FIERER, 2007). When P is the most limiting nutrient, rhizodeposition may be preferentially used to increase P supply (Figure 4) (DIJKSTRA et al., 2013).

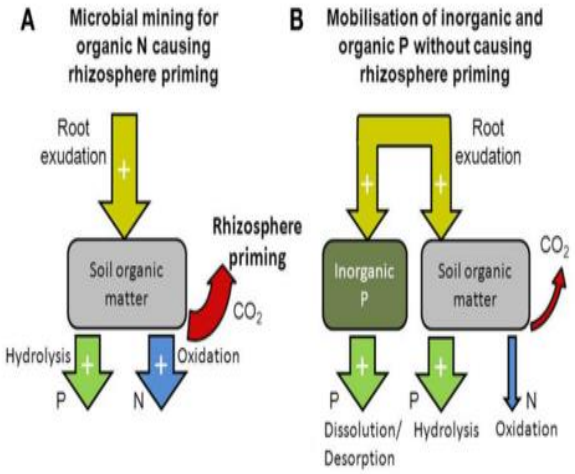

Figure 4. Diagram illustrating how the availability of nitrogen and phosphorus in the soil can influence rhizosphere priming. Source: Extracted from Dijkstra et al. (2013a)

Microbial loop hypothesis

The increased C availability stimulates microbial growth and N uptake and immobilization from SOM, but the protozoa and/or nematodes grazes the microbial biomass, releasing CO_2 and NH_4^+, creating the so-called microbial loop (CLARHOLM, 1985).

Stoichiometric decomposition

According to the hypothesis of "stoichiometric decomposition", when the addition of C and N via substrate is compatible with the microbial demand (stoichiometric C/N ratio), there is an increase in microbial activity and, consequently, in decomposition rates (HESSEN et al., 2004).

According to Chen et al. (2014b), among these hypotheses, there are two that are apparently the opposite of one another: the "stoichiometric decomposition' and 'microbial nitrogen mining'. While the former claims that substrates with lower C/N ratios favor the decomposition of recalcitrant SOM, the latter states just the opposite (i.e., that a lack of

N stimulates SOM degradation) (CHEN et al., 2014a). These hypotheses are clearly linked by the availability of carbon, which is the common element. And when one considers the Fontaine's conceptual model, in which changes in microbial community are related to the priming effect, one can see, for example, the performance of r-strategists on more labile substrates and k-strategists in more recalcitrant substrates (CHEN et al., 2014a).

Chen et al. (2014b) found specific growth rates (μ, h^{-1}) in the presence of different treatments, namely: control; N-mineral; sucrose; sucrose + N-mineral; maize straw; maize straw + N-mineral. The presence of substrates with only C induced the predominance of smaller μ, indicating dominance of k-strategists causing the priming effect, which are more adapted to the conditions of lower availability of N due in part to the higher C/N ratio and the ability to mine recalcitrant SOM (BLAGODATSKAYA et al., 2007; MILCU et al., 2011; NEWMAN, 1985b; SIX et al., 2006). On the other hand, a high C and N availability conditioned larger values of μ, indicating the predominance of r-strategists (CHEN et al., 2014a). Treatments with carbon, but without mineral N, also increased enzyme activity, such as glucosidase, cellobiohydrolase, xylanase, chitinase, and LAP in relation to the control (CHEN et al., 2014a). Treatments with carbon plus N-mineral led to higher enzyme acitivities of glucosidase, cellobiohydrolase, and chitinase, and lower for LAP and xylanase (CHEN et al., 2014a). Therefore, based on enzymatic activity, simultaneous C and N additions induced the activity of cellulose-degrading microorganisms, but decreased the activity of hemicellulose- and protein- degrading microorganisms. This work also points to the fact that the presence of N + straw leads to

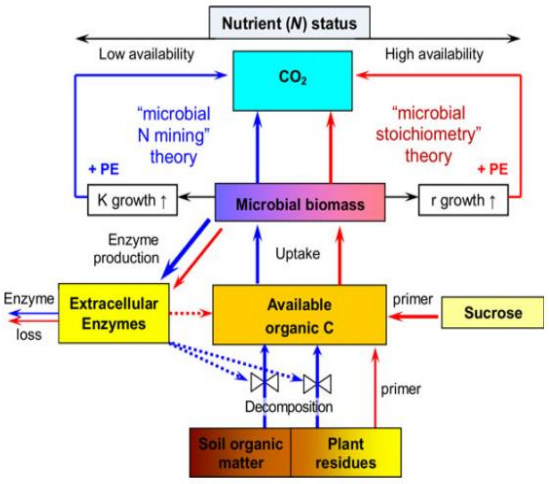

Figure 5. The link between 'microbial N-mining' and 'microbial stoichiometry' hypothesis, considering the effects of C and N availability on priming of soil organic matter. The blue and red lines represent the fluxes controlled by k-strategists and r-strategists, respectively. The dotted lines represent the effect of extracellular enzymes. The availability of the substrates is represented by the darkness of the colour. Source: Chen et al. (2014a)

the preservation of SOM and stimulates degradation of the plant residue (CHEN et al., 2014a).

Since numerous cellular macromolecules contain nitrogen, including proteins, nucleic acids, and cell wall components, nitrogen availability limits microbial growth and is linked to PE (WHITE; DRUMMOND; FUQUA, 2012). Microbes usually respond to N starvation by the nitrogen regulation stress response and by the stringent response (WHITE; DRUMMOND; FUQUA, 2012). In the first case, there is an induction of a specific uptake system to scavenge the environment for the nutrient and/or enzymes are produced that allow the use of alternative N sources (microbial mining) (WHITE; DRUMMOND; FUQUA, 2012). In the second case, changes in metabolic activity, when microorganisms can experience an increased turnover (metabolic breakdown and resynthesis) of proteins and RNA takes place, accounting for part of the CO_2 released during the priming effect. Under this condition, proteins and RNA can serve as an energy source to maintain viability and crucial cell functions, which includes solute transport system, an energized membrane, and ATP pool levels (WHITE; DRUMMOND; FUQUA, 2012).

In this regard, N mineralization processes are linked to the priming effetc (Figure 6) and will be performed by general soil microbes mainly due to three soil conditions: I – microbes are carbon-limited, then they utilize the keto skeletons of amino acids as energy source; II – fluctuations in water and temperature cause microbial death and lysis; consequently, the utilization of the low C/N necromass leads to N-mineralization; III – microbiota is consumed by grazers that release the excess of NH_4^+ (HAWKES; DEANGELIS; FIRESTONE, 2007). Thus, the primary and most important limitation for N mineralization common to the three conditions above is energy/carbon. Once this limitation is overcome, there is a predominance of N immobilization.

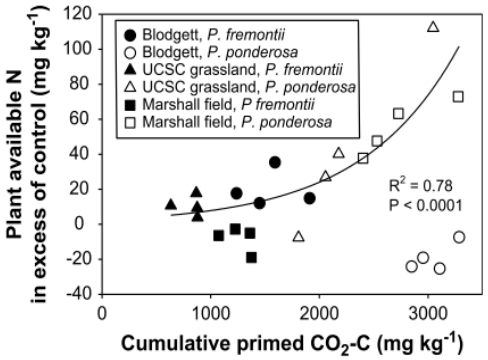

Figure 6. Excess of plant available N as a function of cumulative primed C for each soil type and tree species. Source: Dijkstra et al. (2009)

Table 1, adapted from Cheng and Kuzyakov (2005), presents the dominance of different mechanisms according to the availability of C and N.

Table 1. The hypothesized dominating mechanism under different combination of carbon (C) and nitrogen (N) availability to microbial growth

Soil condition	N limited	N not limited
$C_{available}$ limited	Competition dominates (negative rhizosphere priming)	Substrate preference dominates (negative rhizosphere priming)
$C_{available}$ not limited	Microbial activation or nutrient competition dominates or microbial mining or shifts in microbial communities composition (+ or - rhizosphere priming)	Microbial activation dominates or substrate preference dominates (+ or - rhizosphere priming)

Source: adapted from Cheng and Kuzyakov (2005)

1.4. Experimental evidences

Experiments with the increased CO_2 atmosphere are very important to illustrate the occurrence of RPE. In an experiment with the ^{15}N tracer and CO_2-increased atmosphere (720 vs. 368 p.p.m.), a decreased concentration of ^{15}N labeled in the plant tissues during the 5-years-period of the trial was observed (DIJKSTRA et al., 2008). This decreased concentration along time was explained by unlabeled N mineralization and plant uptake that diluted the ^{15}N in the plant tissues (DIJKSTRA et al., 2008). Indeed, the dilution was faster in the increased CO_2 atmosphere treatment, is probably caused by the higher rhizodeposition of organic compounds with higher C/N ratios than the soil (DIJKSTRA et al., 2008). This may be linked to a microbial mining effect (DIJKSTRA et al., 2009).

Within the Plantae kingdom, woody species present the highest RPE followed by grasses. Crops have the lowest level of RPE, indicating that plant traits and physiology may exert important controls on RPE (HUO; LUO; CHENG, 2017). *Eucalyptus regnans* forests, for example, are able to uptake N amounts that meet their nutritional requirements and maintain normal photosynthetic activity even in soils with low natural fertility (DIJKSTRA, FEIKE A. et al., 2017). As shown Dijkstra et al. (2017), *Eucalyptus* roots themselves induce a greater microbiological activity in the soil, greater respiration, and N mineralization. The authors observed two-fold higher microbial biomass and 5.5 higher gross mineralization in the soil where *Eucalyptus* plantations grew their roots than in the same soil with root exclusion. As a result, a net reduction of 0.50 kg C m^{-2} and 12 g m^{-2} of N was observed in the total C and N contents in plots where roots grew in a relatively short period of time (April 2010 to March 2011) (DIJKSTRA et al., 2017).

Experimental evidence for Brazilian sites in the Vale do Rio Doce region (Minas Gerais state), with a clone of *E. grandis* x *E. urophylla,* also points to the existence of a link between the root activity and the increase in the rates of mineralization of the SOM (DELVAUX, 2014). It was observed a higher microbial biomass, metabolic quotient (q_{mic}), enzymatic activity (laccase and Mn-peroxidase), potential mineralization and, consequently, lower total N in the rhizosphere than in the bulk soil (DELVAUX, 2014) . In greenhouse experiments, Hurtarte (2017) observed that the growth of seedling roots of a clone of *E. grandis* x *E. urophylla* in an oxisol reduced the stocks of C associated to mineral fractions in the rhizosphere, especially when plants were under N limitation (5 % reduction of C). According to the author, the changes are probably related to a higher exudation rate of citric acid in the rhizosphere uncer N limitation. These results are surprising considering the short period of the experiment (20 days). Paradoxically, the priming effect on N mineralization was more intense in treatments with lower nutritional limitation by N, which may be related to the predominant microbial populations in the soil and the mineral mining mechanism.

Dijkstra and Cheng (2007), for example, studied the effect of rhizosphere cycling during 395 days with *Pinus ponderosa* and *Alamos fremont* grown on three different soils. The authors observed that the decomposition of soil organic carbon in planted treatments was up to 225 % higher than in the soil incubated alone. The loss of organic carbon was greater than the formation of new SOM, suggesting that C inputs via roots could result in a net loss of C in soil in the period considered. Under another approach, the effect of exudation on microbial activity was verified in studies with tree girdling (HÖGBERG et al., 2001). Tree girdling involves the removal of the stem bark to the depth of the xylem, interrupting the supply of photoassimilates to the roots and mycorrhizal fungi, without physically disturbing the root system. The authors reported that *Pinus* tree girdling reduced soil respiration within 1-2 months by about 54 % relative to the respiration in the control plots without girdling, and that the decrease was up to 37 % in the first 5 days (HÖGBERG et al., 2001). Murphy et al. (2015) linked the increased availability of labile carbon to N mineralization. These authors observed an increase in N mineralization from SOM of about 54 % in the first three days and of 23 % after eight days compared with control without glucose.

In spite of this, Cook et al. (2016), in a long-term study (over two decades) with short rotations of 6-8 years with *Eucalyptus* trees, observed that trees can increase, reduce or even quantitatively change the SOM stocks from planted depending on the

characteristics of the forest site. However, significant modification of the carbon composition of the soil was observed, changing its isotopic composition from predominantly C4 (original vegetation) to C3 (*Eucalyptus*), suggesting the mineralization of native SOM and its substitution by the organic material of eucalypts. Therefore, it is clear that the studies of the C and N cycling mechanisms in eucalypt plantations are extremely important for understanding the functioning of these ecosystems. As observed, the interactions between eucalypts trees and the forest soil present great importance and complexity, so that its analysis and interpretation can be facilitated through mechanistic modelling. This approach is relevant to this type of study because it comprises multiple simultaneous causal relationships, some of them with feedback networks and time-lagged effects that could hardly be accessed by classical experimentation due to the costs involved and the inherent complexity of the forestry soil.

1.5. Perspectives for the modeling of rhizosphere cycling on an ecosystem scale

Eucalypts plantations occupy an area of approximately 5 million hectares in Brazil and around 20-25 million hectares in the world (COOK; BINKLEY; STAPE, 2016). *Eucalyptus* is a genus in the Myrtaceae Family, whose trees are widely recognized in Australia, Brazil, and other parts of the World due to their unparalleled adaptability to diverse soil and climatic conditions (ATTIWILL; ADAMS, 1996; BARROS; NOVAIS, 1990). These forests are generally confined to regions where average rainfall exceeds 500 millimeters per year. In some regions, forests extend from wetter, coastal, and sub-coastal areas into central, drier parts of the continent (ATTIWILL; ADAMS, 1996). Through these regions, forests grow on soils that vary from ancient, fragile, and infertile soils, to recent, fertile soils of volcanic origin (ATTIWILL; ADAMS, 1996).

Nitrogen (N) is one of the most accumulated nutrients in eucalypts plantations, with values ranging from 120 to 1,300 kg ha^{-1}, depending on the productivity and nutritional efficiency (BARROS; NOVAIS, 1990). Interestingly, stands in Brazil often show little or no response to N fertilization at harvest age (DE MELO et al., 2016; PULITO et al., 2015; SMETHURST et al., 2015). The responses, when present, occur within the first two or three years and cease to exist during the time of harvest (PULITO et al., 2015). Therefore, *Eucalyptus* plants can meet its high N demand without fertilization or with the application of low doses, between 40 and 70 kg ha^{-1} of N (BARROS; NOVAIS, 1990). This low response to N application of some forest sites (not

all) shows that our understanding of N supply in these systems is incomplete. This can be due to the scarcity of information regarding the importance of microbial supply connected to the rhizosphere processes of eucalypts.

Thus, at best, the recommendation of N for eucalypt cultivation is based on soil organic matter content (SOM) and productivity expectancy (GONÇALVES, 1995). Although it represents an improvement over these recommendations without objective criteria, the problem of this system is represented by the low correlations between N accumulated in the stands and SOM concentration, which can lead to both waste of resources and decreasing productivity of agroecosystems. This occurs because the release of nitrogen from the SOM is controlled by soil microorganisms, as highlighted in the previous topic about PE. These microorganisms, in turn, have their dynamics controlled by biotic and abiotic factors with seasonal variation throughout the year, such as water, temperature, and organic substrates (BARROS; NOVAIS, 1990; KUZYAKOV, 2002; PULITO et al., 2015; SMETHURST et al., 2015).

In this regard, modeling can be used to estimate N mineralization from SOM. It is usually performed via empirical, process-oriented or mechanistic (organism-oriented) modeling. The first form of modeling is based on incubation-leaching experiments. The main objective of these studies is to estimate the mineralizable nitrogen (N_0), based on the method proposed by Stanford and Smith (1972); that is, to estimate the probable release of N-mineral (Nm) from the soil stock to the solution in a certain period of time (CAMARGO et al., 2008). Among the several empirical models, it is possible to consider a single compartment (N_0) or two compartments of N (N_1 and N_2), one being more stable than the other, as shown in table 2 extracted from Camargo et al. (2008).

Table 2. Empirical models for the estimation of soil organic nitrogen mineralization

Model	Equation/Reference	Description
Simple exponential	$N_m = N_0(1 - e^{-kt})/$ (Stanford and Smith, 1972)	It considers that N-mineralized is described by only one pool (N_0), which defines N-potentially mineralizable as a function of time (t) at a rate k
Simple exponential	$N_m = N_0(1 - e^{-kt^b})/$(Marion et al. 1981)	Similar to the previous one, except for the exponent (b) in time
Simple exponential	$N_m = N_1 + N_2 - (N_2 e^{-k_2 t})/$ (Jones, 1984)	It considers an initial flux of mineralization (N_1) and an active fraction (N_2) dependent on the time at a rate k_2
Simple exponential	$N_m = N_0(1 - e^{-kt}) + k_0 t/$ (Cabrera, 1993)	It describes the occurrence of two pools, where k_0 is the most stable pool rate
Double exponential	$N_m = N_0 S(1 - e^{-ht}) + N_0(1 - S)(1 - e^{-kt})/$ (Molina et al. 1980)	It describes two pools, where S and (1-S) represent the labile and recalcitrant fraction of N_0, decomposing at a rate k_q and k_s, respectively
Double exponential	$N_m = N_{0q}(1 - e^{-hqt}) + N_{0s}(1 - e^{-kst})/$ (Inobushi et al., 1985)	The first term describes the easily mineralizable N (N_{oq}) and the second most recalcitrant N (N_{os}), decomposed at a rate kq and ks, respectively
Hyperbolic	$N_m = N_0 t(t^{1/2} - t)/$ (Juma et al., 1984)	Estimation of the mineralization half-life ($t^{1/2}$)
Parabolic	$N_m = N_0 t^b$ / (Broadbent, 1986)	Used to adjust to N_0 data preliminarily adopted by Stanford and Smith, 1972

Source: Extracted from Camargo et al. (2008) and originally adapted from Camargo et al. (2002)

Such models have as presupposition experimentally fixed conditions of temperature, moisture, aeration, and availability of organic material (CAMARGO et al., 2008). Gonçalves et al. (2001), tested the equation $Nm = N_0 + b/t$ against $Nm = N_0 (1 - e^{-kt})$ and obtained a better fit to the values obtained in aerobic and anaerobic incubation experiments with the first equation. The total amounts of N_0 (layer 0-15 cm) under aerobic conditions were, on average, 103 ± 53 kg ha^{-1} of N, while under anaerobic conditions they were on average 281 ± 175 kg ha^{-1} of N (GONÇALVES; MENDES; SASAKI, 2001). From this, the authors calculated that the average reserves of N of the sites surveyed were sufficient for three to five crop rotations (7 years each) of *E. grandis*. The research also showed rates of decomposition for *Eucalyptus* comparable to the native ecosystem of the region (cerrado), and higher than the agroecosystem with *Pinus caribaea* var. hondurensis. Finally, it was estimated that only 5 to 15 % of the organic matter content of the soil was susceptible to decomposition in 32 weeks (GONÇALVES; MENDES; SASAKI, 2001).

Despite the desirable simplicity, it seems evident that edaphoclimatic variability, especially in a global context of climate change, should be explicitly considered in the model. This fact is manifested, in part, by the wide range of mineralizable N obtained in

the literature for the same total N content in the soil (CAMARGO et al., 2008). Thus, the same research group that presented the equation Nm = N_0 + b/t (GONÇALVES; MENDES; SASAKI, 2001) parameterized a simple process-based model considering aerobic incubation methods, which explicitly considers the effect of the temperature (Tm) and soil moisture (Wm) in the following equation: Nmin = k × Tm × Wm (SMETHURST et al., 2015). The model, called SNAP (Soil Nitrogen Availability Predictor), was used to estimate mineralizable N in areas with eucalypts in southeastern Brazil. Rates of net mineralization between 150-350 kg ha^{-1} a^{-1} were predicted by SNAP, presenting, in general, a good performance (R^2 = 0.84), with overestimations only during periods of low moisture and temperature (SMETHURST et al., 2015).

The main feature of the nitrogen cycle, which operates the ecosystems, is the integration between the activities of autotrophic and heterotrophic organisms (CAMARGO et al., 2008) (Figure 7). Thus, it can be seen that phenomena in the rhizosphere (and detritosphere) must also explicitly consider the carbon supply, whose importance was highlighted in the previous topics. Otherwise, a single mathematical model could not explain the differences in mineralization between agroecosystems with *Pinus* and *Eucalyptus*, for example, as mentioned above.

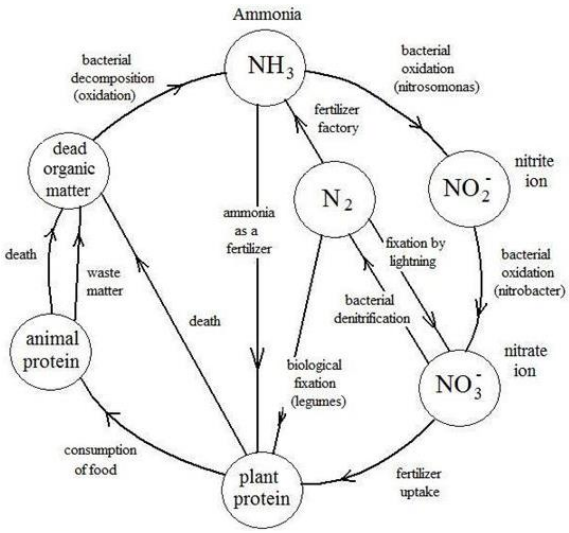

Figure 7. Nitrogen cycle diagram
Source:http://www.brighthub.com/environment/science-environmental/articles/74437.aspx

Therefore, considering the complexity of the N cycle for the proper prediction of N availability, it is necessary to consider the multiple processes that regulate the cycle of this nutrient (RAMBO et al., 2004), including mineralization occurring in the rhizosphere. According to Finzi et al. (2015), the rhizosphere N mineralization may be responsible for supplying up to 1/4 of the total N mineralized in some temperate ecosystems. Several mechanistic, process-based, and empirical models were proposed with the objective of estimating N cycle processes. To a certain extent, factors and processes have been studied in N and organic matter (or C) cycling process models, such as SOMM and ROMUL (CHERTOV et al., 2001), CENTURY (and DayCent) ("NREL-DayCent: Daily Century Model", [S.d.]; PARTON et al., 1987), CANDY (FRANKO;

OELSCHLÄGEL; SCHENK, 1995), CBM-CFS2 (KURZ; APPS, 1999) , DOCMOD (CURRIE; ABER, 1997) , GENDEC (MOORHEAD; REYNOLDS, 1991), MBL - GEN (RASTETTER et al., 1991) , FLDM (ZHANG et al., 2007), Yasso (LISKI et al., 2005) and MCNiP (DRAKE et al., 2013; SCHIMEL; WEINTRAUB, 2003).

Schimel and Weintraub (2003) explain that traditional SOM decomposition models are usually based on first-order kinetics, in which the decomposition rate of a particular C and N pool is proportional to its size and a simple decomposition constant. However, their work with the enzymatic kinetics analysis showed that a non-linear relationship between enzyme concentration and decomposition rate is more likely. According to the same authors, competition for the binding of enzymes on solid substrates is very likely, as described by the Langmuir adsorption isotherm theory. Based on this vision, with the necessary improvements, the MCNiP was elaborated (Figure 8) (DRAKE et al., 2013).

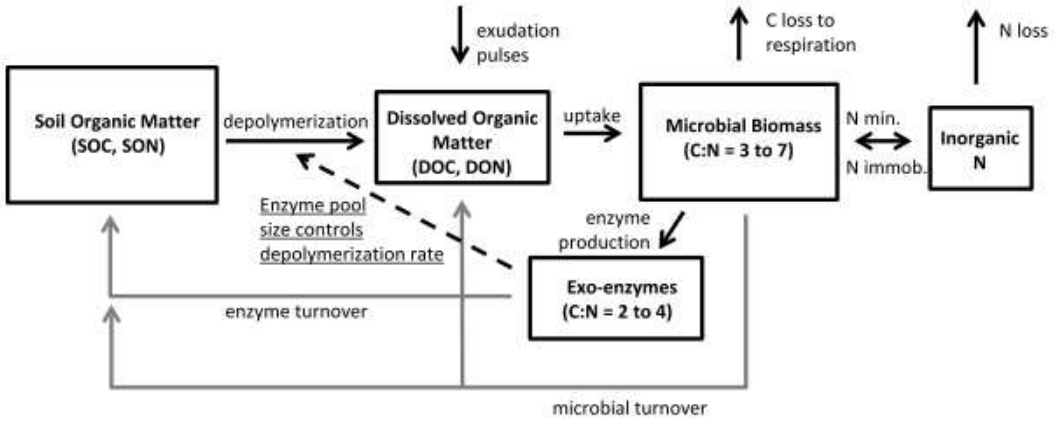

Figure 8. Structure of the decomposition model MCNiP
Source: DRAKE *et al.* (2013)

This model considers the supply of substrates by SOM and exudates and the effect of the stoichiometric relation of inputs and pools of the rhizospheric system (Figure 8) (DRAKE et al., 2013). Tests evaluating the accuracy of the model showed that the model adequately treats microbial responses to the addition of substrates with different C/N ratios (DRAKE et al., 2013). Although it presents good strengths as one of the few organism-oriented models, it still does not consider the edaphoclimatic factor so important for microbial cycling and root growth, necessary for realistic estimates at forest ecosystem level. One perspective of improvement of this model is the adoption of an approach similar to that presented by Smethurst et al. (2015) in the SNAP model mentioned above, regarding the temperature and humidity modifiers. As for the estimation of root growth, it is necessary the coupling to growth models such as 3-PG

(LANDSBERG; WARING, 1997), APSIM (KEATING et al., 2003) or CABALA (BATTAGLIA et al., 2004).

The APSIM model (Figure 9), according to our point of view, seems to be most promising for this purpose because it presents greater sensitivity to soil factors and considers several crops (*Eucalyptus* is considered in the APSIM next generation, see chapter 2), including a general model for N cycling in soil and litter. Therefore, in the future, when considering the rhizosphere system, this model may predict most adequately N supply and feedbacks that are likely to improve the estimates of the eucalypts growth model. Such an accomplishment will not only allow us to have a greater knowledge of the magnitude/importance of the processes in the soil-eucalyptus system but also to better measure the fertilizer doses and produce estimates of growth by a more realistic analysis.

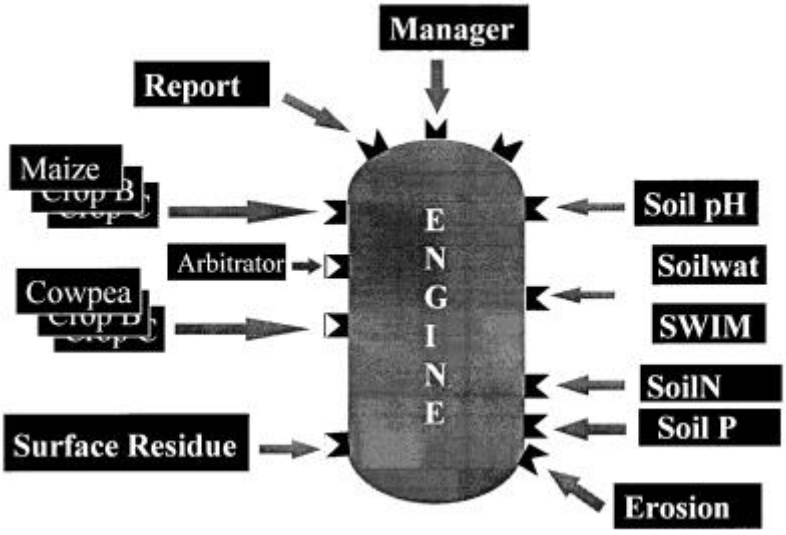

Figure 9. Diagrammatic representation of the APSIM simulation framework with individual crop and soil modules, module interfaces and the simulation engine
Source: Keating et al. (2003**)**

1.6. CONCLUSIONS

The rhizosphere phenomena are ubiquitous in nature, presenting great importance for eucalypt tolerance to biotic and abiotic stresses, as well as explaining part of the evolutionary success of these plants in tropical environments. One of the key phenomena that explain this success is the ability of trees to activate the rhizosphere microbial populations in the so-called rhizosphere priming effect to provide nitrogen from the soil organic matter for its subsequent uptake by trees.

Experimental evidences indicate that this phenomenon is quantitatively important, but the lack of predictive models that consider the simultaneous effects of biotic and abiotic factors on N cycling coupled with growth models, have prevented the estimation of the rhizosphere N supply for eucalypts plantations. This phenomenon, according to experimental observations, has its importance amplified in scenarios of global climate change, which makes their modeling even more urgent.

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HYPOTHESIS

The rhizosphere priming effect (RPE) is quantitatively important for *Eucalyptus* nitrogen nutrition in different climatic and soil conditions.

OBJECTIVE

GENERAL OBJECTIVE

To propose a mechanistic model for estimating the contribution of rhizosphere N mineralization for *Eucalyptus* trees.

SPECIFIC OBJECTIVES

1- To predict the *Eucalyptus* growth under distinct edaphoclimatic conditions of Brazil and Australia.

2- To estimate the contribution of rhizosphere N mineralization for Brazilian and Australian *Eucalyptus* plantations.

CHAPTER 2
Predicting *Eucalyptus* growth using APSIM model in Brazil and Australia

Predicting *Eucalyptus* growth using APSIM model in Brazil and Australia

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ABSTRACT

Our objective with this work was to evaluate a general APSIM *Eucalyptus* growth model and test its sensitivity to the effect of water availability, soil properties, and nitrogen fertilization. The work consisted of a data survey, parametrization, evaluation, and proposing improvements to the previously developed *Eucalyptus* APSIM model for Australia conditions, and also to provide accurate predictions for Brazilian plantations. APSIMs component-based design allows individual models to interact via a common communication protocol, usually on a daily time basis. In this case, the plant module communicates with existing modules for soil processes, such as carbon and nitrogen cycling, surface litter dynamics, water and solute fluxes and soil. The model also has management modules that consider genetic material, fertilization, irrigation, spacing and planting date. With the purpose to evaluate the general APSIM model, twelve sites with a wide variety of climate, soil, and forest management conditions were selected in the following geographical distribution a) Brazil (1-Aracruz - ES; 2 – Curvelo – MG; 3-Itacambira - MG; 4- Monte Dourado - PA; 5- Santana do Paraíso -MG; 6- Ribas do Rio Pardo - MS; 7- Paulistânia – SP; 8- Mogi Guaçú- SP; 9- Luis Antônio) and b) Australia (10 – Gympie -QLD; 11- Coffs Harbour - NSW; 12- Wagga Wagga- NSW). The APSIM model presented satisfactory treatment of growth processes, considering the diverse climatic and edaphic conditions anthe different syvilcultural managements. The performance of the model can still be improved with adjustments to better consider the partitioning of carbon to the roots, as well as other nutritional limitations and nutrient flows in the forest ecosystems, like rhizosphere cycling.

Key-words: above-ground growth; fertilizer response; soil factor; simulation

2.1. INTRODUCTION

Eucalyptus has been planted in more than 20 million hectares worldwide (GAHAGAN, 2010), being found mainly in Latin America, Europe, Asia, Africa, and Oceania. The genus is recognized worldwide due to its unparalleled fast growth capacity and by the adaptability to grow in the diverse soil and climatic conditions around the world (MERCHANT et al., 2007). The trees are naturally found in Australia, where *Eucalyptus* forests extends from wetter regions, in the coastal and sub-coastal areas, into central drier parts of the country; and under low to high latitudes and on soils that vary from ancient and infertile to young and fertile soils (DAFF, 2017).

According to the forest site conditions, management and genotype, *Eucalyptus* trees may present a very different growth patterns in each part of the globe (BARROS; NOVAIS, 1990; GONÇALVES; BARROS, 1999). For instance, Brazilian planted forests mark the world-record of productivity, reaching average values of about 40 m^3/ha/year, meanwhile other countries present productivities levels of 25, 10, and 4 m^3/ha/year, respectively (SOARES; GOMES, 2010). Thus, to understand the factors and processes underlying these productivity variations, intense research efforts have been done by the national and international scientific communities aiming at the improvement of *Eucalyptus* yields, product quality, resource use efficiency, and the selection of the appropriate planting areas.

Most of these productivity variations can be explained by increases in photosynthesis and changes in the photoassimilate partitioning for the different components of the plant, and underground flow or respiration (RYAN et al., 2010). In general, these changes are related to limitations in water, light, temperature, and nutrients (GONÇALVES, BARROS, 1999). Focusing on Brazil and Australia, light and temperature are not considered the main limiting factor in most of their territories (BARROS, NEVES, NOVAIS, 2005). Therefore, differences in the productions of plant biomass between sites are primarily related to water and nutrient availability (BARROS et al., 2005).

Water increases wood net primary productivity mainly because of increases in light interception, photosynthetic efficiency, gross primary productivity, and partitioning to wood (RYAN et al., 2010). On the other hand, nutrients are important because they are part of most of the plant cells components, such as enzymes, pigments, nucleotides, and structural elements. They also play a fundamental role in regulating plant responses to

environmental stimuli (MARSCHNER, MARSCHNER, 1995). Thus, good soil nutrient levels are often related to greater leaf area index and, consequently, to higher above-ground net primary productions (CROMER et al., 1993). The importance of nutrient availability for eucalyptus growth is evident when it is observed that a simple omission of fertilization from one rotation to another can lead to losses of 40 to 60 % in relation to the initial productivity (FARIA et al., 2002).

Modelling the influence of each above-mentioned factor and process is a very challenging task, because that requires the determination of which are the most important ones and how they interact generating a certain pattern of growth response. Despite these difficulties, an impressive advance has been achieved in the last decades, especially regarding the mathematical representation of the processes related to the light interception, vegetal biomass conversion, and partitioning as a function of the variation in the availability of light and water (LANDSBERG, WARING, 1997; LANDSBERG, WARING, COOPS, 2003; ALMEIDA, LANDSBERG, SANDS, 2004; BORGES, 2009). However, the prediction of the effect of soil properties, nutrient availability, and their relationships with water availability on growth has been little studied in the current models, even considering the poor nutrient availability of many soils under *Eucalyptus* plantations and the high nutritional demand of *Eycalyptus* in short rotations.

Our objective with this work was to evaluate a general APSIM *Eucalyptus* growth model and test its sensitivity to the effect of water availability, soil properties, and nitrogen fertilization.

2.2. MATERIAL AND METHODS

The present work was carried out as a partnership between the Commonwealth Scientific and Research Organization (CSIRO, Australia) and Federal University of Viçosa (UFV, Brazil). The work consisted of a data survey, parametrization, evaluation, and improvement of the *Eucalyptus* APSIM model, previously developed by Huth et al. (2008) for Australia conditions and, also, to provide accurate predictions for Brazilian plantation sites.

2.2.1. Model overview

The growth model was developed based on the eucalyptus modeling structure of Huth et al. (2008), within the Agricultural Production Systems Simulator (APSIM; Keating et al., 2003). APSIM allows individual models to interact through a common communication protocol on a daily time scale. Thus, the plant module communicates with the existing modules for soil processes, such as carbon and nitrogen cycling, dynamic surface residues, water and solute flows, and soil temperature (PROBERT et al., 1998).

The model also has management modules that consider genetic material, fertilization, irrigation, spacing, and planting date. The main model input data are: precipitation (mm/day); radiation (mJ/m²); maximum and minimum temperature (ºC); moisture in the field capacity and in the permanent wilting point (mm/mm); soil organic matter content (%); C/N ratio of organic matter (g/g); amount of vegetal residue over the area (kg/ha); C/N ratio of the residue (g/g); soil pH; profile depth (cm). Here, the essential details for the understanding of the work will be presented based in the APSIM website (<http://www.apsim.info/Documentation.aspx>). More information can be obtained in the documentation section of this website.

Photosynthesis

Biomass production is estimated by the product of the amount of radiation intercepted and its conversion efficiency, called radiation use efficiency (RUE) (MONTEITH et al., 1977). In this estimation, the RUE is deducted by the effect of stress factors related to plant nutrition (Fn), air temperature (Ft), vapor pressure deficit (Fvpd), and water supply (Fw), as shown in equation 1.

Growth is calculated as,

$$\Delta G = Rint\ x\ \varepsilon\ x \min(Ft, Fn, Fvpd)\ x\ Fw \qquad \text{Eq. 1}$$

Where ΔG is daily growth, R int is the daily intercepted solar radiation (MJ/m^2), ε is the radiation use efficiency (g/MJ) and Ft, Fn, Fvpd, and Fw are growth modifiers for temperature, nitrogen, vapour pressure déficit, and soil water supply, respectively. Rint is calculated using crown cover, leaf area, and an assumption of exponential light extinction. Ft and Fvpd are based on average daily temperature and vapour pressure deficit, respectively. Fn is based on leaf nitrogen concentration. Fw is calculated as the ratio of soil water demand and supply.

Partitioning of daily growth

The biomass produced is allocated to different compartments of the plant, among which are: foliage, branches, bark, wood, and roots. The above-ground biomass allocation changes throughout the plant growth cycle, consistent with that observed for plants growing in the field. Leaf area growth is calculated from leaf growth and a specific leaf area. Similarly, root length calculations use a specific root length.

Senescence and detachment of biomass

The senescence of the growth compartments (foliage and roots) is calculated by means of simple first order equations. The user specifies an average residence time (in days) that is inverted within the model to provide a decay coefficient. Senescence of foliage is often observed to show a certain seasonality, depending on the presence of stress factors, such as those related to temperature and shading. Biomass that has been senesced above the soil is added to surface residues. Root biomass is added to soil organic matter.

Plant water uptake and use

The plant water demand is calculated using the Micromet module, while the plant water supply is calculated using the water module available in APSIM. The potential uptake of water by the root system is calculated for each soil layer with root growth. In each layer, the potential absorption is calculated as the product of the available water in the layer and a factor that controls the rate of extraction. If water absorption does not meet the plant demand, trees experience water stress.

Plant nitrogen uptake and use

Plant nitrogen demand is based on the size of the biomass pools and a target nitrogen concentration for each pool. When nitrogen supply is insufficient to meet all this demand, nitrogen is partitioned according to the sink strength in each pool. If this results in a decrease in leaf nitrogen concentration the plant may experience nitrogen stress.

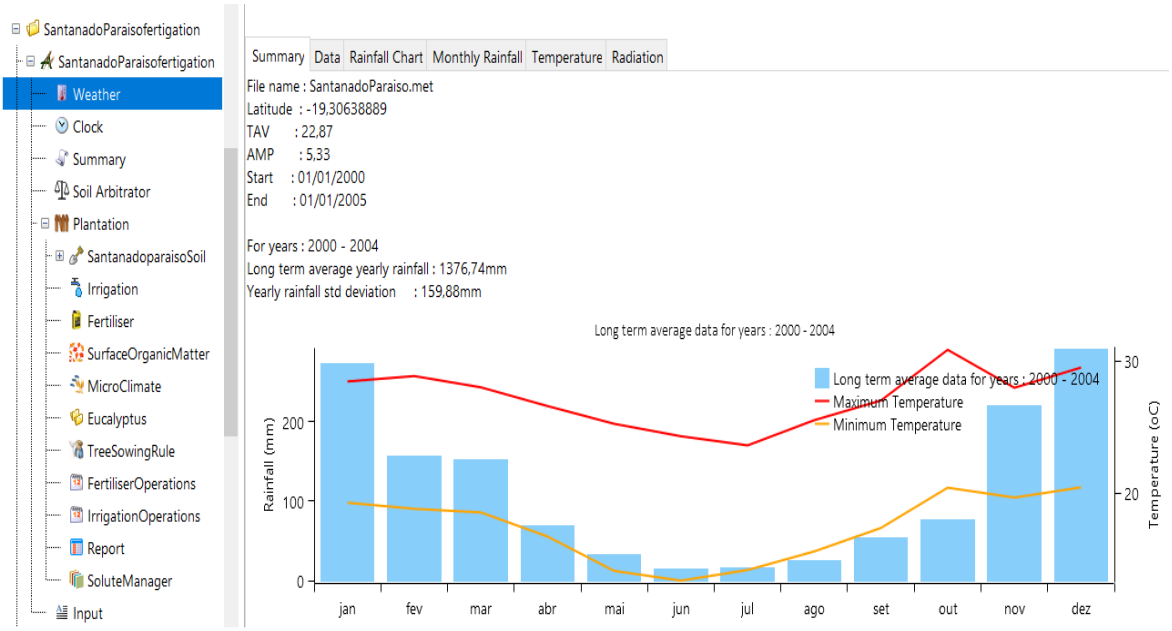

Figure 1. *Eucalyptus* model plataform

2.2.2. Site descriptions

With the purpose of evaluating a model adequate for the most important *Eucalyptus* genetic materials growing under Brazilian and Australian environmental conditions, selected twelve sites with a wide variety of climate, soil, and forest management conditions were selected. The datasets used for these sites were collected from the works of Turner (1986), Ross and Thompson (1991), Cromer et al. (1993), Myers et al. (1996), Almeida et al. (2004), Borges (2009), Nogueira (2005), Silva (2006), and Melo et al. (2016). The geographic distribution of these sites are shown in the Figures 1a and 1b.

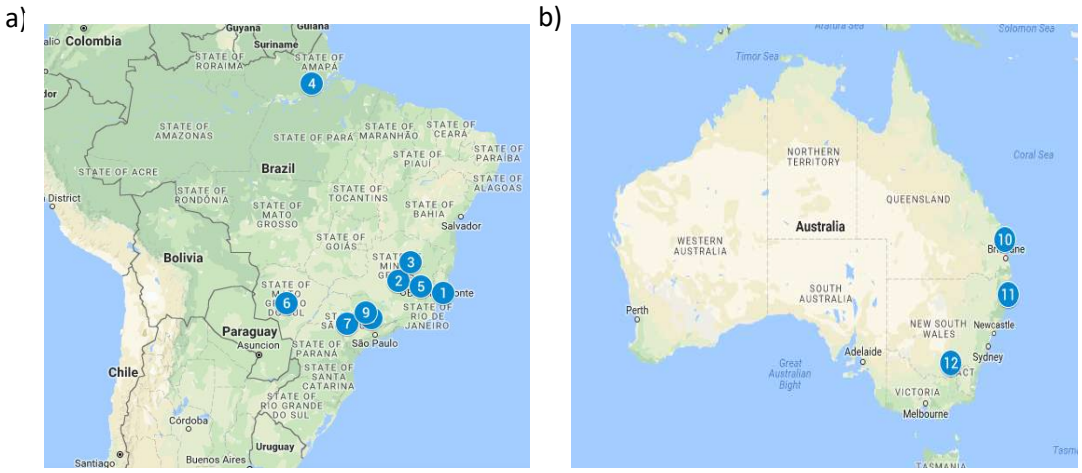

Figure 2. Geographical distribution of the studied forest sites in a) Brazil (1-Aracruz - ES; 2 – Curvelo – MG; 3- Itacambira - MG; 4- Monte Dourado - PA; 5- Santana do Paraíso -MG; 6- Ribas do Rio Pardo - MS; 7- Paulistânia – SP; 8- Mogi Guaçú- SP; 9- Luis Antônio) and b) Australia (10 – Gympie -QLD; 11- Coffs Harbour - NSW; 12- Wagga Wagga- NSW)

The forest sites were chosen considering the main *Eucalyptus* producing regions in these two countries and the availability of data. The datasets encompass different altitude, precipitation, temperature, and soil conditions (Table 1). We have also selected sites that allowed the evaluation of differences between genetic materials, fertilization, irrigation and fertirrigation (Table 2). The soil characteristics of each site were extracted from Turner (1986), Ross and Thompson (1991), Cromer et al. (1993), Almeida et al. (2004), Borges (2009), Nogueira (2005), Silva (2006), and Melo et al. (2016). In the absence of information on soil water characteristics, the values of field capacity and permanent wilting point were estimated according to equations proposed by Andrade and Stone (2011) and Klein, Baseggio, Madalosso and Marcolin (2010).

Table 1. Geographic and climatic information of the studied sites

Sites	State	Latitude *	Longitude *	Elevation (m)	Rainfall (mm)	Mean temperature (°C)
Aracruz	ES[1]	-19.81	-40.23	69.0	1179.0	23.5
Curvelo	MG[1]	-18.76	-44.43	600.0	1360.0	22.8
Itacambira	MG[1]	-17.07	-43.31	1100.0	900.0	20.6
Monte Dourado	PA[1]	-0.51	-52.67	65.0	2115.0	26.4
Santana do Paraiso	MG[1]	-19.31	-42.38	220.0	1163.0	25.2
Ribas do Rio Pardo	MS[1]	-20.75	-54.98	530.0	1472.0	24.5
Paulistânia	SP[1]	-22.55	-49.32	610.0	1387.0	22.5
Mogi Guaçu	SP[1]	-22.07	-47.03	591.0	1446.0	22.0
Luis Antônio	SP[1]	-21.58	-47.52	610.0	1213.0	21.5
Gympie	QLD[2]	-26.0	152.83	54	1267.5	21.1
Coffs Harbour	NSW[2]	-30.12	153.18	21	1635.4	19.0
Wagga Wagga	NSW[2]	-35.0	147.35	147	703.6	16.3

[1]Brazilian states: Espírito Santo (ES); Minas Gerais (MG); Pará (PA); Mato Grosso do Sul (MS); São Paulo (SP); [2]Australian states: Queensland (QLD) and New South Wales (NSW); *Latitude and longitude in decimal degrees.

Table 2. Forest sites used in the study

Site	Specie/hybrid	Age	Treatments	Source
Aracruz	*E. urophylla x E. grandis*	5	Clones 15 and 22	Almeida et al. (2004)
Curvelo	*E. grandis x E. urophylla*	7	Clones 3334 and 3336	Borges (2009)
Itacambira	*E. grandis x E. urophylla*	7	Clones 3334 and 3337	Borges (2009)
Monte Dourado	*E.grandis x E. urophylla*	4	Control and rates of NPK	Silva (2006)
Santana do Paraiso	*E. grandis*	3	Control, irrigation and fertirrigation	Nogueira (2005)
Ribas do Rio Pardo	*E. grandis x E.urophylla*	5	Rates of N	Melo et al. (2016)
Paulistânia	*E. grandis x E. urophylla*	6	Rates of N	Melo et al. (2016)
Mogi Guaçu	*E. urophylla x E. globulus*	7	Rates of N	Melo et al. (2016)
Luis Antônio	*E. urophylla x E. globulus*	8	Rates of N	Melo et al. (2016)
Gympie	*E. grandis*	6	Rates of N	Cromer et al. (1993)
Coffs Harbour	*E. grandis*		-	Turner (1986)
Wagga Wagga	*E. grandis*	5	Irrigation	Myers et al. (1996)

2.2.3. Parameter estimation

Most of the parameters in APSIM were selected based on observation values from previous studies. For instance, reference values for specific leaf area, leaf residence time, and radiation use efficiency were based in the range of data presented by Almeida et al. (2004), Laclau et al. (2008), and Stape, Binkley and Ryan (2008). The remainder was estimated by systematical variations until a "best fit" was obtained between the APSIM output and the corresponding observed data. Essentially, the model is executed and the outputs compared to the measured data. A number of parameter values can be varied to change the output, but the normal procedure is to use standard or the best empirical values available for as many parameters as possible.

2.2.4. Model evaluation

The following are the main statistics used to describe the performance of the model in predicting the *Eucalyptus* growth under different site conditions presented in Table 1.

1- It was used a linear regression of observed (O) microbial biomass vs predicted (P) data and its coefficient of determination (R^2).

2- Nashe 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 standardised value of the root mean square error.

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

2.3. RESULTS

2.3.1. Model evaluation

The model presented excellent performance considering the diverse conditions of soil, management, climate, and *Eucalyptus* genotypes in the Brazilian and Australian sites. According to Fig. 2, our model explained, approximately, 91 % of the observed data variation ($p<0.01$). The index Nashe Sutcliffe efficiency (NSE) was of 0.89, demonstrating lower ratio between the variance of predicted and observed data. The mean (ME) and the mean absolute error (MAE) of -0.07 and 1.26, respectively, are considered adequate for the average of observed values of field experiments (mean +/- standard deviation: 6.02+/- 6.2), as well as the RMSE of 2.07. The Root Mean Square Error to Standard Deviation Ratio (RSR) corresponded to 0.34, which is considered low by Moriasi et al. (2007). The latter authors suggest that RSR values below of 0.6 indicates a good to a very good performance

In general, there was a trend of overestimation of the initial values and underestimation of the final values. As the plants grow there is a convergence between observed and predicted values, which is evident by the approximation and overlapping of the predicted line with the line of ideal values (P = O line). It is interesting to note that there was a slight prevalence of overestimation, in about 56 % of the results, being the other results equal or underestimated when compared to the observed data. In 64 % of the cases of overestimation of the initial growth, irrigation, and/or fertilization treatments were involved. The other cases were related to genetic material and control treatment. It is noteworthy, however, that the predicted/observed relationship was on average for adult plantations close to 1 (0.94) and that the prediction interval encompasses a large part of the observed values, with 95 % confidence, disregarding only a few observations of Gympie, Curvelo, Itacambira, and Coff Harbour.

In general, the following sites were highlighted by the results of initial overestimation in one or more treatments: Gympie; Santana do Paraíso (Irrigation and Control), Aracruz, Curvelo, Luís Antônio, Mogi Guaçú and Ribas do Rio Pardo. The adult phase overestimation was much lower, being found at a higher level for the sites of Gympie (fertirrigation), Mogi Guaçú (all the treatments) and Ribas do Rio Pardo (control and dose 150 kg/ha of N). The underestimation in the adult growth stage was highlighted by the simulations for the sites: Gympie (control and irrigated); Santana do Paraíso

(control); Curvelo (clone 3334); Monte Dourado (sandy soil) and Paulistânia (doses 0 and 50 kg/ha of N). The other sites presented simulation values close to the observed ones.

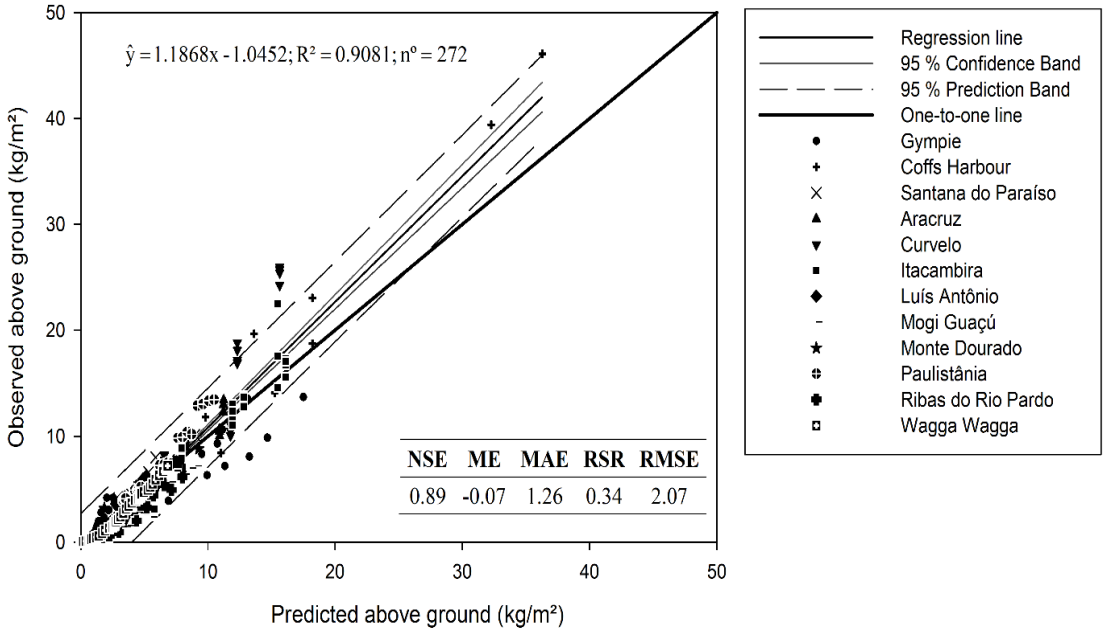

Figure 2. Linear regression of observed vs predicted above ground data

2.3.2. Soil effect

Soil organic matter content

The growth of *E. grandis* vs *E. urophylla* was simulated over five years in the city of Monte Dourado, Pará, Brazil (Figure 2). To analyze the sensitivity of the model to soil factors, two databases with different soil characteristics of water retention capacity and organic matter content were selected. Soil 1, more clayey and with higher levels of organic matter conditioned higher growth of *Eucalyptus*. Soil 2, on the other hand, led to lower plant growth. By the graphical analysis of the predicted and observed values, it can be deduced that the APSIM was able to predict with considerable accuracy the situation of the clayey soil, and underestimated growth in the sandy soil.

Since the two sites were under the same climatic conditions, the APSIM model considered that the productivity difference is due, first, to the effect of organic matter on nitrogen supply in soil 1 (4.3 dag/kg MOS) compared to soil 2 (1.9 dag/kg MOS) (Fig. 4). Water stress was the second most influential factor (Fig. 5). Both stress index (Fn and Fw) show an amplitude of variation between 0 and 1, where the closer to 1 the lower the stress. In the case of the nutritional stress index by N, it was observed that, throughout

growth, these values were higher for soil 1, richer in organic matter, indicating a higher N supply for the plants. Water availability of soil 2 was also more restrictive for *Eucalyptus* growth (Figure 5), although, in this case, it was not the most important factor to explain the productivity differences between the sites for APSIM.

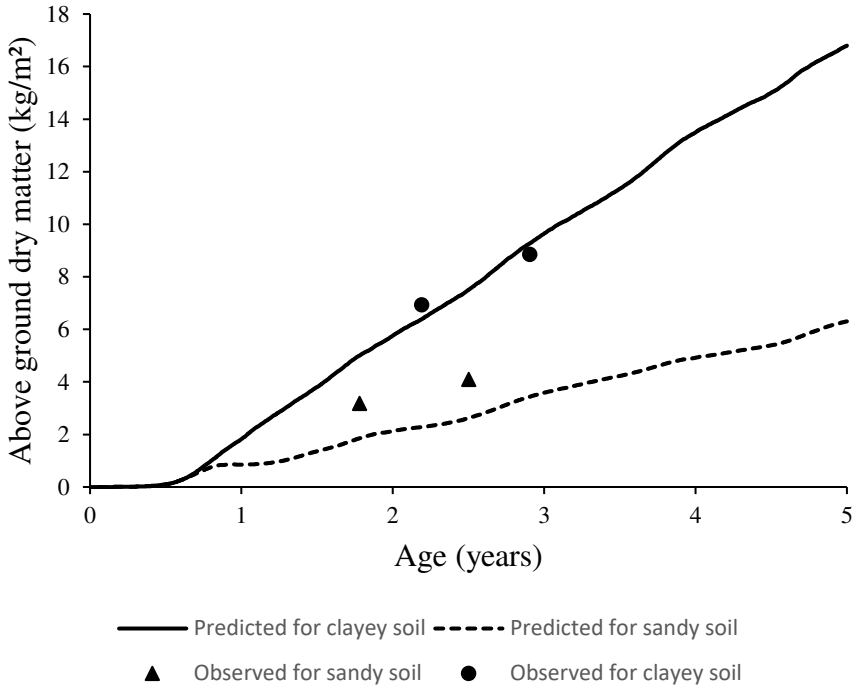

Figure 3. Simulation of wood production as a function of the effect of two soils with distinct clay and organic matter contents from the region of Monte Dourado, Pará, Brazil

Figure 4. Simulation of the *Eucalyptus* N nutritional stress factor in two soils with different clay and organic matter contents of the region of Monte Dourado, Pará, Brazil

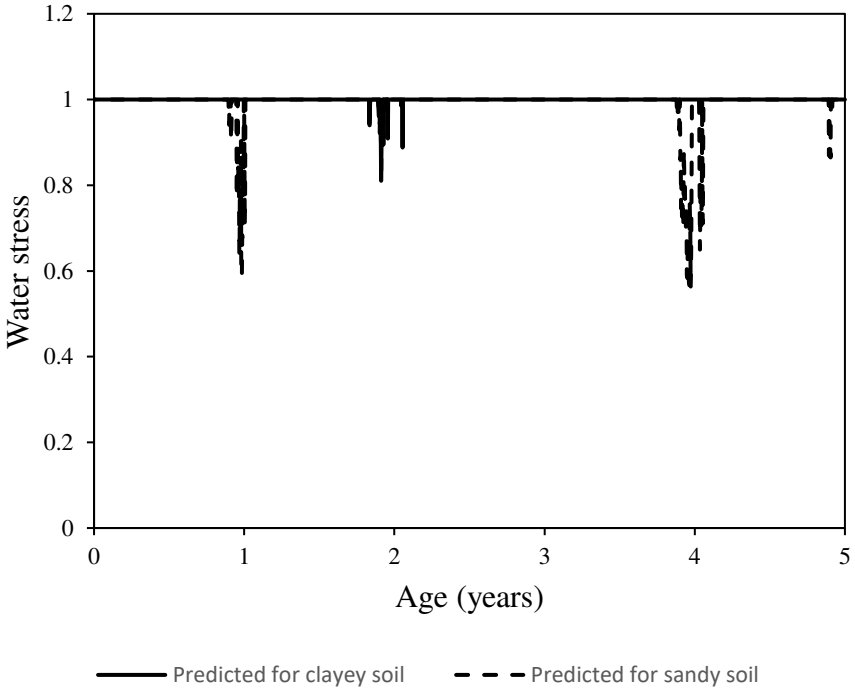

Figure 5. Simulation of the water stress factor in two soils with distinct clay and organic matter contents from the region of Monte Dourado, Pará, Brazil

2.3.3. Nitrogen fertilizer and irrigation effect

The model simulated the response to fertilization and irrigation closer to the o bserved values, but presented a considerable deviation for the control treatment (figure 6). Figure 7 represents the main source of variation expected for the treatments under st udy, which refers to the nutritional factor and water stress. Stress due to nitrogen defici ency increased markedly from the age of 1 year, which is expected as a consequence of canopy formation. Stress due to water deficit was very low (Figure 8), showing that in s uch situations nutrients rather than water are the most limiting factors.

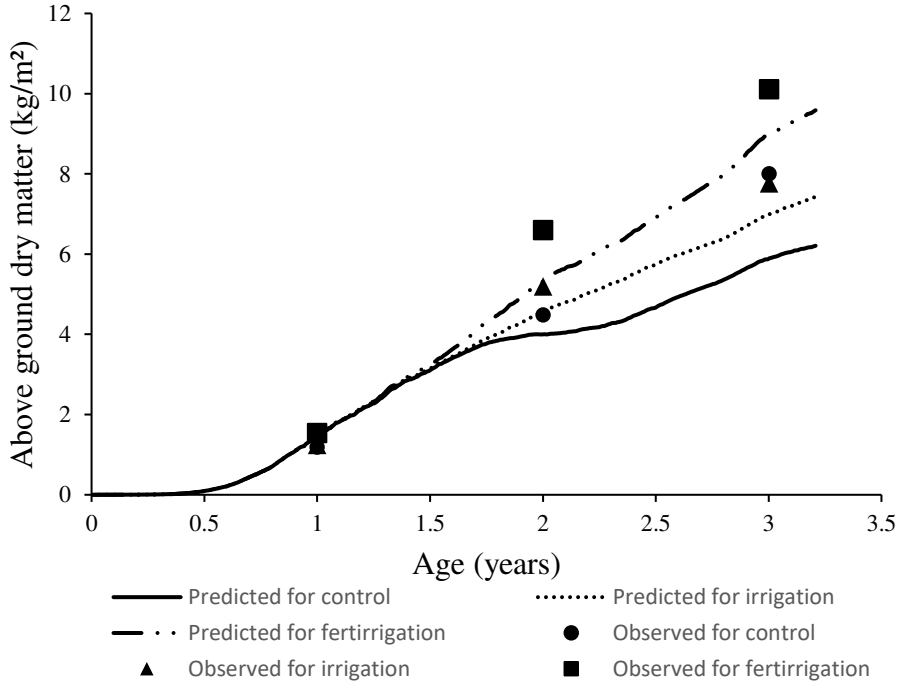

Figure 6. Simulation of the above ground production as a function of irrigation and fertigation at Santana do Paraíso, Minas Gerais, Brazil

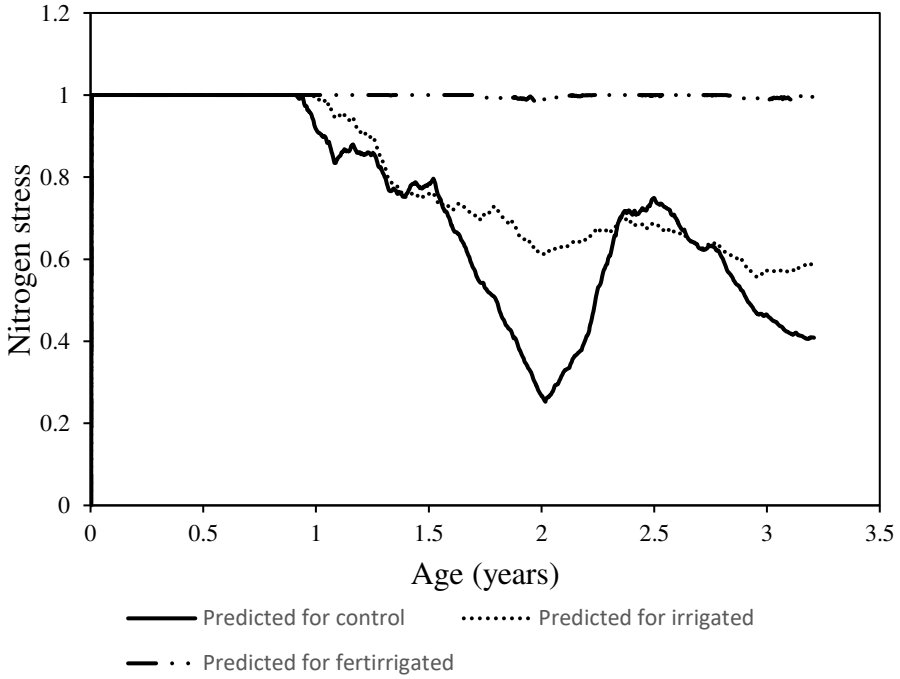

Figure 7. Simulation of the N nutritional stress as a function of different treatments at Santana do Paraíso, Minas Gerais, Brazil

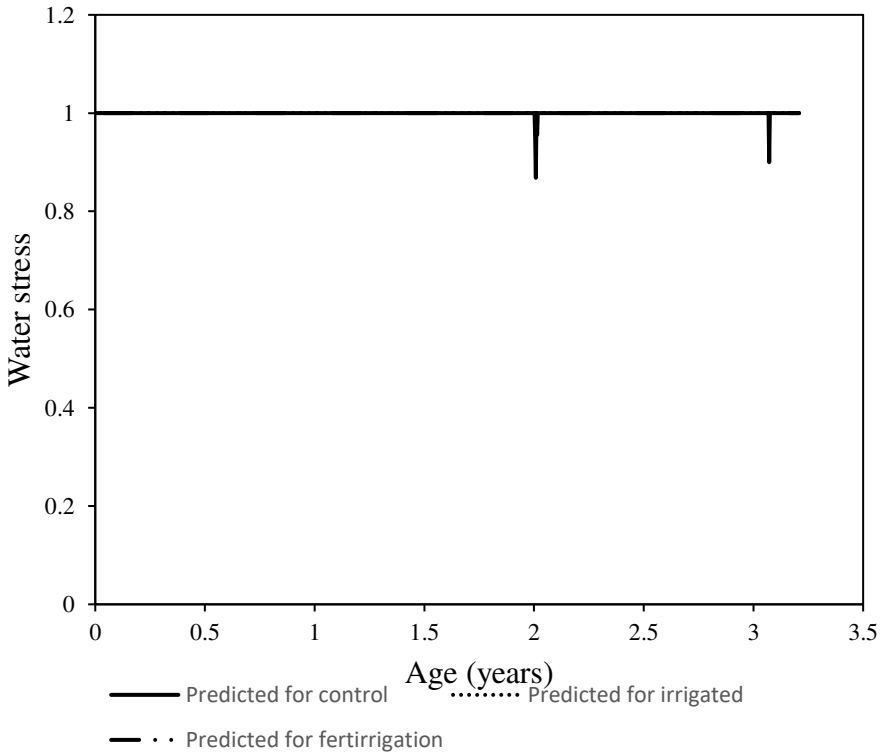

Figure 8. Simulation of water stress as a function of different treatments at Santana do Paraíso, Minas Gerais

2.4. DISCUSSION

The model simulated the growth of eucalyptus in a wide range of conditions, from latitudes -30.12 to -0.51 (decimal degrees), with mean rainfall varying from 703.6 to 2115 mm and with average temperatures from 16.3 to 26.4 ° C. Considering the complexity of factors involved in these datasets (and observing figure 2), the R^2 value of 0.91 indicates an adequate approach for the considered processes. The current version of APSIM presented an MAE/average ratio of 0.20 and RMSE/average of about 0.34. Therefore, it can be concluded that MAE and RMSE are within an uncertainty pattern for field experiments, where one can idealize values until 0.3 (or 30 %) (sd / mean) as adequate.

Part of the observed deviations may be related to the fact that some information was missing, such as the soil profile depth and the water soil properties (LL, DUL, and SAT), which had to be estimated for some sites (Ribas do Rio Pardo, Mogi Guaçú, Paulistânia and Luis Antônio). As mentioned above, we have calculated some of these hydrological soil parameters based on soil texture according to the equations proposed by Andrade and Stone (2011) and Klein, Baseggio, Madalosso and Marcolin (2010). Such information is extremely important for this type of study, since, according to Stape, Binkley and Ryan (2004), water soil regime is the most important factor causing changes in productivity in tropical regions, followed by nutrients. Another important factor is the different partition pattern observed for the genus *Eucalyptus*, which can hardly be predicted with average parameters. Considering the root biomass partitioning in the current version of APSIM, a simple equation of partition rate (root/shoot) was assumed for *Eucalyptus* genus. However, important changes in the pattern of tree biomass allocation may be related to plant species, age, nutritional status, among other factors (CHEN et al., 2015). *E. pelita*, for example, typically allocates more carbon to the roots than other species (BARROS, NOVAIS, 1990). Within the same genotype, when fertilized or under broader spacing, a reduction in the partitioning of biomass to the roots may be observed (OLIVEIRA NETO et al., 2003).

However, the significant fact it is the characteristic feature of the genus *Eucalyptus* to present decreasing root/shoot biomass ratios with the increase of growth. This is evident in the study carried out by Chen et al. (2015) where a decreasing partition ratio (root / shoot) was observed for *E. urophylla* from 0.35 to approximately 0.28 for trees with 1 to 6 years, respectively. Reis et al. (1985) also observed a different root/shoot ratio for *E. grandis* in sites of better quality and worse quality (lower fertility and higher

water deficiency), ranging from 0.6 to 0.47 and 0.25 to 0.20, respectively. For hybrids of *E. grandis* vs. *E. urophylla*, Almeida, Landsberg and Sands (2004) observed that the less productive clone (named 22) partitioned more to roots (mean root/shoot ratio of 0.2) than a more productive clone (named 15) (mean root/shoot ratio of 0.15). It is notorious that the all above mentioned authors observed larger partition for the initial root growth, which precedes the rapid growth phase and formation and closure of the tree canopy. In this phase, where the importance of geochemical cycling is emphasized, the greater partitioning to the roots in relation to that assumed in the APSIM would explain the prevalence of overestimated initial growth values. Therefore, changes in the model with respect to the root/shoot partition functions should improve the performance of the model (see supplementary material).

It interesting to note in figures 3 and 6 that, under conditions of soil moisture close to the ideal and higher fertility, the model tends to simulate values closer to those observed. In this line, in Figure 6, irrigated and fertirrigated treatments showed higher convergence between simulations and predictions. The exception is the control treatment in which a higher underestimation of the final growth was observed. This latest result illustrates a typical condition in which the initial root growth of the control treatment may present a compensatory effect by exploring deeper layers of the profile, what would increase the uptake of water and nutrients. The opposite can be observed in sites such as Paulistania and Ribas do Rio Pardo. In these cases, it is interesting to note that the availability of N is not the greatest limitation, as already reported in Pulito et al., (2015) and Smethurst et al., (2015). In this scenario, the model estimates responses to N fertilizer where they are not expected to occur. Improvements to the model performance can still be gained if we consider other limitations such as K, P, and B, besides water and N deficiencies focused in our study.

2.5. CONCLUSIONS

The APSIM model satisfactorily predicts the growth of *Eucalyptus* above ground biomass, presenting potential to simulate the plantations in diverse climatic and edaphic conditions and under different sylvicultural managements. Adjustments to better consider the partitioning of carbon to roots, as well as other nutritional limitations and nutrient flows in the forest ecosystems may improve the performance of the model.

Supplementary material

Table 3. Partitioning and allometrics equations suggested to improve APSIM model

Description	Equation	Description	Equation
Leaf/shoot partitioning[1]	$\hat{y} = 0.0104 + \frac{(0.3680-0.0104)}{(1+\left(\frac{shoot}{2169.2210}\right)^{1.3721})}$; R^2 = 0.99	Leaf/shoot partitioning[3]	$\hat{y} = \frac{1}{(1.6008+0.0009shoot^{1.0333})}$; R^2=0.98
Stem/shoot partitioning[1]	$\hat{y} = 1.0061 + \frac{(-10.4516-1.0061)}{(1+\left(\frac{shoot}{12.1780}\right)^{0.7876})}$; R^2 = 0.99	Stem/shoot partitioning[3]	$\hat{y} = \frac{(0.3695*856.6625+1.0275*shoot^{0.9212})}{(856.6625+shoot^{0.9212})}$; R^2=0.98
Bark/shoot partitioning[1]	$\hat{y} = 0.1773 + 3.0546\ 10^{-6}Shoot - 8.7825\ Shoot^2$; R^2= 0.56	Specific leaf area[1,3,4]	$\hat{y} = 18.9258shoot^{0.0993}$; R^2=0.85
Branch/shoot partitioning[1]	$\hat{y} = 0.085 + \frac{(0.2867-0.085)}{(1+\left(\frac{shoot}{8142.964}\right)^{74.3069})}$; R^2 = 0.88	Branch+Bark/shoot partitioning[3]	$\hat{y} = -0.1582(-0.7765 - \exp^{(-0.00006shoot)})$; R^2= 0.32
Root/shoot partitioning[2]	High quality site $\hat{y} = 0.15364 + \frac{(0.2519-0.1536)}{(1+\left(\frac{shoot}{3026.15}\right)^{3.446014})}$; R^2 = 0.99 Low quality site $\hat{y} = 0.4467 + \frac{(0.58-0.4467)}{(1+\left(\frac{shoot}{1947.877}\right)^{194.554})}$; R^2 = 0.99	Root/shoot partitioning[4]	General $\hat{y} = 0.7889 - 0.6797e^{(-8798.1622*shoot^{-1.2949})}$; $R^2 = 0.96$ Clone 15 $\hat{y} = -1410.837 + \frac{(0.1722515 + 1410.837)}{\left(1+\left(\frac{shoot}{10471930}\right)^{1.476136}\right)}$; R^2 = 0.99 Clone 22 $\hat{y} = 0.18 + \frac{(0.25-0.18)}{(1+(\frac{shoot}{7025.867})^{46.2987})}$; R^2 = 0.83
Diameter at breast height[1]	$\hat{y} = \frac{(-3.7441*77.6625+36.911*shoot^{0.4869})}{(77.6625+shoot^{0.4869})}$; R^2 = 0.88	Diameter at breast height[3]	$\hat{y} = \frac{0.19409shoot}{(0.0029+shoot)}$; R^2=0.96
Height[1]	$\hat{y} = \frac{(0.7600*738.5755+30.28438*shoot^{0.7440})}{(738.57553+shoot^{0.7440})}$; R^2=0.93	Height[3]	$\hat{y} = 0.1920\ (0.9999^{shoot}) * (shoot^{0.5159})$; R^2=0.97

[1]Partitioning relationships for *E. grandis*, considering shoot in g/m²; Data source: Coffs Harbour; Root/shoot relationships based in the work of REIS, M. das G.F.; KIMMINS, J.P.; REZENDE, G.C. de; BARROS, N.F. de. Acumulo de biomassa em uma sequencia de idade de Eucalyptus grandis plantado no cerrado em duas areas com diferentes produtividades; [3]Partitioning relationships for *E. grandis* vs *E. urophylla* hybrids, considering shoot in g/m²; Data source: Curvelo and Itacambira; Root/shoot relationships based in the dataset from Aracruz .

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CHAPTER 3
Modeling rhizosphere carbon and nitrogen cycling in *Eucalyptus* plantation soil

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} a^{-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.

Key-words: root grouth, rhizodeposition, priming effect, nitrogen nutrition

3.1. INTRODUCTION

Nitrogen is a nutrient essential for plant growth and sustainability of natural and managed ecosystems, including *Eucalyptus* plantations (BARROS, 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, 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, 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, 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.

3.2. MATERIAL AND METHODS

3.2.1. 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.

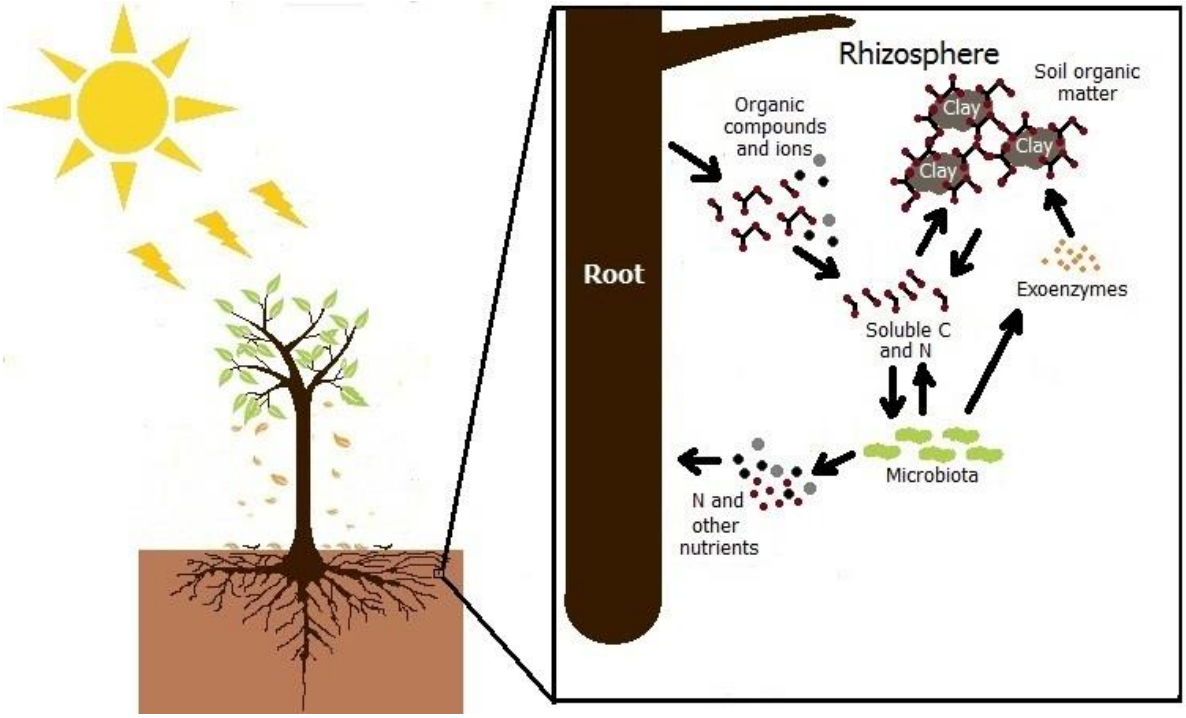

Figure 1. Illustration of rhizosphere C and N cycling processes in the ForPRAN model

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; shoot dry matter); 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).

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).

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, 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).

Factors that affects microbial turnover

Soil moisture affects microbial metabolism because of its role as a universal solvent (i.e. all microbial reactions depend on water) (BROCK, 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, 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, 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, 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, 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, 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).

3.2.2. 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 APSIM *Eucalyptus* model (Chapter 2) to represent the conversion of light energy to dry vegetable matter. The APSIM model is used widely for

this purpose by researchers and managers (HOLZWORTH et al., 2014). Root biomass and depth are estimated in APSIM, 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. Further details of the model are presented in the Supplementary Material section.

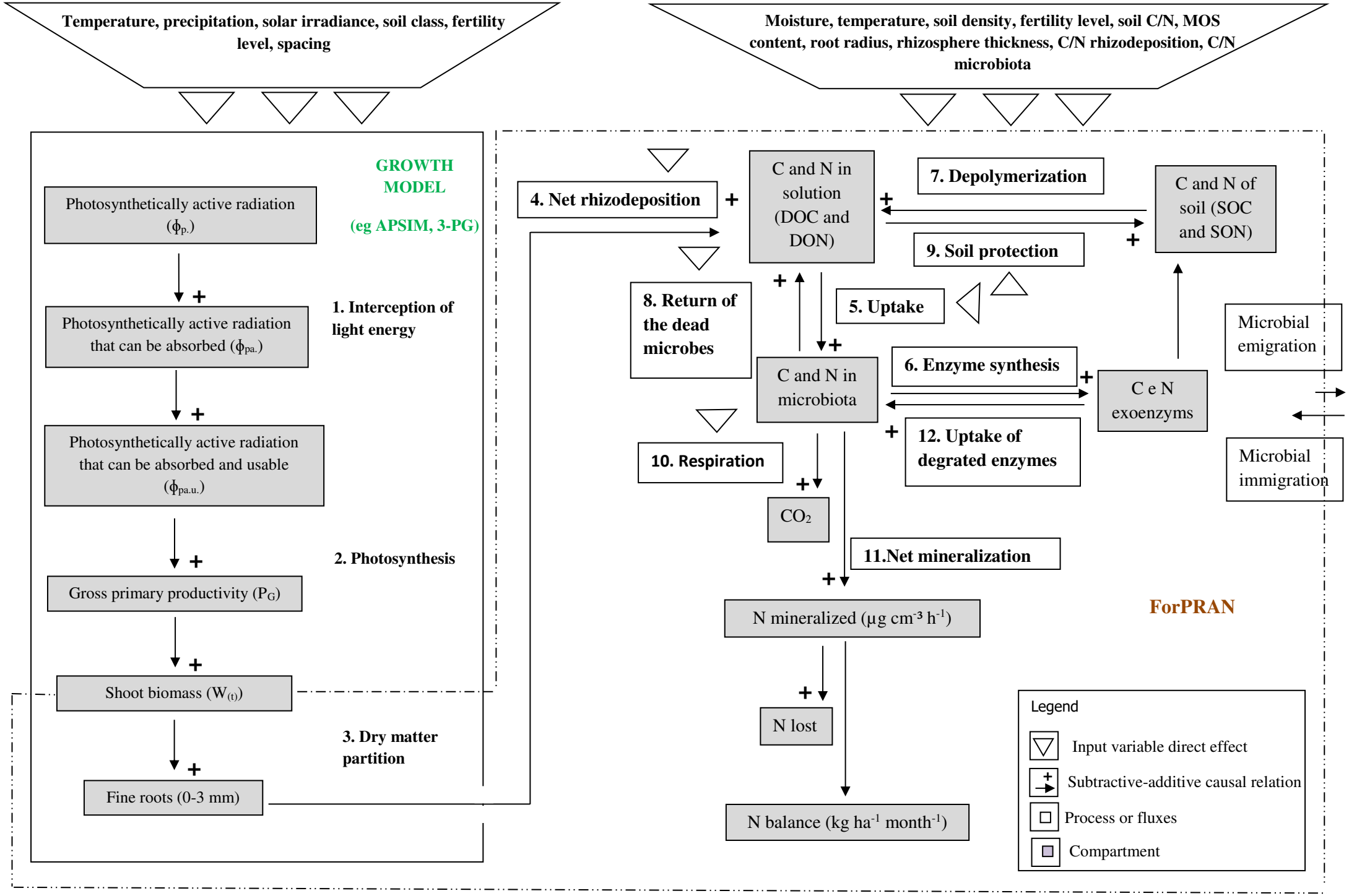

Figure 2. Flow chart of processes represented in the ForPRAN model

3.2.3. 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.

3.2.4. Evaluation of the rhizosphere model

During model development, substrate use efficiency was assumed to be 0.3 $\mu g\ \mu g^{-1}$ (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 $\mu g\ \mu g^{-1}$). We also assumed a low rate of enzyme production of 0.0075 μg C $\mu g^{-1}\ h^{-1}$ (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 $\mu g^{-1}\ h^{-1}$), and 0.02 μg C $\mu g^{-1}\ h^{-1}$ 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 $O = \beta_1 P + \beta_0$ 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 β_1 was tested for significant difference from 1, and coefficient β_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.

3.2.5. Sensitivity analysis of the ForPRAN model

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).

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

3.3. RESULTS AND DISCUSSION

3.3.1. Statistical parametrization and evaluation of the model

3.3.1.1. 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 ($MSfr = aClay^b\ TSL^c\ MDAP^d$).

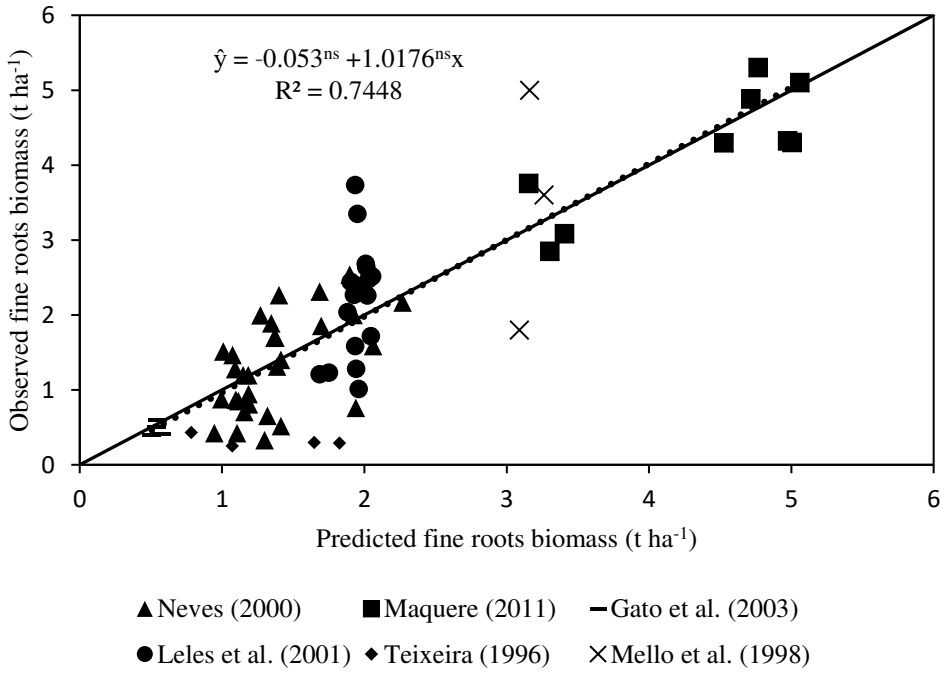

Figure 3. Regression of fine root biomass reported in literature against values predicted using the ForPRAN model. The dotted line is the mean regression, with neither intercept nor slope significantly different from 0 or 1, respectively. Solid line: 1:1 relationship.

3.1.1.2. 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.

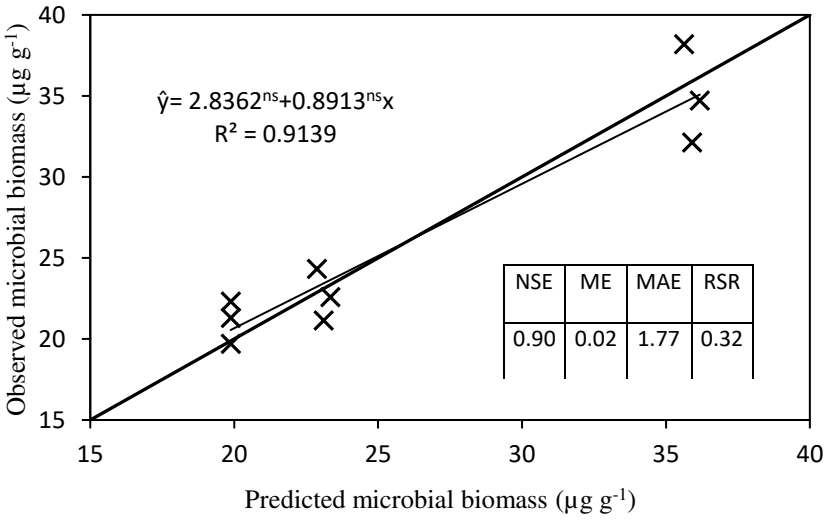

Figure 4. Regression of microbial biomass observed by Drake et al. (2013) against ForPRAN results. Regression parameters were not significantly different from 1 (slope) and 0 (intercept), respectively. Nash Sutcliffe Efficiency (NSE), Mean Error (ME), Mean Absolute Error (MAE), and Root Mean Square Error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

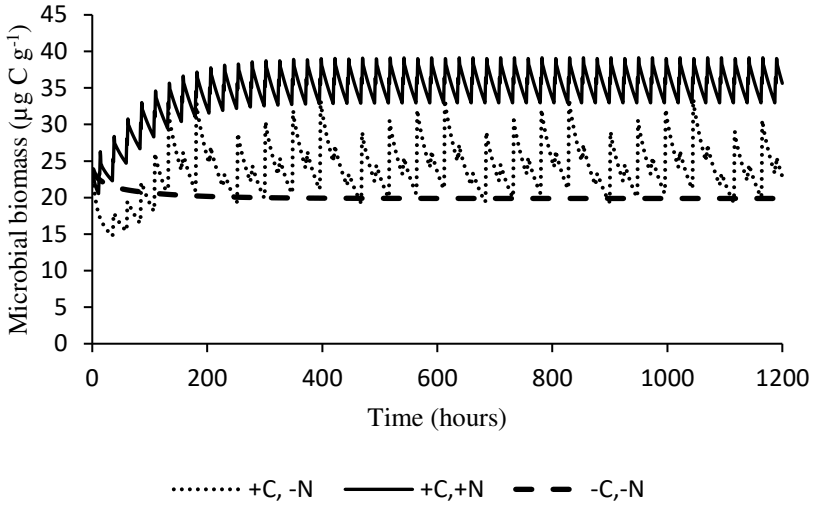

Figure 5. Predicted effect of daily pulses of substrates containing water, water+C or water+C+N (as occurred in DRAKE et al., 2013) on microbial biomass during 50 days of treatment.

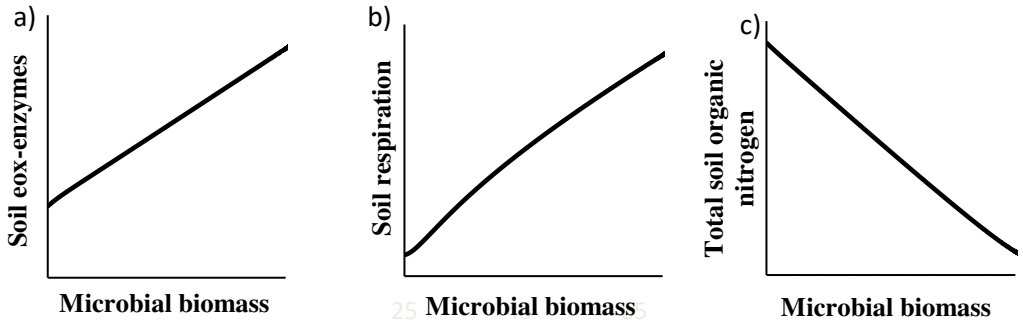

Figure 6. General trends predicted by the ForPRAN model of a) soil exo-enzymes b) soil respiration, and c) total soil organic N as a function of microbial biomass under conditions of increasing availability of C and N

3.3.2. Model sensitivity analysis

3.3.2.1. 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 $\mu g\ cm^{-3}\ h^{-1}$, 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.

3.3.2.2. Modeling C and N cycling in the rhizosphere soil (bacteria + fungi)

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.

3.3.3. Biological meaning

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 concentration 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 the 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 concentration (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 protection (%)	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
Microbial immigration (µg µg^{-1} h^{-1})	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
Clay concentration in soil (%)	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: $Sensitivity\ (S) = \frac{|\log|z+|y|+1|-\log|y+|y|+1||}{|\log|higher\ input|-\log|lower\ input||}$

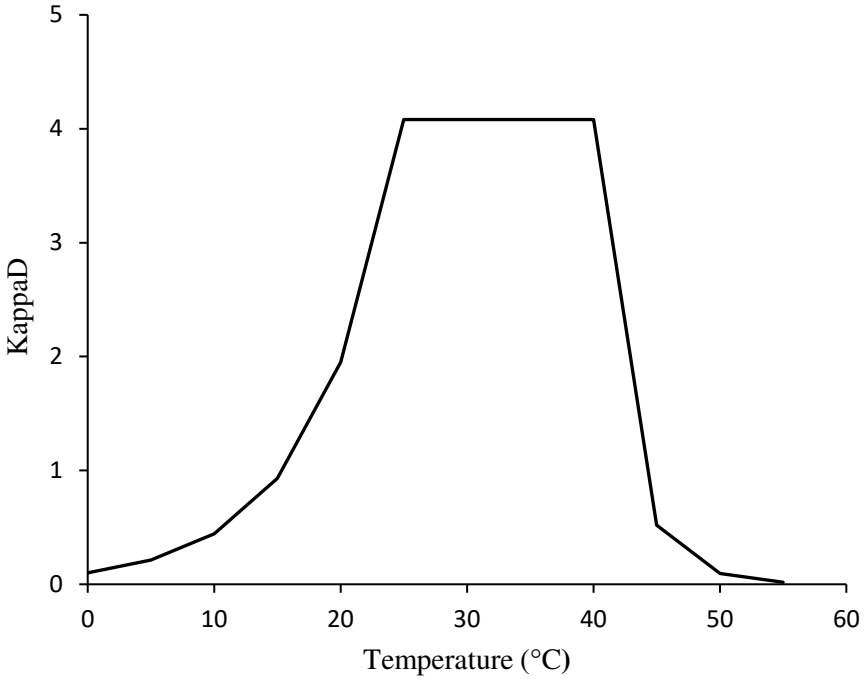

Figure 7. Temperature dependence the kinetic enzyme variable KappaD used in ForPRAN model simulations.
(Based on theoretical representation of BROCK and MADIGAN, 1991).

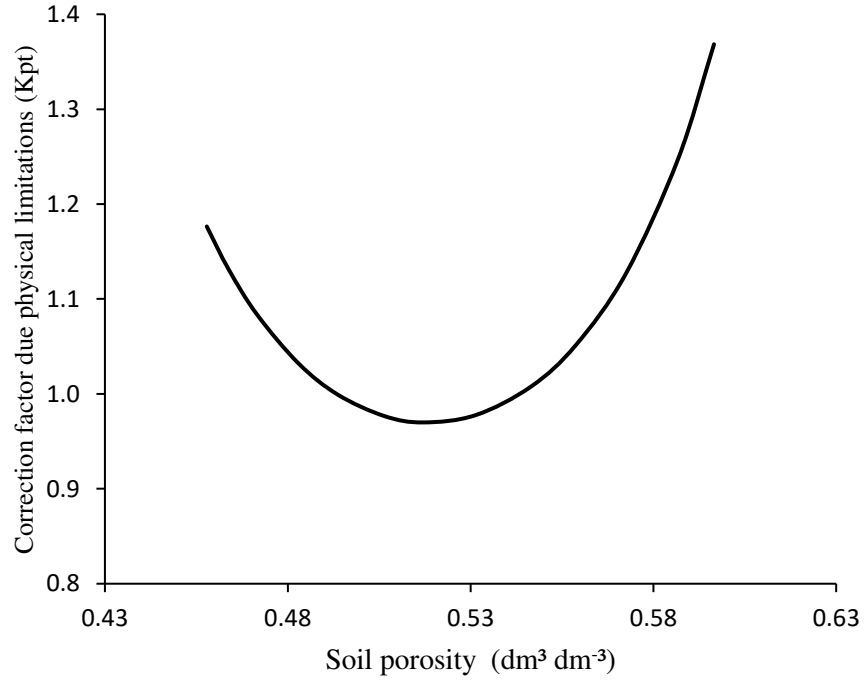

Figure 8. Soil porosity dependence of the modifier of microbial death rate due to limitations of physical conditions (Kpt) used in ForPRAN model simulations.
(Source: The equation used in the Kpt modifier was parameterized with data presented in SILVA et al., 2011).

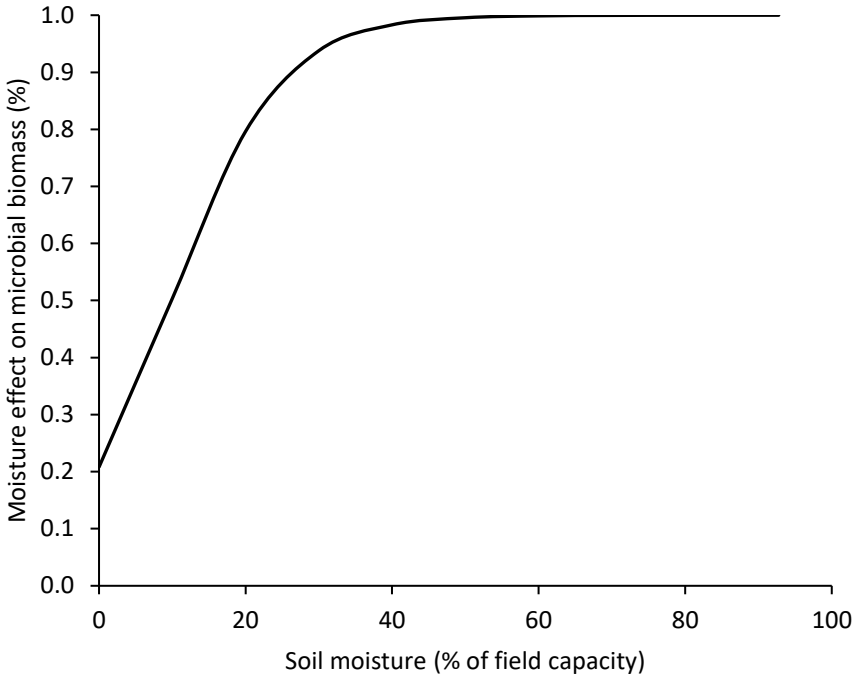

Figure 9. Soil moisture dependence of the modifier of microbial death rate due to water limitation (Ku) used in ForPRAN model simulations. (Source: The equation used in the Ku modifier was parameterized with data presented in SATO et al., 2000)

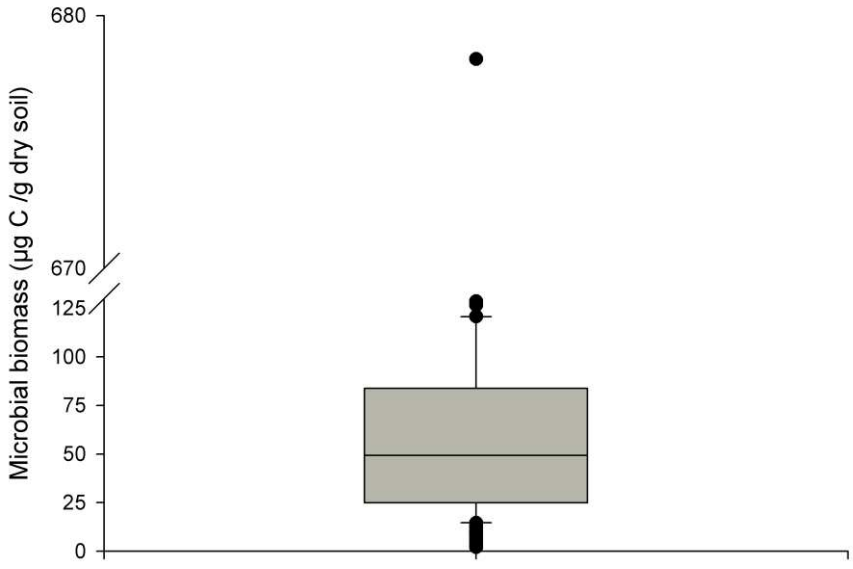

Figure 10. Boxplot of 206 observations of microbial biomass of soils under *Eucalyptus* growing in southeast Brazil (0-10 cm depth) (M. R. Tótola pers. comm.)

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.

3.4. CONCLUSIONS

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.

SUPPLEMENTARY MATERIAL

Part 1 – modeling fine root growth and rhizodeposition

1.1. Converting light energy in Eucalyptus dry matter

We used the ASPIM ecophysiological process model 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. We used shoot mass estimated by the APSIM model as input to the next step, i.e. estimation of 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. ForPRAN model is currently 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.

Estimation of carbon partitioning to fine roots (MSfr, t/ha)

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.

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

1.2. 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.

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

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

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).

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

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

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]	EN	$\mu g\ g^{-1}\ h^{-1}$	-
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 compartiments of the microbial rhizosphere model

Name	Symbol	Unit	Default
Immigration constant flow[2]	Ki	µg g^{-1} h^{-1}	0.01
Emigration constant flow[2]	Ke	µg 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	µg g^{-1} h^{-1}	-
N loss[2]	Nloss	unl*	0.4
Inorganic N in one hour[4]	Nin	µg g^{-1} h^{-1}	-
Microbial respiration rate for enzymatic production	Re	µg g^{-1} h^{-1}	-
Rate of microbial respiration for growth	Rg	µg g^{-1} h^{-1}	-
Maintenance respiration rate	Rm	µg g^{-1} h^{-1}	-
Overflow respiration rate	Ro	µg g^{-1} h^{-1}	-
Substrate use efficiency	SUE	µg $µg^{-1}$	0.3
Soil temperature	Ts	°C	-
Rate of C uptake by microbes	Uc	µg g^{-1} h^{-1}	-
Rate of N uptake by microbes	Un	µg g^{-1} h^{-1}	-
Maximum inflow of C and N by microbiota	Vmaxuptake	µg C $µg^{-1}$ h^{-1}	-
Pre-exponential rate of C uptake	Vmaxuptake0	µg 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	µg 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 microbiota

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.

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

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

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

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

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.

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

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

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

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

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 (KU) 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 O2, 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 (Kpt), 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 (Kft), 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

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

Death by physical conditions limitations

$$Kpt = \frac{1}{-12.206+ 51.060Pt -49.239\ Pt^2} \quad \text{Eq. 32}$$

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

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

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

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 (CYc) and DON (CYn) 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 rhizospheric 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)

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CHAPTER 4
The importance of the rhizosphere priming effect for *Eucalyptus* nitrogen nutrition in Brazil and Australia

The importance of the rhizosphere priming effect for *Eucalyptus* nitrogen nutrition in Brazil and Australia

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ABSTRACT

Nitrogen (N) is one of the most accumulated nutrients in *Eucalyptus* plantations, with values ranging from 120 to 1,300 kg ha^{-1}. Interestingly, the stands often present little or no response to N fertilization in tropical countries, like Brazil. The responses, when present, occur within the first two or three years. Then, they may cease to appear by the time of harvest. Therefore, *Eucalyptus* plants can meet their high N demand without fertilization, or with the application of low doses, between 40 and 70 kg ha^{-1} of N during the entire growth cycle. To explain this phenomenon, we hypothesized that rhizosphere priming effect (RPE) is quantitatively important for *Eucalyptus* nitrogen nutrition. To test this hypothesis, *Eucalyptus* growth and rhizosphere processes were simulated using the general *Eucalyptus* APSIM and the ForPRAN models, respectively. *Eucalyptus* growth was projected in four sites, two in Brazil (Aracruz/ES and Curvelo/MG) and two in Australia (Wagga Wagga/NSW and Coffs Harbour/NSW). The planting space was of 3 x 3 m for all the sites and the soil and climatic conditions were specific for each location. N cycling in the first 20 cm layer of the soil was considered. At the end of seven-year rotations, 12, 11, 10 and 5 % of the total soil was estimated to be occupied by the rhizosphere at Aracruz, Coffs Harbour, Wagga Wagga and Curvelo sites, respectively. Because of the rhizodeposition, the ForPRAN model suggests, in all four sites, an increase in the rhizosphere microbial biomass compared with bulk soil standard values, being between 70.3 μg cm^{-3} and 246.1 μg cm^{-3} of C. In general, RPE has the potential to

meet between 15 and 38 % of the forest ecosystem N demand (root + shoot + litter) under the studied situations. Higher temperatures and rainfall may contribute to a more significant rhizosphere contribution to N nutrition (in absolute values) in Brazil than in Australia, thus explaining the less frequent N limitation in the former country.
***Keywords**:* fine roots, rhizosphere priming effect, microbial population.

4.1. INTRODUCTION

Eucalyptus trees are widely distributed in the world from wet to dry regions, and from fertile to infertile soils. These trees are planted in over 20 million hectares (GAHAGAN, 2010), being present in Latin America, Europe, Asia, Africa, and Oceania. They show very distinct growth and nutritional behavior depending on the interactions with biotic and abiotic factors. For instance, in Brazil the average productivities are around 40 $m^3\ ha^{-1}\ a^{-1}$, while in other countries the productivity levels may be two to four times lower (SOARES, GOMES, 2010).

An important factor that determines the adaptive success of *Eucalyptus* genus in some parts of the World (e.g., Brazil) is related to the ecological interaction between its roots and soil microorganisms (GONZALEZ et al., 2009; PYLRO et al., 2013; SANTOS, 2011; MASSENSSINI et al., 2016). It was observed recently that the rhizosphere populations of *Eucalyptus* mineralize nitrogen from the soil surrounding the fine roots much faster than the bulk soil populations, through a process named positive rhizosphere priming effect (RPE) (HURTARTE, 2017). Löhnis (1926) described for the first time the priming effect (PE) when studying the decomposition of green manures. He observed that the soil presented an intensified humus mineralization following the addition of the fresh organic residues to the soil. It is currently well known that PE is common for most of the plant species and may be caused by other composts besides plant residues, such as dead microorganisms, high- and low-molecular-weight organic substances, or mineral N (KUZYAKOV, 2002; BLAGODATSKAYA; KUZYAKOV, 2008; CHENG et al., 2014; DIJKSTRA et al., 2013; ZHU et al., 2014).

In the *Eucalyptus* rhizosphere, RPE is caused by the rhizodeposition of significant amounts of citric, malic, and oxalic acids, as well as sucrose, alose, fructose, glutamine, inositol, and asparagine (HURTARTE, 2017). The release of these organic compounds has been associated with decreases in total N in the rhizosphere soil, suggesting a nutritional benefit for *Eucalyptus* plants (HURTARTE, 2017). Considering that these trees may reach 448.1 km $tree^{-1}$ of root length within the first 30 cm of soil (MELLO et al., 1998), we have hypothesized that rhizosphere priming effect is quantitatively important for *Eucalyptus* nitrogen nutrition and may help to explain why stands often present little or no response to N fertilization in tropical countries, despite the high N demand of *Eucalyptus* trees.

This work was done with the objective of studying the quantitative importance of RPE for *Eucalyptus* through the simulation of rhizosphere microbial N cycling for four sites, two in Brazil, where productivity records have been reported, and two in Australia, the origin center of *Eucalyptus*.

4.2. MATERIAL AND METHODS

The present work consisted of the simulation of fine root growth and N cycling in the rhizosphere of *Eucalyptus* plantations in Brazil (1-Curvelo/MG and 2- Aracruz/ES) and Australia (3- Coffs Harbor/NSW and 4- Wagga Wagga/NSW). Plant growth was simulated using APSIM *Eucalyptus* software as evaluated and improved in Chapter 2. Afterward, the shoot biomass and soil temperature and moisture APSIM outputs were used to simulate the rhizosphere cycling in the ForPRAN model (see Chapter 3). The simulations represent real plantations located in the geographical positions shown in figure 1.

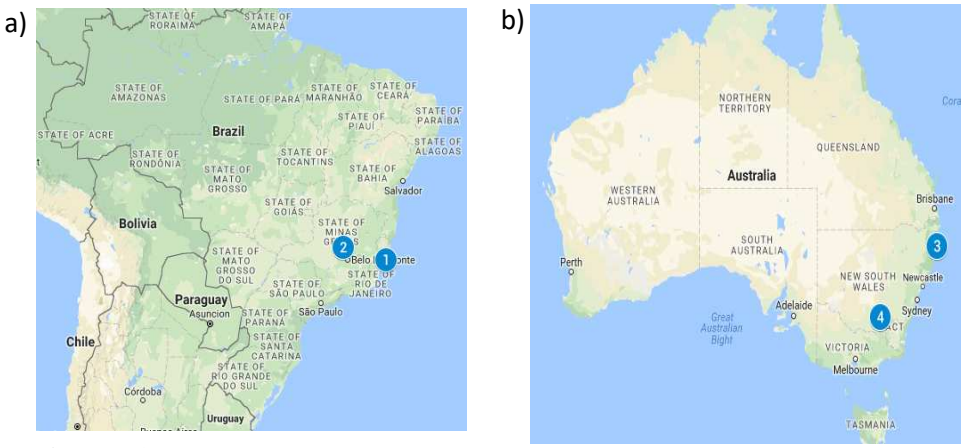

Figure 1. Geographical distribution of the simulated forest sites at a) Brazil (1-Aracruz - ES; 2 – Curvelo – MG) and b) Australia (3- Coffs Harbour - NSW; 4- Wagga Wagga- NSW)

4.2.1. Sites description

The forest sites were chosen considering the main *Eucalyptus* producing regions in these two countries and the availability of data. The datasets encompass contrasting altitudes, precipitation regimes, temperatures and soil conditions, according to table 1 and 2. Therefore, it was possible to evaluate the rhizosphere N cycle in sites with different biological productivities. The daily climatic values of air temperature, solar irradiance, and precipitation used in the simulations were collected from the websites of the National Meteorological Institute (INMET, at www.inmet.gov.br) and from the Agroclimatology of the National Aeronautics and Space Administration (NASA, at www.power.larc.nasa.gov). The soil characteristics of each site were collected from Almeida, Landsberg, and Sands (2004) (Aracruz), Borges (2009) (Curvelo), and from *Eucalyptus* APISM datasets (Coffs Harbour and Wagga Wagga – Chapter 2).

Table 1. Geographic and climatic information of the simulated sites

Sites	State	Lat.*	Long.*	Elevation	Rainfall	Mean temperature
				m	mm	°C
Aracruz	ES[1]	-19.81	-40.23	69.0	1269.4	24.3
Curvelo	MG[1]	-18.76	-44.43	600.0	1361.5	23.8
Coffs Harbour	NSW[2]	-30.12	153.18	21	1635.4	19.0
Wagga Wagga	NSW[2]	-35.0	147.35	147	703.6	16.3

[1]Brazilian states: Espírito Santo (ES); Minas Gerais (MG); [2]Australian states: New South Wales (NSW); * Latitude and longitude in decimal degrees.

Table 2. Soil characteristics of the simulated sites

Sites	State	Clay	SOC	C/N[3]	F. Capacity	P. Wilt Point
		dag/kg	dag/kg	kg/kg	mm/mm	mm/mm
Aracruz	ES[1]	31.8	1.40	14.5	0.20	0.11
Curvelo	MG[1]	79.0	2.45	14.5	0.39	0.15
Coffs Harbour	NSW[2]	28	2.00	14.5	0.22	0.11
Wagga Wagga	NSW[2]	28.0	2.00	14.5	0.23	0.12

[1]Brazilian states: Espírito Santo (ES); Minas Gerais (MG); [2]Australian states: New South Wales (NSW); [3] The values of this variable were assumed

4.2.2. Scenarios simulation

The simulations were performed to represent the growth of *Eucalyptus* plantations in the different regions, considering the following planting dates: 01/04/1953 (Coffs Habour); 01/01/1990 (Wagga Wagga); 11/10/2001 (Curvelo); 15/12/1997 (Aracruz). The first two locations were planted with *E. grandis* and the last two with *E. grandis* vs *E. urophylla* hybrids. The dates were selected to coincide with the real plantings so that it was possible to compare the results of the growth simulations with the observed data. In the case of the Wagga Wagga simulation, the contribution of water via fertigation was disregarded aiming the estimation of the rhizosphere activity under natural precipitation conditions. The standard spacing of the simulations was 3 m between plants and 3 m between planting lines (3 x 3 m).

Based on the dry matter biomass projected by APSIM *Eucalyptus* for the period of seven years, a ForPRAN module (see Chapter 3) was used to estimate the growth of fine roots (<3 mm). The rhizosphere cycling was simulated considering the period of seven years, a rhizosphere thickness of 3 mm and a soil depth of 20 cm. Considering that APSIM provides results in a daily time scale and ForPRAN in hourly time scale, the daily value output of the first model was adopted as input for the 24 hours simulated in the second model. Further details about the input coefficients and variables used in each of the simulations see Chapter 3 (supplementary material section) and Eucalyptus documentation file on < http://www.apsim.info/>.

To compare the rhizosphere supply results with the N accumulation of *Eucalyptus*, it was adopted the model for estimating the biological utilization coefficient (CUB) developed by Valadares (2015) (Equation 1). The division of CUB by the stand dry matter mass provided the accumulation of N in the different plantations.

$$\hat{y} = \frac{409.088\, e^{\left(-\frac{28.276}{cl} + \frac{443.592}{ar}\right)}}{1 + 7.919\, e^{[(-0.086 + 0.00265\, a)\, t]}} \quad \text{Eq. 1}$$

Where,

$\hat{y}$ = biological utilization coefficient (CUB) predicted, in kg kg^{-1};
cl = Clay concentration, in g kg^{-1};
ar = Annual precipitation, in mm;
a = Area per plant, in m^2;
t = forest stand age, in month.

4.2.3. Data analysis

It was performed a graphical analysis of the main ForPRAN outputs over the time (seven-years simulation). When appropriate, we described the system using the general mean, median, maximum and minimum values, and standard deviation.

4.3. RESULTS

4.3.1. Main factors controlling rhizosphere processes

The four simulated sites naturally presented considerable variation in shoot biomass production at the end of seven years in the following order: Curvelo (177.9 t ha^{-1}), Aracruz (164.65 t ha^{-1}), Coffs Harbour (73.4 t ha^{-1}), and Wagga Wagga (44.3 t ha^{-1}). As expected, higher yields coexisted with conditions of higher precipitation, solar irradiance (at lower latitudes), and air temperatures (Table 1). With respect to root growth, the highest yield of fine roots was projected for Aracruz site, the second most productive in shoot mass, corresponding to 16,664 km ha^{-1} under the first 20 cm of soil (Fig. 1c). This site was followed by Coffs Harbor, with 16,080 km ha^{-1} (Fig. 1a), and Wagga Wagga (Fig. 1b), with 14,610 km ha^{-1} fine roots. Curvelo site (79 % of clay) presented a remarkable trend for lower fine root growth (7,323 km ha^{-1}, Fig. 1d). As will be explored further, this factor was not as decisive for rhizosphere cycling as might be inferred.

Interestingly, the fine root growth projected by ForPRAN was extremely fast up to two years of age (Fig. 2a, b, c, d), a period characterized by canopy formation and by the predominance of geochemical and chemical cycling. In this

period, all four stands would have reached 75 % of the fine root length compared to the total length projected at the end of seven years. It can be deduced that, after the first two years, occurs a net increase of only 5 % in the length of fine roots per year. This is not to say that *Eucalyptus* plantations decrease their investment in fine roots. The plants must keep their absorbent roots, whose half-life is of about 4 months, and still produce 5 % of net growth. Therefore, there is still a considerable allocation of carbon from photosynthesis to the fine roots compartment.

The estimates of the rhizosphere volume, with a thickness of up to 3 mm, as indicated by observations made by Hurtarte (2017), shows a high occupation rate of the soil by the rhizosphere till the first two years of the trees growth, similarly to the pattern of fine root growth (Fig. 2a, b, c, d). At the end of seven years, it was estimated that 12, 11, 10 and 5 % of the arable layer was rhizosphere soil for the sites of Aracruz, Coffs Harbor, Wagga Wagga, and Curvelo sites, respectively. This proportion of rhizosphere soil is higher under the upper part of the soil layer, as it is already known that fine roots are concentrated close to the soil surface.

The rhizodeposition, as presented in Valadares et al. (2017), has a rather simple behavior when compared to the complexity of the phenomenon, which varies greatly according to the species and the environment. Since there is no other work dealing with the modeling of the rhizosphere process for *Eucalyptus* plantations, it is natural that certain doubts arise are answered with presuppositions. Therefore, a rhizodeposition value close to zero was assumed in the first hours and a maximum value from eight hours onwards of 0.25 and 0.013 $\mu g\ cm^{-3}\ h^{-1}$ of C and N, respectively (Fig. 2e). For the Aracruz site, at the end of seven years, the root+rhizodeposition investment would represent 16.1 % of the accumulated C in the trees (shoot + roots), assuming a final root/shoot ratio of 0.15. For Curvelo, Coffs Harbor, and Wagga Wagga sites these values would be in the range of 14.3, 19.6, and 23.2 %, respectively. The total rhizodeposition for these four sites would be around 403 $mg\ g^{-1}$ of total roots.

Soil moisture and temperature were also factors that greatly affected rhizosphere microbial cycling and, consequently, the phenomena derived from it, such as the priming effect. Soil moisture and temperature patterns can be observed for the four sites used in this study (Figure 3).

In Australia, higher precipitations and temperatures were observed from November to April in the Coffs Harbor site. The average soil moisture (as a percentage of field capacity) over the seven-year period was 58 %, with maximum and minimum values of 100 and 6.25 % and standard deviation of 31.4 % (Fig. 3a1). The soil temperature at the same site had an estimated APSIM value of 21.9 °C, with maximum and minimum values of 29.9 and 14.9 °C, and a standard deviation of 3.26 °C (Fig. 3a2). Although with an average precipitation of only 689 mm a^{-1}, the rains were better distributed in the Wagga Wagga site, where presented lower temperatures from April to August. Soil moisture presented an average of 43 % and maximum and minimum values of 100 and 6.25 %, and a standard deviation of 33.3 % (Fig. 3b1). The average soil temperature corresponded to 19.7 °C and the maximum and minimum values estimated were 37 and 7 °C, and the standard deviation of 6.7 °C (Fig. 3b2).

In Brazil, Curvelo site presented an average annual precipitation of 1361 mm a^{-1}, with rainfall concentrated from November to March, when temperatures were also higher. The average soil moisture was equivalent to 73 % of field capacity, with maximum and minimum of 100 and 2.6 %, and standard deviation of 27 % (Fig. 3d1). The average soil temperature for this site was 26.9 °C, with maximum and minimum values of 31.6 and 21.4 ° C, and standard deviation of 1.7 °C (Fig. 3d2). In the eastern portion of the country, in the municipality of Aracruz, the average annual rainfall was 1269.41 mm and average soil moisture of 69 %, with maximum and minimum values of 100 and 5 %, and a standard deviation of 31.4 % (Fig. 3c1). The soil temperature, on the other hand, presented an average of 26 °C, maximum and minimum of 33.6 and 20 °C, and standard deviation of 2.3 °C (Fig. 3c2).

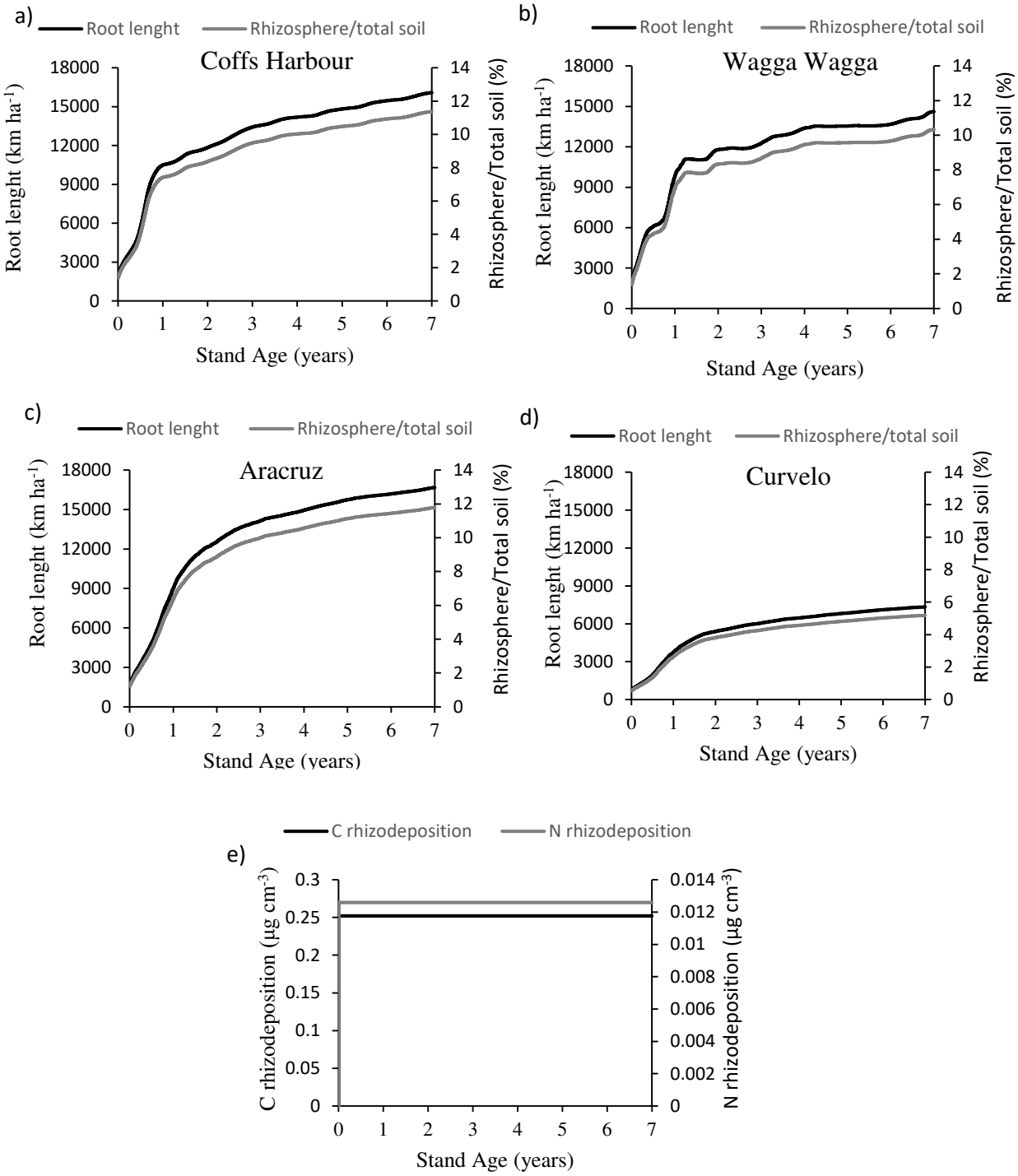

Figure 2. Simulated root length, percentage of the rhizosphere soil in the 0-20 cm layer for the sites, and C and N rhizodeposition: a) Coffs Harbour; b) Wagga Wagga; c) Aracruz; d) Curvelo; e) C and N rhizodeposition

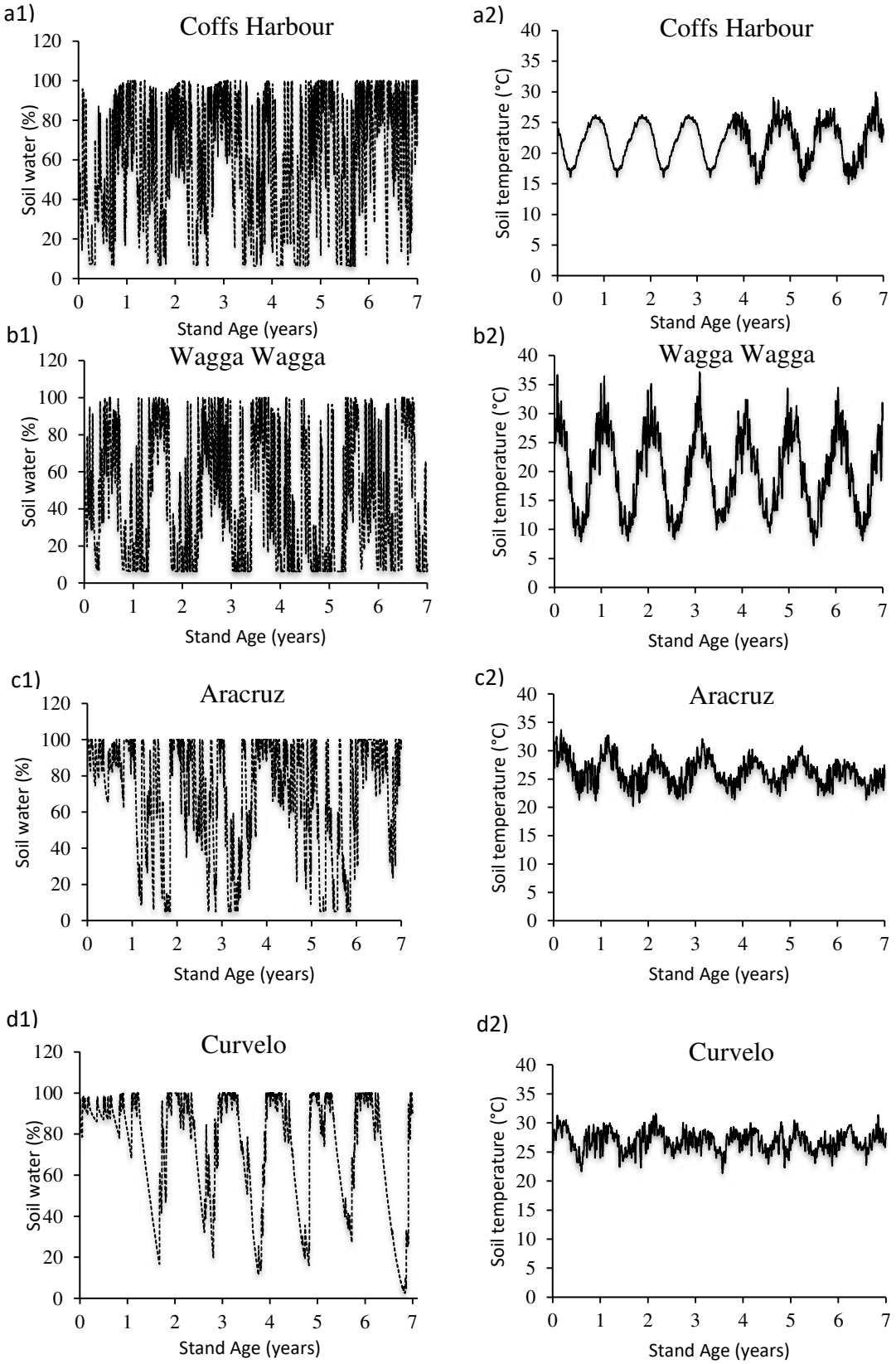

Figure 3. Simulated soil water and soil temperature for the sites: a1 and a2) Coffs Harbour; b1 and b2) Wagga Wagga; c1 and c2) Aracruz; d1 and d2) Curvelo

4.3.2. Rhizosphere microbial dynamics and N flux

Because of the factors previously presented, a very different microbial biomass pattern was observed in the rhizosphere of each of the simulated sites. As all of them showed similar rhizodeposition rates, the differences observed in microbial biomass were defined by the seasonal patterns of rainfall, organic matter, and temperatures in each of the regions. Microbial growth peaks were linked to periods of higher soil moisture and temperature, what was particularly evident for Australian sites. In those sites, the percentage of water and the lower temperatures led to microbial biomasses considerably lower than those simulated values for the Brazilian sites.

In Coffs Harbor, for example, it was simulated an average value of 134 μg cm^{-3} of C in microbial biomass, with maximum and minimum values of 264.2 and 18.4 μg cm^{-3}, and standard deviation of 73.8 μg cm^{-3} (Fig. 4a1). Meanwhile, in the southernmost part of the Australian continent, at Wagga Wagga, where is also drier and colder, the simulations showed an average microbial biomass of 70.3 μg cm^{-3} with maximum and minimum values of 247.4 and 14.7 μg cm^{-3} and standard deviation of 47.8 μg cm^{-3} (Fig. 4b1). In Brazil, as described in the previous topic, the volume of rhizosphere did not necessarily define its importance for the ecosystem. This was the case of the Curvelo site, which presented a much larger microbial biomass than the two Australian sites, with an average of 246.1 μg cm^{-3} and a maximum and minimum value of 265.4 and 23.8 μg cm^{-3}, and a standard deviation of 37 μg cm^{-3} (Fig. 4d1). In the case of Aracruz, predicted values were slightly lower, with an average of 186.5 μg cm^{-3} and a maximum and minimum value of 231.2 and 23.8 μg cm^{-3}, and a standard deviation of 49.4 μg cm^{-3} (Fig. 4c1).

Microbial uptake peaks were greater under conditions of higher soil moisture and temperature, which was particularly evident for Australian sites and less evident for sites in Brazil, especially Curvelo (figures 4 a,b,c,d). Apparently, the higher rainfall and greater soil water retention capacity contributes to the maintenance of a more stable microbial activity in the Brazilian sites. Such observations obtained through simulation should be better studied under experimental conditions. When the demand for C estimated by ForPRAN (black line) is considered, the microbiota's demand was still unsatisfied, although the rhizosphere is a more carbon-rich soil compartment. For this reason, it is prevalent

the mineralization of N over the immobilization in the rhizosphere environment (dotted line) of all the studied sites (4 a,b,c,d).

It was observed annual N rhizosphere supplies of 24.4, 4.4, 41.7, and 29.4 kg ha^{-1} for the Coffs Harbor, Wagga Wagga, Aracruz, and Curvelo plantations, respectively (Figure 5 a,b,c,d). The present demonstration establishes a link between factors related to forest productivity, such as rainfall, temperature, and organic matter stocks and the intensity of rhizosphere cycling. Factors that condition higher forest productivity also contribute to the existence of a more intense rhizosphere activity. Thus, for the maintenance of the high yields in the Brazilian sites, rhizosphere cycling present relevant contribution according to our simulations.

Aracruz represented the site whose cycling would have the largest cumulative contribution to *Eucalyptus* nutrition, with about 292.4 kg ha^{-1} of N at the end of seven years. When N losses of 40 % are considered, this value is close to 175.2 kg or 47.3 % of the N accumulated in the trees (about 370.7 kg ha^{-1}) or 30 % of the ecosystem demand (about 582.3 kg ha^{-1}: root + shoot + litter). Since a perfect system efficiency cannot be expected, it is reasonable to assume that there are losses. Thus, the gain from the interaction between *Eucalyptus* and the rhizosphere microbiota for Curvelo would be close to 123.5 kg ha^{-1}, which would represent about 31.9 % of tree demand and 20.2 % of ecosystem demand. The estimated net rhizosphere supply for the Coffs Harbor site was 102.7 kg ha^{-1}, equivalent to about 56.5 % of tree demand or 38.2 % of ecosystem demand. In the case of Wagga Wagga, the estimated balance of the interaction was only 18.5 kg ha^{-1} of N at the end of seven years, when considered losses of 40 %. It would represent 24 % of the demand for N of the trees or 15.3 % of the demand of the ecosystem.

The rhizosphere cycling would have a greater potential for reducing organic matter stocks in the Aracruz site, followed by Curvelo, Coffs Harbor, and Wagga Wagga. In the case of the Curvelo site, a relatively high cycling is observed in view of the smaller root surface, which highlights the role of factors other than rhizosphere volume, such as soil water retention capacity, temperature, and organic matter content. In the case of Australian sites, the lower N cycling average converges to greater responses to nitrogen fertilization and to a less problematic situation in relation to the exhaustion of the N stocks from MOS.

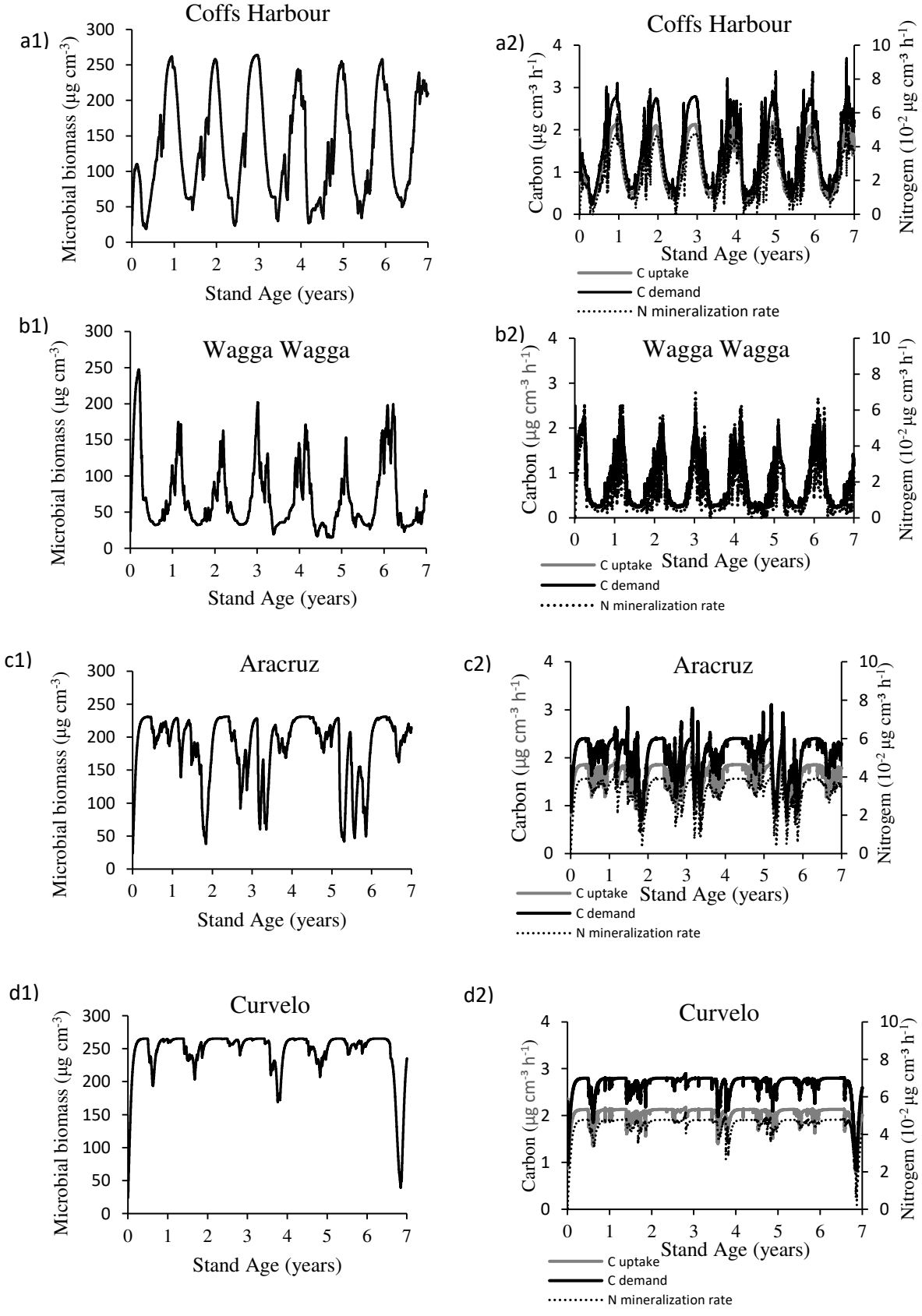

Figure 4. Simulated microbial biomass and C uptake and demand and N mineralization rates for the sites: a1 and a2) Coffs Harbour; b1 and b2) Wagga Wagga; c1 and c2) Aracruz; d1 and d2) Curvelo

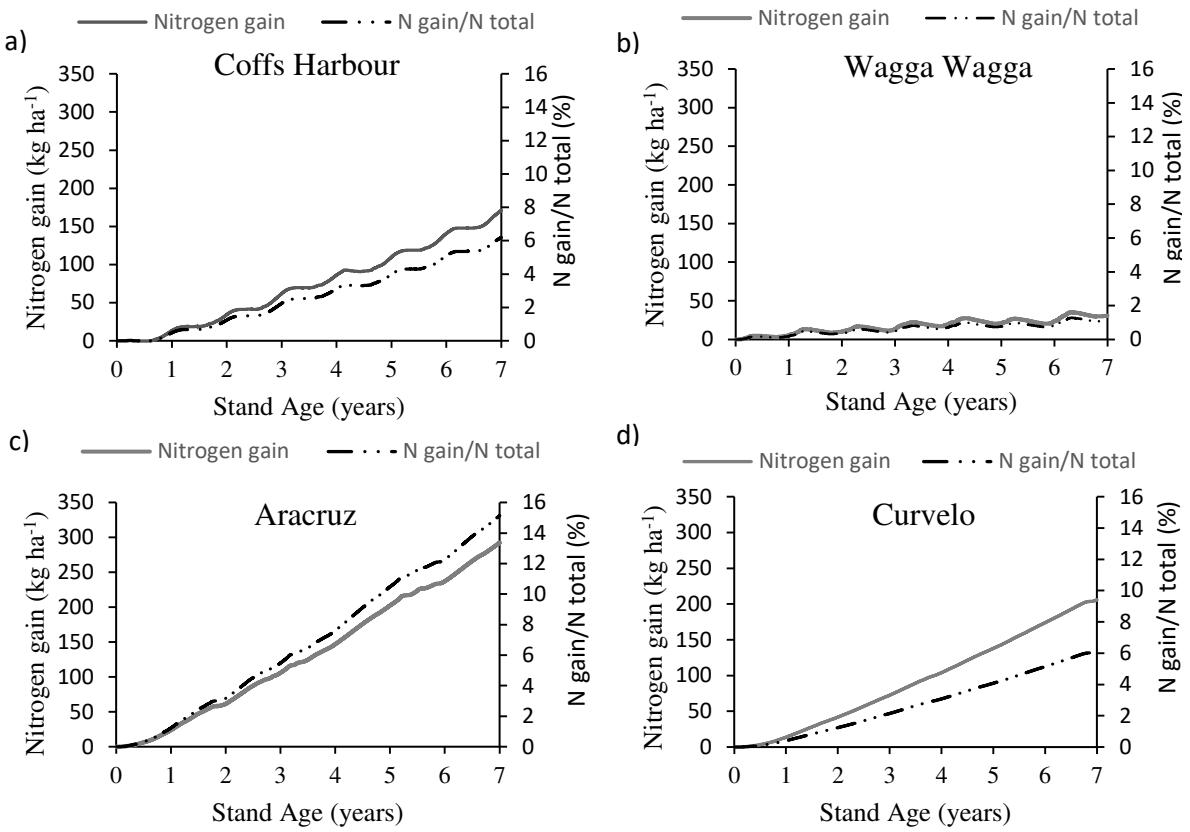

Figure 5. Simulated nitrogen gain and percentage compared total soil N: a) Coffs Harbour; b) Wagga Wagga; c) Aracruz; d) Curvelo

4.4. DISCUSSION

The study of processes related to fine roots is of fundamental importance for the understanding of many aspects of forest nutrition. The thin roots of *Eucalyptus* are commonly related to the functions of water and nutrient uptake, in a more passive perspective, but little or no quantitative approach has been devoted to their role as active organs in the acquisition of nutrients, such as nitrogen, from SOM. Due to their low degree of suberification, fine roots are more permeable to water and nutrients but are also more susceptible to the release of compounds that favor microbial growth and the occurrence of the so-called positive priming effect, with its implications for the release of N to trees.

One of the capital points for the discussion of the quantitative importance of this phenomenon in an ecosystem perspective is the root length. The simulations showed a link between forest productivity and site characteristics, such as soil clay concentration (Fig. 2d). Generally, the higher simulated yields (e.g., Aracruz site) correlated with a larger surface of active fine roots, with values ranging from 16,080 km ha^{-1} to 7,323 km ha^{-1}, in the upper 20-cm soil layer. This high root surface in a few centimeters of soil represents reasonably well the axial development of the roots of *Eucalyptus*, where, from a supporting root, numerous secondary roots, with differnt branching orders, grow. Among these, the fine roots (<3 mm diameter) concentrate about 70 % of their final length in the first 30 cm of soil (MELLO et al., 1998).

According to Ford and Deans (1977), in a survey of several forest species, fine roots corresponded to more than 96 % of the extension of the root system. In the present case, a root system of 16.080 km ha^{-1} (for Aracruz) would represent about 14.5 km $tree^{-1}$ (at 3 x 3 m spacing), which is not too far from estimates for other species, such as those for conifers, whose normal values are between 13-15 km $tree^{-1}$ (FORD; DEANS, 1977). But in the case of *Eucalyptus*, as observed in Mello et al. (1998), these trees may have wide root plasticity, ranging from 4.4 km $tree^{-1}$ to 448.1 km $tree^{-1}$ as a normal range for the first 30 cm of soil, depending on the genotype, propagation type, and environmental conditions (e.g., precipitation regime and temperatures).

This high plasticity explains why the Curvelo site with high yield (177.9 t ha^{-1}) had the lowest growth of fine roots. 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 of Coffs Habour and Wagga (Fig. 2a,b). While root biomass of low-quality sites may represent 32 % of the shoot biomass, that of high-quality sites is about 13 % of the shoot biomass (at 67 months) (REIS et al., 1985). The greater investment in roots under conditions of greater scarcity of resources is intended to enlarge absorptive root surface to guarantee tree survival. The same pattern was identified for other forest species, such as *Pseudotsuga mensiesii*, for which at 40 years of age, 2.5 folds more carbon was allocated to fine roots in soils with low water and nutrient contents, compared to soils with higher availability of these resources (KEYES; GRIER, 1981).

Our results for the ForPRAN root growth module revealed lower root surface in soils with higher clay concentration, such as in the Curvelo site, due to the greater water and nutrient retention capacity of the soil compared with sites with lower clay concentration, such as Aracruz, Coffs Harbor, and Wagga Wagga. Clayey soils of the tropics are generally nutrient-poor, and therefore, the results obtained for the Curvelo site were more closely related to the water retention capacity. Future improvements in the ForPRAN root growth module may consider issues related to soil fertility.

When analyzing the highest value of 448.1 km $tree^{-1}$ presented by Mello et al. (1998), it can be deduced that the simulated rhizosphere volume of 5 to 12 % may be still modest for some situations. Considering the rhizosphere as a perfect cylinder around the root, it can be represented by the equation $2 \times \pi \times R \times L \times E$, where: R is the rhizosphere radius; L is the length; E is the thickness. Considering a mean diameter of fine roots of 1.5 mm, one has a radius of 0.75 mm and about 3 mm of thickness (Hurtarte, 2017), the rhizosphere volume for this site would be: $2 \times 3.14 \times 0.075 \times 4.98 \times 10^{10} \times 0.3 =$ 7,035,157,440 cm^3 = 7,035,157.44 dm^3. This value, considering the depth of 0-30 cm, would be 2.34 times the volume of the soil layer. This means that, under certain conditions, it is not possible to distinguish the rhizosphere soil from the non-rhizosphere soil, and there is certainly a high overlap between rhizospheres in these cases. Such a demonstration serves as a warning since it can be deduced that there is no difference in the intensity of the processes between rhizosphere and non-rhizospheric soil in field experiments, when, in fact, the whole soil volume may be under the influence of rhizodepositions.

Thus, future improvements may consider the different fine root growth rates, according to plant genotype and environment, as well as larger specific root lengths. However, it is noteworthy that our estimates were in line with those presented by Finzi

et al. (2015), who estimated that about 5-17 % of the first 30 cm of temperate conifer forest soil would be occupied by the rhizosphere.

When analyzing rhizodeposition, they presented absolute cumulative values at the age of 7 years of 2.9, 1.2, 2.8, and 2.58 t ha^{-1} of C for Aracruz, Curvelo, Coffs Harbor, and Wagga Wagga, respectively. Finzi et al. (2015) suggest as a reasonable release value 45 g m^{-2} a^{-1} of C for temperate forests, which, at the end of 7 years would be equivalent to 3.15 t ha^{-1} of C. This is not a value far from those presented in our simulation, mainly if we consider the roots of deeper soil layers. As mentioned before, the mean value of rhizodepositions for the four sites was around 403 mg g^{-1} of total roots, which is close to the upper range of values estimated by Newman (1985) for soluble and insoluble exudates (350 mg g^{-1} of root). Our estimates were also close to the observations made by Pausch and Kuzyakov (2017), who concluded that an average rhizodeposition value for annual crops, grasses, and trees of 500 mg g^{-1} of root would be reasonable.

However, trees can invest 40 % (VAN VEEN et al., 1991) to 73 % of the assimilated carbon from photosynthesis into roots plus rhizodeposition (FOGEL; HUNT, 1983). In the case of the Curvelo, Coffs Harbor, and Wagga Wagga sites, C transfered to roots+rhizodeposition were 14.3, 19.6, and 23.2 %, respectively. At this point, it should be understood that productive *Eucalyptus* commercial plantations do not present root-to-shoot ratios much higher than 0.25 at harvest period (ALMEIDA et al., 2004), while other species may have values above 0.4. High productive *Eucalyptus* plantations have values close to 0.15 (ALMEIDA et al., 2004) so that there is a certain trend for the total root + rhizodepositions to be lower than those reported in the literature for slower growth or native species. Considering the relatively short period of growth used in our simulations (7 years), typical for *Eucalyptus* rotations in Brazil, it is reasonable to expect that rhizodeposition represents a higher percentage of photosynthesized carbon when longer rotations are taken into accounts, such as those in South Africa (8-10 years), Chile (10 - 12 years), Portugal (12-15 years), and Spain (12-15 years) (SOARES; GOMES, 2010).

The ForPRAN model indicated for all four sites an increased microbial biomass with average values between 70.3 μg cm^{-3} and 246.1 μg cm^{-3} of C. This behavior of the model reflects the views presented by Grayston et al. (1997), according to whom the trees affect microbial cycling and, consequently, the supply of N by the creation of environments more conducive to microbial activity and that this occurs by the addition of carbon into the soil as litter, dead roots, and rhizodeposition. In accordance with the

ForPRAN model, this is due to increases in microbial biomass, because of higher C and N inputs, and by a greater C use efficiency and higher rates of enzymatic production under copiotrophy conditions (rhizosphere environment).

The model considers a low rate of enzymatic production and low microbial C use efficiency coefficient (CUE) for complete oligrotrophy conditions. But in the presence of only C, an increase in enzymatic synthesis was considered to meet the demand of N. And in the presence of both elements, an average rate of enzymatic synthesis and an ideal CUE were assumed. According to Phillips et al. (2006), several amino acids are released by roots (e.g., arginine, alanine, proline, tyrosine, lysine, and leucine), which can be rapidly reabsorbed by the plant itself or lost to the soil, altering the dynamics of the rhizosphere populations. As a consequence of the rhizodeposition, in the rhizosphere, microbial biomass range from two to 1,000 times larger than that in the bulk soil (BONKOWSKI et al., 2000) and increases in enzyme activities ranging from 42 (DRAKE et al., 2013) up to over 1,000 % (not published data) can also be found. This behavior was explained by ForPRAN by the simultaneous occurrence of a higher CUE (ideal of 0.5 $\mu g\ \mu g^{-1}$) and a medium enzymatic production rate (0.0001 $\mu g\ \mu g^{-1}\ h^{-1}$).

The model showed that the microbial biomass presented a seasonal behavior throughout the year when averages were around 134, 70.3, 246.1, and 186.5 $\mu g\ cm^{-3}$ for the sites of Coffs Harbor, Wagga Wagga, Curvelo, and Aracruz (Fig. 5), respectively. Valadares et al. (2017) reported an average microbial biomass value of 50 $\mu g\ cm^{-3}$ for 256 forest sites, supporting the hypothesis that the processes in the rhizosphere are more intense compared with the bulk soil. Gama-Rodrigues et al. (2008) observed values for microbial biomass for a site in Aracruz-ES, for the bulk soil, that were 2.3 times smaller than those simulated for the same site by the ForRAN. Silva et al. (2010), on the other hand, reported values close to the maximum values observed in our simulations, corresponding to 358 $\mu g\ g^{-1}$ of C for an Oxisol planted with *Eucalyptus* in the Campos das Vertentes region, Minas Gerais State, Brazil. In this case, values of this magnitude for the bulk soil could be explained by the effect of the rhizosphere itself, since such measurements do not exclude roots; or even by the effect of the so-called “detritosphere” (the litter zone of influence).

As all the simulations presented the same rhizodeposition rate but showed different results for microbial biomass, environmental factors effect, such as water availability and temperature, likely had a significant effect on the microbial biomass. The

ForPRAN took into account water availability because of its role as a universal solvent in which all microbial reactions occur (MADIGAN et al., 2017). Therefore, we report a positive effect of increasing moisture on the microbial processes studied. Water availability is certainly one of the most important factors for microbial activity in tropical environments, reflecting its large variability throughout the year. Under conditions of low soil moisture, prevalent in Wagga Wagga site, soil microorganisms probably spend more energy to adjust their electrochemical balance often by the synthesis of proline, glutamine, or by K^+ uptake (MADIGAN et al., 2017). However, it is well known that such mechanisms do not always compensate the water deficit and this, according to the ForPRAN logic, leads to a decrease in microbial biomass by death, as already observed in the work of Sato et al. (2000). Therefore, water availability must have been the main reason for the lower rate of microbial growth in the Australian sites.

In relation to temperature, theoretically, lower temperatures tend to reduce the costs for maintaining the rhizosphere microbial biomass, thus reducing the energy demand and increasing the use efficiency of organic substrates (STEINWEG et al., 2008). Thus, microbial communities are generally more efficient at using C at 15 °C than at 25 °C, for example (STEINWEG et al., 2008). However, this behavior is not always presented by the microbiota in field studies, so that to maintain our results consistent with reality, a fixed substrate use efficiency idealized for the rhizosphere (CUE = 0.5) was adopted. Temperature displays a more consistent effect on enzymatic activity. Higher temperatures increase the rates of chemical and enzymatic reactions and, consequently, promotes fast microbial growth (MADIGAN et al., 2017). Thus, the temperature increase promoted the higher microbial biomass values simulated for Aracruz and Curvelo. Increases in temperature have a positive impact on microbial biomass and, therefore, are related to increases in CO_2 evolution and N mineralization rates (MADIGAN et al., 2017), as observed in our simulations with ForPRAN for N, mainly for the Brazilian sites. Although not simulated in the present work, above certain temperatures (>40 °C), it is expected that microbial cellular components, such as exo-enzymes, are denatured, causing the rates of the microbial process to fall sharply (MADIGAN et al., 2017).

The changes induced in microbial activity by rhizodeposition increase the rhizosphere N supply to *Eucalyptus* mainly by the mineralization of N contained in native SOM and by the degradation of dead microbial biomass. Besides these two sources, mineral N availability can also be raised by the degradation of exoenzymes produced by the microbiota. The N mineralization in the rhizosphere has the potential to contribute

with 15 to 38 % of the N demand of the forest ecosystems (shoot + root + litter) under study. This conclusion sheds light into the numerous works in which high accumulations of N are observed in *Eucalyptus* trees grown in N-poor soils and also helps to explain the lack of or low response to N fertilization, as reported in Melo et al. (2016), Pulito et al. (2015), and Smethurst et al. (2015).

4.5. CONCLUSIONS

This work represents the first attempt to address the quantitative importance of rhizosphere N mineralization for nutrition of the genus Eucalyptus. According to ForPRAN calculations, the supply from the rhizosphere reaches values between 15 and 38% of the N demanded by plantations in Brazil and Australia. Such simulations can aid in balance models to optimize nitrogen fertilization, as well as to improve the Eucalyptus growth estimates of models such as APSIM, which consider N cycling. The simulations also highlight the role of the higher temperatures and rainfall volumes to a more significant rhizosphere N contribution to *Eucalyptus* nutrition in Brazil than in Australia sites.

5. FINAL CONSIDERATIONS

Like our economic system, based on surplus exchange, plants provide their surplus of carbon/energy, and receive in exchange of the soil microbiota, nitrogen (N) and/or other nutrients. Such interactions not only affect nutrient fluxes, but also have the potential to affect the stability and dynamics of these agroecosystems. Therefore, the pattern of carbon fixation and redistribution through rhizodeposition is an important component to explain the differences in the availability of nutrients, such as N, in different forests, such as *Eucalyptus*. Thus, to evaluate the quantitative importance of this phenomenon for nitrogen nutrition of eucalyptus, the present thesis aimed to present a mechanistic model that represented the cycling system of C and N in the rhizosphere coupled to a growth model (APSIM).

We elaborated the Forest plantation rhizosphere available nitrogen model (ForPRAN) for estimates of the C and N mineralization fluxes in the rhizosphere soil. As results, it was observed that the performance of the model was satisfactory quantitatively and qualitatively when compared to the data observed in the literature. In average, the rhizosphere N mineralization in a typical *Eucalyptus* plantation producing 42 $m^3\ ha^{-1}\ a^{-1}$ of shoot biomass, was estimated in 24.6 % of the N demand of N of planted forest (root + shoot + litter), with assumed losses of N of 40 % by different processes. However, it was observed that the rhizosphere priming effect (RPE) has the potential to explain about 15 to 38 % of the N accumulated in the forest ecosystem (root + shoot + litter), depending on the site conditions. Higher temperatures and rainfall volumes contribute to higher rhizosphere N supply in absolute values in Brazilian sites than in Australians, for example. These percentages present proximity to other estimates of the literature for temperate ecosystems (FINZI et al., 2015). From this, it was concluded that the rhizosphere cycling model should be considered for adaptation of other models of forest and agricultural production, such as APSIM, where the inclusion of these processes offers the potential to improve the performance of the estimates.

Among the perspectives of future studies, we emphasize the importance of evaluating whether the assumption of a fixed enzyme production rate is adequate for a dynamic system such as the rhizosphere. Likewise, it is necessary to study the potential of water in the *Eucalyptus* rhizosphere soil throughout the year and throughout the day. The seasonal pattern of water in the rhizosphere, with lower potentials during the day, and higher at night, may accelerate microbial turnover and affect simulation results.

Another important point is to study if *Eucalypts* plants can produce molecules inducing microbial quorum sensing, affecting the expression of degrading enzymes of organic matter, for example. This could explain differentiated patterns of decomposition across different forest ages. The N losses in the *Eucalyptus* rhizosphere are also a crucial factor for the better understanding of this system. Finally, the expansion of this model to consider the general soil system and interaction with other processes can help in the understanding of the overall pattern of N cycling in *Eucalyptus* plantations soil in different regions and may aid in the recommendation of N fertilizers rates that contribute to greater environmental and economic sustainability of the planted forests.

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