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Spatial heterogeneity in nitrification and soil exploration by trees favour source–sink dynamics in a humid savanna: A modelling approach

Sarah Konaré[1] | Simon Boudsocq[2] | Jacques Gignoux[1] | Jean-Christophe Lata[1,3] | Xavier Raynaud[1] | Sébastien Barot[1]

[1]Sorbonne Université, Université de Paris, UPEC, IRD, CNRS, INRA, Institute of Ecology and Environmental Sciences, iEES Paris, Paris, France

[2]Eco&Sols, INRA, CIRAD, IRD, Montpellier SupAgro, Univ Montpellier, Montpellier, France

[3]Department of Geoecology and Geochemistry, Institute of Natural Resources, Tomsk Polytechnic University, Tomsk, Russia

Correspondence
Sarah Konaré
Email: ksarahfaike@yahoo.fr

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Abstract

1. Savannas are structured ecosystems characterized by a grass layer interspersed with trees. Trees strongly modify their local environment and favour nutrient accumulation under their canopies. Tree roots can also forage horizontally far beyond the canopy projection to increase nutrient uptake. In the Lamto savanna (Côte d'Ivoire), grasses are able to inhibit nitrification while trees stimulate it.
2. Here, we used a two-patch model simulating nitrogen (N) dynamics in a humid savanna between an open patch (without tree) associated with a low nitrification rate and a patch of tree clump associated with a high nitrification rate. The model also includes horizontal N fluxes between these two patches corresponding to horizontal soil exploration by tree roots. We analysed the impact of spatial heterogeneity in nitrification and soil horizontal exploration on N budget and plant biomass.
3. Despite high N losses under trees due to nitrification stimulation by trees, our results show that the ability of trees to explore horizontally the open allows them to uptake more nutrients in total. This leads to an asymmetric N flux from the open to tree clumps, which contributes to nutrient enrichment under tree clumps and thereby to tree growth.
4. Although trees have the ability to horizontally explore the soil to accumulate nutrients under their canopy, increasing the surface occupied by tree clumps increases N losses per hectare of savanna due to the increased nitrification under trees and the subsequent increase in NO_3^- leaching.
5. While perennial savanna grasses show a restricted horizontal soil exploration to control nutrient availability, our results predict that the extension of tree roots outside their canopy increases their nutrient acquisition in the Lamto savanna. This study is the first one emphasizing the influence of horizontal exploration of trees and tree cover on savanna N budget and functioning. Overall, the proportion of tree cover and horizontal soil exploration are important factors to consider in savannas characterized by spatial heterogeneity in N cycling created by trees and grasses. These factors appear critical to the functioning of West African humid savannas and should be investigated in other savanna types.

KEYWORDS

grasses, horizontal soil exploration, nitrification control, nitrogen cycling, preference for NH_4^+ versus NO_3^-, savanna, trees

1 | INTRODUCTION

Savannas are spatially structured ecosystems dominated by C_4 grasses and trees that are more or less clumped (Scholes & Archer, 1997). Savanna functioning is determined by the interactions between plants, disturbances and resource availability (Hoffmann et al., 2012; Sankaran et al., 2005; Scholes & Archer, 1997). In particular, plants directly affect the availability of soil nutrients through litter deposition or root exudation, which feedbacks on their capacity to take up nutrients (Hobbie, 1992, 2015). Many studies have focused on the effects of savanna trees on soil properties and on understorey vegetation beneath their canopies (Belsky et al., 1989; Isichei & Muoghalu, 1992; Ludwig et al., 2004; Mordelet et al., 1993; Ward et al., 2018). They generally showed that soils under tree canopies have significantly higher concentrations of organic matter and nutrients (N, P, K and Ca) than in the open (Belsky et al., 1989; Mordelet et al., 1993). The increase in nitrogen (N) concentration under tree clumps leads to a lower C/N ratio that likely increases microbial activity (Mordelet et al., 1993). Besides the influence of throughfall (foliar and branch leachates) on inputs of nutrients to the soil, some trees (*Acacia* species) increase soil fertility through symbiotic N fixation (Belsky et al., 1989; Kambatuku et al., 2013), which constitutes an important N source for the herbaceous vegetation under tree canopies but can also change nutrient limitation from N-limited in open areas to P-limited under tree canopies (Ludwig et al., 2004). Taken together, trees modify their environment and create spatial heterogeneity in the soil characteristics of savannas.

Most savannas tend to be nutrient-limited (Pellegrini, 2016), particularly for N. This is due to heavy rains and low soil cationic exchange capacity (due to low soil organic matter and clay contents, and to clay types) that cause high N losses by leaching. Besides, frequent fires burn above-ground biomass, which leads to the volatilization of a part of the N it contains (Abbadie, 2006). Despite these constraints, primary production is often as high in humid savannas as in tropical forests (Lieth & Whittaker, 1975). In the Lamto humid savanna (Côte d'Ivoire), this high productivity is partly due to the capacity of dominant perennial grasses to prevent nitrification in the soil surrounding their root system (Boudsocq et al., 2009; Lata et al., 2004; Srikanthasamy et al., 2018). Such a 'biological nitrification inhibition' (BNI) has been identified in other tropical grasses such as *Brachiaria humidicola* and *Andropogon gayanus* (Rossiter-Rachor et al., 2009; Subbarao et al., 2013). Suppressing nitrification keeps N in the ammonium (NH_4^+) form, thus minimizing N losses through nitrate (NO_3^-) leaching and denitrification. In addition, Srikanthasamy et al. (2018) found that the dominant non-fixing tree species of the Lamto savanna stimulate nitrification. While grasses have been shown to inhibit nitrification through particular root exudates, the mechanism by which trees affect nitrification in savannas is still unclear. Higher amount of organic matter under tree canopies could increase N availability and microbial activity including mineralization and nitrification (Mordelet et al., 1993). Trees could also release specific molecules through root exudates that specifically stimulate nitrification. These different plant–soil feedbacks create a spatial heterogeneity in nitrification fluxes that should strongly influence N cycling and suggests differences between trees and grasses in their preference for NH_4^+ versus NO_3^- (Boudsocq et al., 2012; Konaré et al., 2019).

Horizontal N flows may occur between the open and tree clumps through soil exploration by tree roots. Savanna trees are able to extend their roots horizontally beyond their canopy extent to absorb nutrients from surrounding open areas occupied by grasses. These nutrients are used for tree growth (leaves, branches) and thus return to the soil of tree clumps through litterfall, improving soil fertility under the canopy (Belsky et al., 1989; Rhoades, 1997). This leads to horizontal fluxes of nutrients from open patches to tree clump patches while grasses in open patches can receive nutrients from tree clump patches via the mortality of exploring roots. In the Lamto savanna, tree roots can extend more than 30 m away from the centre of a tree canopy rarely wider than 5 m (Mordelet, 1993) and are found almost everywhere outside tree clumps (Menaut, unpublished data; Mordelet, 1993). Tree roots in the open could create source–sink dynamics leading, for example, tree clumps to be nutrient sinks. Moreover, horizontal fluxes between the open and tree clump patches and their impact on plant biomass should also depend on the proportion of tree cover in the savanna. For a given surface of savanna, and for a given proportion of roots outside the tree canopy, increasing tree cover increases tree sink capacity, but decreases the quantity of N available in the open. Hence, for a low (high) proportion of tree cover, each unit area of tree patch could benefit from a high (low) N input from the open. This should, in turn, influence the relative tree and grass biomass.

This study aims to analyse how spatial heterogeneity due to nitrification control by plants and horizontal N fluxes between the open and tree patches influence the N budget and plant biomass of the Lamto savanna. To do so, we used a two-patch model (an open patch with low nitrification and a tree clump patch with high nitrification) to test the following hypotheses: (a) increasing horizontal soil exploration leads to an increasingly asymmetric net N flux from the open to tree clumps, which increases tree biomass and contributes to the fertility of tree clump soil and (b) because trees stimulate nitrification, increasing the proportion of the surface occupied by trees increases total N losses and decreases the amount of mineral N available by unit of tree cover surface. As a corollary, spatial heterogeneity in nitrification fluxes and horizontal soil exploration by tree roots strongly alter the overall N budget of the Lamto savanna. Interestingly, we can consider savanna ecosystems as meta-ecosystems (Gounand et al., 2018; Loreau et al., 2003), whose 'ecosystems', that is, two types of patches, are linked by N fluxes. We thus study within a savanna three key features of meta-ecosystems: the structure of the meta-ecosystem (the relative surface of the open and tree clump patches), the heterogeneity between patches (high nitrification vs. low nitrification patches) and the intensity of fluxes between patches (N fluxes).

2 | TWO-PATCH MODEL

2.1 | Model description

The model is a spatial version of a published mean-field model (Konaré et al., 2019). It simulates N dynamics between an open patch with a low nitrification rate (patch 1) and a tree clump patch with a high nitrification rate (patch 2). The open patch is occupied by grasses and some tree roots (see below) while the tree clump patch is occupied by trees and grasses (Figure 1). This model includes grass biomass in both patches (*G_1*, *G_2*) and tree biomass (*T*) in patch 2 as well as organic matter (*O*) and soil mineral N, ammonium (*N_A*) and nitrate (*N_N*) in both patches. Model compartments are N stocks expressed in kilograms of N per hectare of patch (kg N/ha) and exchange rates between compartments and patches are N fluxes, expressed in kilograms of N per hectare of patch per year (kg N ha^{-1} year^{-1}). Note that the term 'plant biomass' only refers to the size of N pools in plants (trees or grasses). All parameters except for nitrification rate and tree preference for NH_4^+ versus NO_3^- are equal between the two patches to focus on the impact of nitrification heterogeneity and horizontal fluxes (Table 1).

Following Boudsocq et al. (2012), grasses and trees can use N in two mineral forms NH_4^+ and NO_3^- with the parameter β quantifying the preference for NH_4^+ versus NO_3^-. β ranges from 0 to 1 and the closer to 1, the higher the preference for NH_4^+. This preference has never been precisely assessed in savanna grasses and trees but has been shown to be very influential for the N budget of ecosystems (Boudsocq et al., 2012),

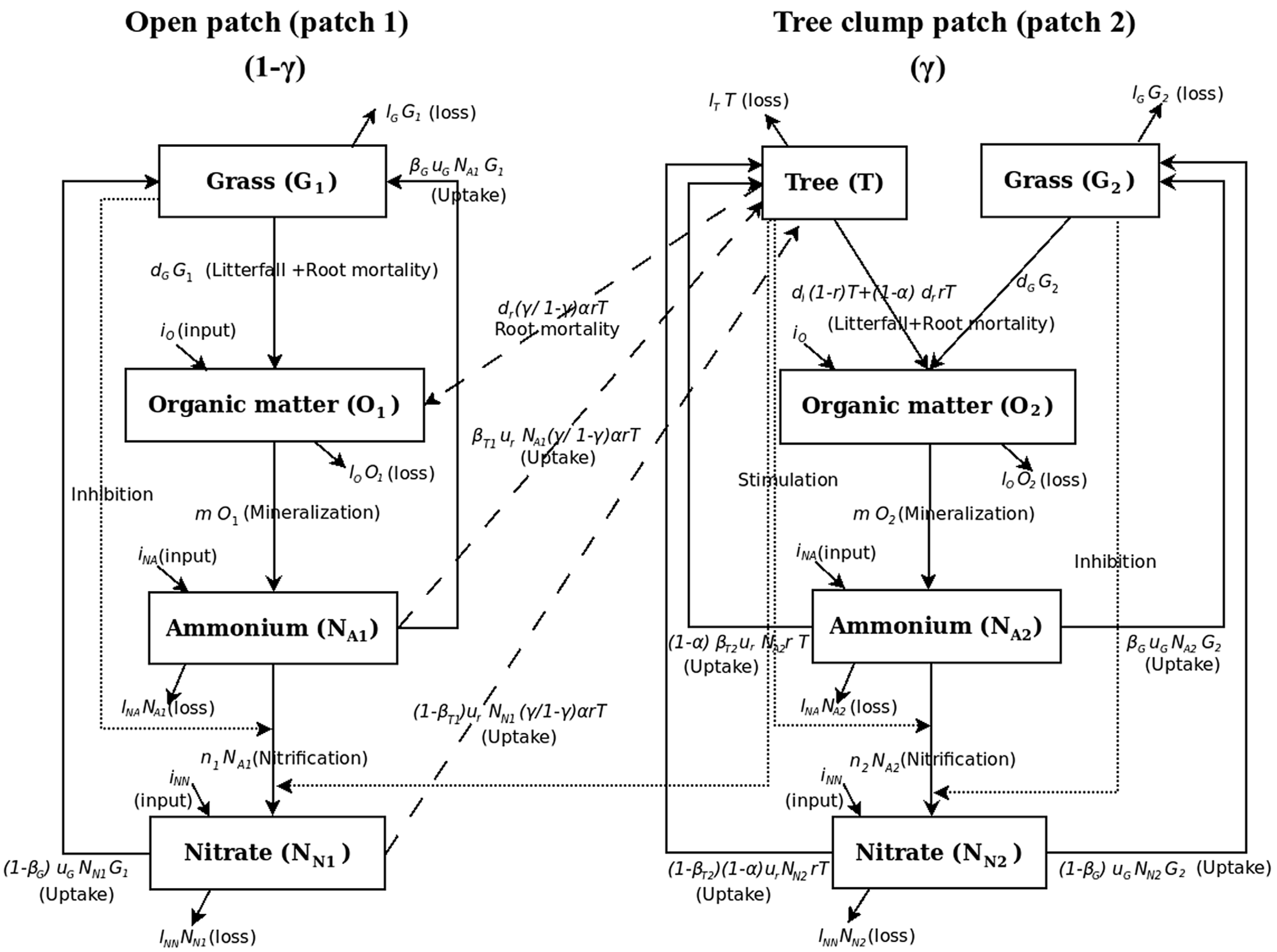

FIGURE 1 Two-patch model representing N dynamics between an open patch and a patch of tree clump in savanna ecosystem. Dashed lines correspond to horizontal exploration of tree roots under grasses and dotted lines correspond to the influence of plants on nitrification. All fluxes are multiplied by the proportion of the surface occupied by the open ($1 - \gamma$) and the proportion of the surface occupied by tree clumps (γ), respectively, for the open and tree clumps patches to perform simulations at the savanna scale

TABLE 1 Model parameters

Parameters	Definition	Unit	Values	References
Grass parameters				
d_G	Turnover rate of grass	year^{-1}	0.6	Lata (1999)
l_G	Rate of N losses from grass compartment	year^{-1}	0.4	Lata (1999)
u_G	N uptake rate	$\text{ha kg}^{-1}\text{ N year}^{-1}$	0.14186	Boudsocq et al. (2012)
β_G	Preference for NH_4^+	No unit	—	
Tree parameters				
d_r	Turnover rate of tree roots	year^{-1}	0.08	Estimated
d_l	Turnover rate of tree leaves	year^{-1}	0.073	Menaut (1974)
l_T	Rate of N losses from tree compartment	year^{-1}	0.11	Menaut and César (1979)
u_r	N uptake rate by tree roots	$\text{ha kg}^{-1}\text{ N year}^{-1}$	0.08	Estimated
β_{T1}	Preference for NH_4^+ in the open patch	No unit	[0,1]	
β_{T2}	Preference for NH_4^+ in the tree clump patch	No unit	0.25	
α	Fraction of roots in the open	No unit	[0.1,0.5]	
γ	Tree clumps proportion	No unit	[0.15,0.6]	
r	Root shoot ratio	No unit	0.5	Menaut and César (1979)
Soil parameters				
i_O	N organic input to the savanna	$\text{kg N ha}^{-1}\text{ year}^{-1}$	16.5	Villecourt and Roose (1978)
m	N mineralization rate	year^{-1}	0.025	Abbadie et al. (2006)
l_O	N loss from the N organic compartment in surface soil layer	year^{-1}	0.0027	Abbadie et al. (2006)
i_{NA}	NH_4^+ inputs to the savanna	$\text{kg N ha}^{-1}\text{ year}^{-1}$	23	Villecourt and Roose (1978)
n_1	Nitrification rate in the open patch	year^{-1}	0.09	Srikanthasamy et al. (2018)
n_2	Nitrification rate in the tree clump patch	year^{-1}	4.16	Srikanthasamy et al. (2018)
l_{NA}	NH_4^+ loss rate	year^{-1}	0.0133	Villecourt and Roose (1978)
i_{NN}	NO_3^- inputs to the savanna	$\text{kg N ha}^{-1}\text{ year}^{-1}$	4.1	Villecourt and Roose (1978)
l_{NN}	NO_3^- loss rate	year^{-1}	2.7	Boudsocq et al. (2009)

and grass and tree biomass (Konaré et al., 2019). Moreover, trees are able to extend horizontally a certain proportion of their roots outside their canopy projection (α) to absorb nutrients in the open (patch 1). Thus, the tree root biomass in the open is $\alpha\, r\, T$, where r is the proportion of roots in the tree biomass (root biomass/total biomass). As nutrient uptake depends on both plant biomass and nutrient availability, N uptake fluxes are modelled using donor–recipient functions, that is, proportional to the sizes of both the donor and the recipient pools. The N uptake rate by trees is represented by $\beta_{T1}u_r$ and $\beta_{T2}u_r$, respectively, for NH_4^+ uptake by tree roots in the open and under tree clump, and $(1-\beta_{T1})\,u_r$ and $(1-\beta_{T2})\,u_r$, respectively, for NO_3^- uptakes. The N uptake by trees in the open depends on α but also on the proportion of the surface occupied by tree clumps (γ) and by the open ($1-\gamma$). We thus considered the tree root biomass in the open ($\alpha\, r\, T$) and we multiplied this biomass by $\gamma/(1-\gamma)$ to compute the uptake of N by trees in the open and to ensure mass conservation. The term $\frac{\gamma}{1-\gamma}$ thus expresses N uptake by trees in kg N per hectare of the open so that N uptake by trees in the open at the savanna scale becomes $\gamma\,(\beta_{T1}u_rN_{A1}\alpha rT)$. This leads to the following expressions: $\beta_{T1}\left(\frac{\gamma}{1-\gamma}\right)u_rN_{A1}\alpha rT$ for NH_4^+ uptake and $(1-\beta_{T1})\left(\frac{\gamma}{1-\gamma}\right)u_rN_{N1}\alpha rT$ for NO_3^- uptake.

It must be noted that in the field, the observed α depends on (a) the proportion of roots outside the canopy projection of each individual tree, (b) the proportion of tree cover (γ) and (c) the spatial distribution of individual trees. Nevertheless, to analyse the respective influence of α and γ on N fluxes and plant biomass, we considered in our simulations the two parameters as independent.

Grass mortality (constant rate d_G) constitutes an input to the organic compartment (compartment O). Tree above-ground and below-ground parts have distinct mortality rates d_l and d_r, respectively, for tree leaves and roots. The dead organic matter resulting from the decay of plant material is mineralized into NH_4^+ at rate m. Then, NH_4^+ is transformed into NO_3^- at rate n. External inputs of mineral N through dry and wet depositions (dust and rain) bring N in organic or mineral forms (Abbadie, 2006) and are represented by fixed inputs, independent of model compartments, i_O, i_{NA} and i_{NN}, respectively, for O, N_A and N_N compartments. Non-symbiotic fixation contributes to the input of NH_4^+ and is included in i_{NA} (Abbadie, 2006). N is lost from the ecosystem at rates l_G, l_T, l_O, l_{NA} and l_{NN} mainly due to fire for plant compartments, leaching for other compartments and denitrification in the case of NO_3^-. Symbiotic N fixation by trees and herbivory are not taken into account in the model because tree species in the Lamto savanna are not N-fixing plants and the density of large herbivores is low (Abbadie, 2006; Le Roux et al., 2006). The equations below hold for compartments measured at the scale of each patch, but the equations for a hectare of savanna can be easily derived by multiplying them by $(1 - \gamma)$ and γ in the open and tree clump patches, respectively (Appendix S1).

Overall, the two-patch model is represented by the following system of equations:

Open patch (patch 1):

$$\frac{dG_1}{dt} = \beta_G u_G N_{A1} G_1 + (1 - \beta_G) u_G N_{N1} G_1 - (d_G + l_G) G_1, \tag{1}$$

$$\frac{dO_1}{dt} = i_O + d_G G_1 + d_r \left(\frac{\gamma}{1-\gamma}\right) \alpha r T - (m + l_O) O_1, \tag{2}$$

$$\frac{dN_{A1}}{dt} = i_{NA} + mO_1 - \left(\beta_G u_G G_1 + n_1 + l_{NA} + \beta_{T1} u_r \left(\frac{\gamma}{1-\gamma}\right) \alpha r T\right) N_{A1}, \tag{3}$$

$$\frac{dN_{N1}}{dt} = i_{NN} + n_1 N_{A1} - \left((1 - \beta_G) u_G G_1 + l_{NN} + (1 - \beta_{T1}) \left(\frac{\gamma}{1-\gamma}\right) u_r \alpha r T\right) N_{N1}, \tag{4}$$

Tree clump patch (patch 2):

$$\frac{dG_2}{dt} = \beta_G u_G N_{A2} G_2 + (1 - \beta_G) u_G N_{N2} G_2 - (d_G + l_G) G_2, \tag{5}$$

$$\begin{aligned}\frac{dT}{dt} = &(1-\alpha)(\beta_{T2} u_r N_{A2} rT + (1-\beta_{T2}) u_r N_{N2} rT) + \alpha(\beta_{T1} u_r N_{A1} rT \\ &+ (1-\beta_{T1}) u_r N_{N1} rT) - (d_l(1-r) + d_r r + l_T)T,\end{aligned} \tag{6}$$

$$\frac{dO_2}{dt} = i_O + d_G G_2 + (1 - \alpha) d_r r T + d_l (1 - r) T - (m + l_O) O_2, \tag{7}$$

$$\frac{dN_{A2}}{dt} = i_{NA} + mO_2 - (\beta_G u_G G_2 + (1 - \alpha) \beta_{T2} u_r r T + n_2 + l_{NA}) N_{A2}, \tag{8}$$

$$\frac{dN_{N2}}{dt} = i_{NN} + n_2 N_{A2} - ((1 - \beta_G) u_G G_2 + l_{NN} + (1 - \beta_{T2})(1 - \alpha) u_r r T) N_{N2}. \tag{9}$$

Note that in our model, grasses do grow within tree clumps as observed in reality (Mordelet et al., 1997).

2.2 | Model analysis and parameterization

Because the model could not be analytically solved, we analysed it through numerical simulations. The model has been implemented in R (R Development Core Team, 2019) and the numerical integration of the differential equations was performed using the DESOLVE package (Soetaert et al., 2010). All displayed results correspond to compartment size after 3,000 years of simulation, which was a time sufficient to reach steady states of all compartments.

Parameter values used are summarized in Table 1 and are based on data from the Lamto reserve in Côte d'Ivoire (06°13′N, 05°02′W; Abbadie et al., 2006). The vegetation in this site is a mosaic of savannas composed of perennial grasses, small tree clumps and tall palm trees. The climate is characterized by a mean annual temperature of 27°C and a mean annual rainfall of 1,200 mm divided between two dry seasons (from November to February and in August) and two rainy seasons (from March to July, and from September to October). We mostly used the same parameter values as in Konaré et al. (2019) but some tree parameters and nitrification rate. The ratio of roots in the tree biomass (r) was estimated from Menaut and César (1979). N uptake by tree roots (u_r) was estimated by exploring parameter values to obtain a tree biomass close to the one measured in the Lamto savanna (86.1 kg N ha^{-1} $year^{-1}$; Menaut & César, 1979). Regarding the mortality rate of tree leaves (d_l), we divided the annual leaf fall by total tree biomass (Menaut, 1974; Menaut & César, 1979). Spatial heterogeneity was included in the model by considering a low nitrification rate in the open patch (n_1) and a higher nitrification rate under trees (n_2). Those rates were determined by dividing nitrification fluxes under grasses and under trees by their respective ammonium stocks (Srikanthasamy et al., 2018). Tree cover varies depending on the different facies observed in the Lamto savanna: from grass savanna (tree cover <7%) to savanna woodland (tree cover >62%; Menaut & César, 1979; Gautier, 1990). To understand the impact of soil exploration by tree roots in the open and the proportion of tree cover on N dynamics, we tested the impact of four combinations of two values of α (0.25 and 0.5) and γ (0.15 and 0.3). $\gamma = 0.15$ and $\gamma = 0.3$ roughly correspond to a sparse tree savanna and a tree savanna in the Lamto site (Gautier, 1990). The net horizontal N flux corresponds to the difference between inflow in the tree clump patch (N uptake by trees) and outflow (tree roots mortality in the open patch).

Although existing data do not allow estimating the preference of plants for NH_4^+ versus NO_3^-, nitrification stimulation under tree clumps suggests a preference of trees for NO_3^- for tree roots inside tree clump patch. On the contrary, if trees extend their roots outside their canopy projection to take up N, these roots should have a preference for NH_4^+. Such a within-species difference in the preference for NH_4^+ versus NO_3^- is possible due to the diversity of underlying mechanisms (Britto & Kronzucker, 2013). We therefore decided to distinguish the preference of trees for NH_4^+ versus NO_3^- in the open patch (β_{T1}) and under tree clumps (β_{T2}) and to fix tree preference under tree clumps ($\beta_{T2} = 0.25$). All N stocks and N fluxes were determined according to different combinations of plant preference for NH_4^+ versus NO_3^- (β_G and β_{T1}) varying between 0 and 1 with an increment of 0.01. All simulations were run for 3,000 years, which was sufficient to reach steady states for all compartments.

3 | RESULTS

3.1 | Soil N pools in the open and tree clump patch at the patch scale

Soil N pools at the patch scale can be strongly affected by the grass and tree preference for NH_4^+ versus NO_3^- (Figure 2). For a given proportion of tree roots outside tree canopy (α) of 25% and a surface of 15% occupied by tree clumps (γ), two main trends appear (Figure 2a): when tree preference for NH_4^+ in the open patch is lower than grass preference for NH_4^+, the organic N pool is lower in the tree clump patch than in the open. Conversely, the organic N pool is higher in clumps than in the open when tree preference for NH_4^+ in the open patch is higher than grass preference for NH_4^+. This ratio sharply increases and leads to a zone where soil organic matter under tree clumps is about eight times higher than in the open patch. The NH_4^+ stock is always higher in the open patch than under tree clumps (Figure 2b). When tree preference for NH_4^+ in the open patch is lower than grass preference for NH_4^+, the NO_3^- pool is higher in clumps than in the open. The clump/open NO_3^- ratio (i.e. the ratio between NO_3^- pool beneath the tree clump patch and in the open patch) increases up to 10 (10 times more NO_3^- per unit area in the tree clump patch than in the open patch). However, when tree preference for NH_4^+ in the open is higher than grass preference for NH_4^+, the NO_3^- pool is generally lower in clumps than in the open (Figure 2c).

3.2 | α and γ have contrasting effects on horizontal N fluxes and tree biomass

The proportion of tree roots outside their canopies (α) and the proportion of the savanna surface occupied by tree clumps (γ) affect the intensity of horizontal N fluxes at the savanna scale (i.e. at the regional scale in the terminology of meta-ecosystems, Figure 3). At low values of α and γ ($\alpha = 0.25$ and $\gamma = 0.15$; Figure 3c), the net horizontal N flux (per ha of savanna) from the open to the tree clump patch is high only when tree preference for NH_4^+ in the open patch is sufficiently higher than grass preference for NH_4^+ ($0 < \beta_G < 0.6$). When grass preference for NH_4^+ increases ($\beta_G > 0.6$), the net horizontal N flux varies from 31 kg N ha^{-1} $year^{-1}$ to zero depending on tree preference for NH_4^+ in the open patch. With increasing α ($\alpha = 0.5$ and $\gamma = 0.15$; Figure 3a), the size of the zone, where the net horizontal N flux is high, increases. Contrary to α, the net horizontal N flux to the tree clump patch decreases with increasing γ. When tree preference for NH_4^+ in the open patch is higher than grass preference for NH_4^+, the net horizontal N flux is above 30 kg N ha^{-1} $year^{-1}$ (Figure 3c). But when γ increases ($\alpha = 0.25$ and $\gamma = 0.3$, Figure 3d), the net horizontal N flux does not exceed 27 kg N ha^{-1} $year^{-1}$ in this zone. When grass preference for NH_4^+ increases, the net horizontal N flux decreases from 27 kg N ha^{-1} $year^{-1}$ to zero depending on tree preference for NH_4^+ in the open patch. We also observe a small part of the parameter space where the net horizontal N flux is negative when tree roots in the open patch have a strict preference for NO_3^- and $0.05 < \beta_G < 0.85$. The overall pattern is similar for tree biomass as in horizontal N fluxes (Figure 4). Horizontal N fluxes to the tree clump patch feedback to tree biomass at the savanna scale and leads to a zone where tree biomass is unrealistically high when tree preference for NH_4^+ in the open patch is higher than grass preference for NH_4^+ (Figure 4c). Tree biomass per ha of savanna increases with α (Figure 4a,c) but decreases with γ (Figure 4b,d). The higher the grass preference for NH_4^+ ($0 < \beta_G < 0.6$), the higher tree preference for NH_4^+ in the open patch required for trees to stay in the system. When grass preference for NH_4^+ is higher than tree preference for NH_4^+ in the open patch, tree biomass decreases to values lower than 100 kg N/ha (Figure 4a,b) or 200 kg N/ha (Figure 4c,d). Appendix S2 also shows that the effects of α and γ

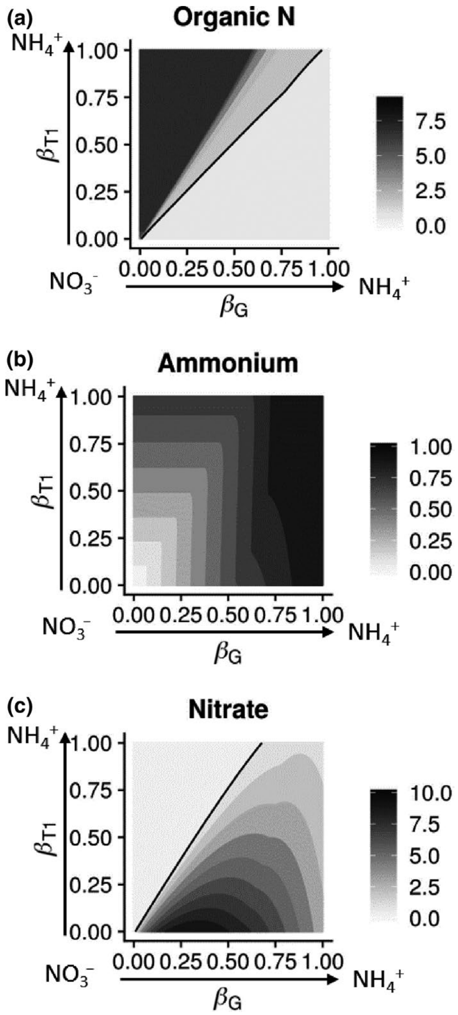

FIGURE 2 Ratio of the soil N pools in the tree clump patch over the N pools in the open patch as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+ in the open patch: (a) organic N pool O_2/O_1, (b) NH_4^+ pool N_{A2}/N_{A1} and (c) NO_3^- pool N_{N2}/N_{N1}. The solid line represents the isocline 1 of the ratio of pools, that is, where the N pools are equal in both patches. These figures correspond to simulations with $\alpha = 0.25$ and $\gamma = 0.15$

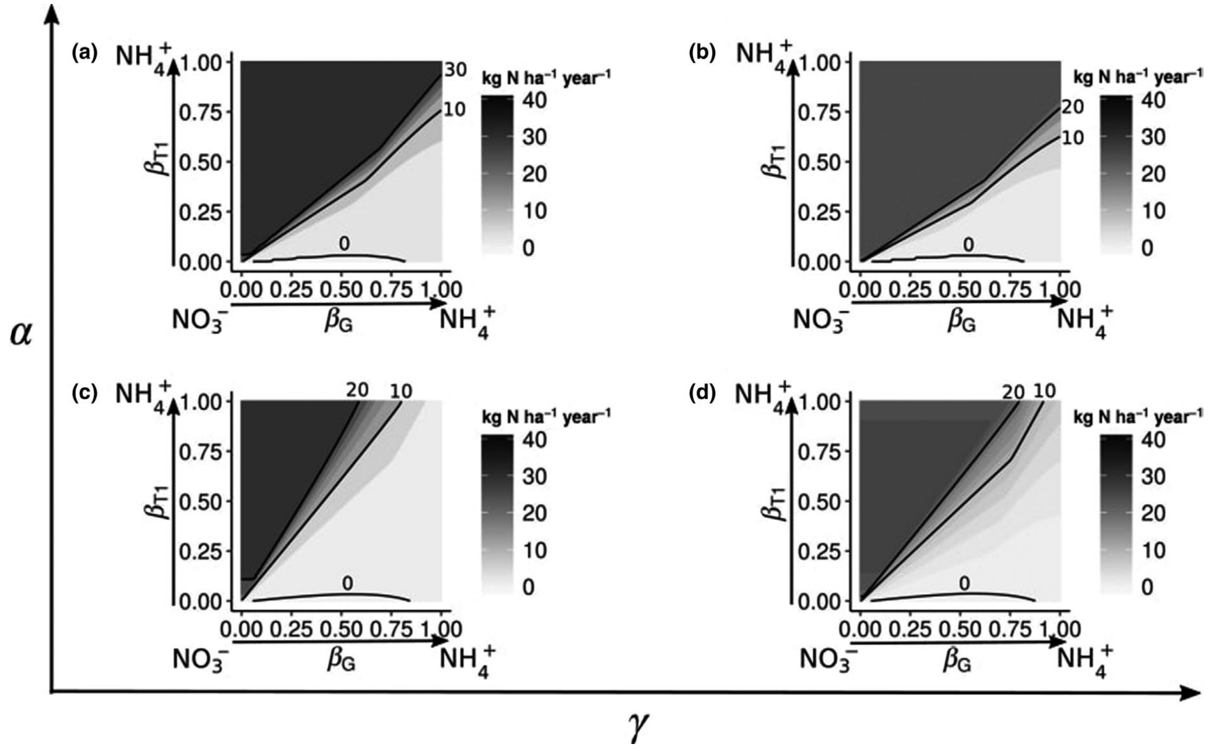

FIGURE 3 Net horizontal *N* flux from the open to the tree clump patch as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+ in the open patch according to different values of α and γ at the savanna scale. The proportion of roots outside tree canopy (α) increases from the bottom to the top, and the surface occupied by tree clumps (γ) increases from the left to the right (a: $\alpha = 0.5$ and $\gamma = 0.15$, b: $\alpha = 0.5$ and $\gamma = 0.3$, c: $\alpha = 0.25$ and $\gamma = 0.15$, d: $\alpha = 0.25$ and $\gamma = 0.3$). Solid lines show N flux contours

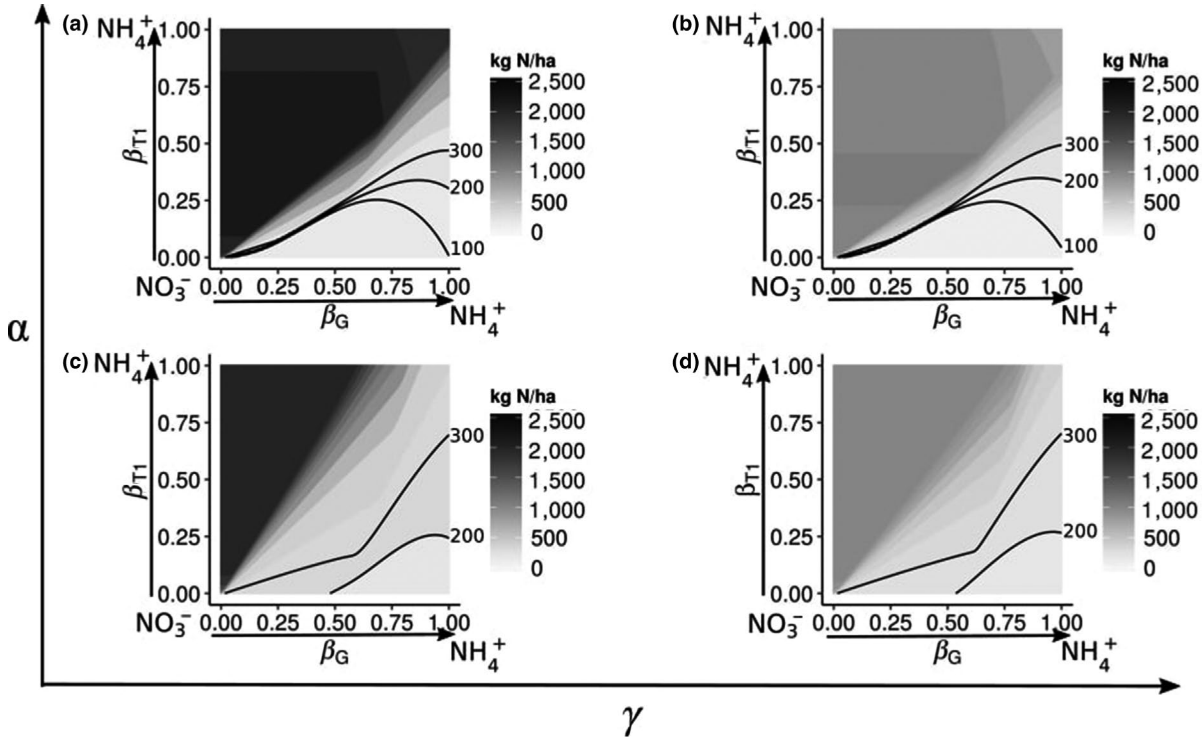

FIGURE 4 Tree biomass as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+ in the open patch, according to different values of α and γ at savanna scale. The proportion of roots outside tree canopy (α) increases from the bottom to the top, and the surface occupied by tree clumps (γ) increases from the left to the right (a: $\alpha = 0.5$ and $\gamma = 0.15$, b: $\alpha = 0.5$ and $\gamma = 0.3$, c: $\alpha = 0.25$ and $\gamma = 0.15$, d: $\alpha = 0.25$ and $\gamma = 0.3$). Solid lines show contours of tree biomass in the range of values observed in the field

impact the grass and total biomass (in kg N per ha of savanna). The decrease in tree biomass favours the growth of grasses beneath tree clump and in the open.

3.3 | N budget in the Lamto savanna

Figure 5 displays the result of a simulation of the N budget of the Lamto savanna for a proportion of tree roots in the open of 25% and a surface of 15% occupied by tree clumps at the savanna scale. We observe that NH_4^+ stock is slightly higher in the open (9.11 kg N/ha) than in the tree clump patch (8.50 kg N/ha) while the NO_3^- stock is about three times higher in the tree clump (2.51 kg N/ha) than in the open patch (0.88 kg N/ha). Organic N content is lower under tree clump than in the open patch. Moreover, nitrification flux is much higher in the tree clump (5.31 kg N ha^{-1} $year^{-1}$) than in the open patch (0.70 kg N ha^{-1} $year^{-1}$) but total N losses are more important in the open (7.21 kg N ha^{-1} $year^{-1}$) than in the tree clump patch (1.84 kg N ha^{-1} $year^{-1}$).

To better investigate the effects of spatial heterogeneity on N budget, a case of spatial homogeneity in nitrification rates was simulated (Appendix S6). When nitrification rate is as high in the open patch as in the tree clump patch ($n_1 = n_2 = 4.16$ $year^{-1}$), nitrification flux in the open patch increases (23.97 kg N ha^{-1} $year^{-1}$) and is about five times higher than in the tree clump patch (5.30 kg N ha^{-1} $year^{-1}$). This high nitrification flux in the open patch increases NO_3^- losses (19 times higher in the open patch) and leads to total N losses higher in the open (21.13 kg N ha^{-1} $year^{-1}$) than in the tree clump patch (1.83 kg N ha^{-1} $year^{-1}$). In the case of spatial heterogeneity, mineral N losses represent 3.0% of N inputs (mineralization and depositions) in the open and 8.90% in the tree clump patch at the savanna scale. In the case of spatial homogeneity, mineral N losses represent 36.28% of these N inputs in the open and 7.85% in the tree clump patch at the savanna scale. In both cases, grass biomass is lower under tree clumps than in the open patch. Regarding horizontal fluxes, mineral N uptake is still higher than tree root mortality and leads to a positive net horizontal N flux to tree clumps higher in the case of spatial homogeneity (5.89 kg N ha^{-1} $year^{-1}$) than in the case of

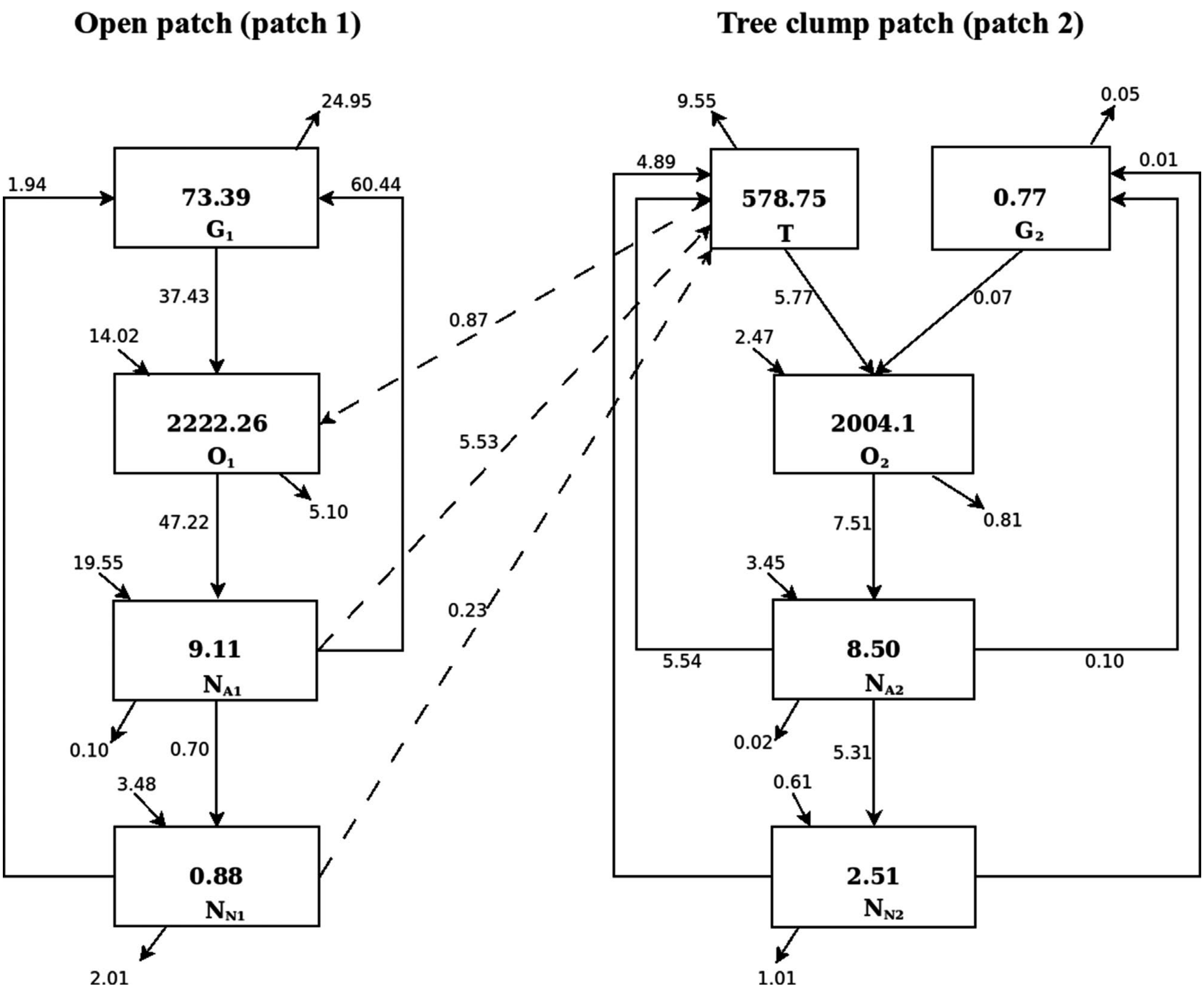

FIGURE 5 Estimate of the *N* stocks (kg N/ha) and *N* fluxes (kg N ha^{-1} $year^{-1}$) at model equilibrium at the savanna scale. We fixed $\beta_G = 0.75$ and $\beta_{T1} = 0.7$

spatial heterogeneity in nitrification fluxes (4.89 kg N ha^{-1} $year^{-1}$). Horizontal N fluxes at the savanna scale, respectively, represent 35.58% and 38.08% of total N uptake by trees in the spatial heterogeneity and homogeneity cases.

4 | DISCUSSION

Trees have the ability to access resources from deeper soil layers to limit competition with grasses (Holdo, 2013; Walter, 1971). Our two-patch model suggests that horizontal soil exploration by tree roots can also play an important role in resource acquisition and confirms our hypotheses that (a) the horizontal extension of tree roots creates an asymmetric N flux from the open to the tree clump patch, which contributes to N enrichment under tree clumps and increases tree biomass at the savanna scale; (b) although soil exploration by trees increases N acquisition and favours tree growth, increasing tree cover can increase N losses due to nitrification stimulation under tree clump, thus reducing the quantity of N available for tree growth and (c) overall, a large part of the savanna N budget depends on horizontal N fluxes (about 35% of the total N uptake by trees). In the following sections, we discuss in detail the implications of soil exploration and spatial heterogeneity on source–sink dynamics, plant biomass and the N budget of the Lamto savanna.

4.1 | Impact of horizontal soil exploration on source–sink dynamics and N enrichment

Our results show that the horizontal spread of tree roots beyond tree canopy projection induces spatial transfers of N between the open and tree clump patches. In our results, N uptake by trees (inflow) at the savanna scale (i.e. at the regional scale in the meta-ecosystems terminology) is, in most cases, higher than tree roots mortality (outflow) regardless of plant preference for NH_4^+ versus NO_3^-. This leads to an asymmetrical N flux between the two patches that increases soil fertility under tree canopy and supports the idea that savanna trees can be considered as nutrient pumps (Scholes, 1990): they take up N from surrounding grassy areas and appear as an N sink. These N exchanges between the open and tree clump patches contribute to the N enrichment under tree canopy and also confirm that savannas can be considered as small-scale meta-ecosystems with source–sink N dynamics (Gounand et al., 2018; Loreau et al., 2003). Increasing the proportion of tree roots in the open increases the net horizontal N flux and consequently increases tree biomass at the savanna scale (Figures 3 and 4). This suggests that it is beneficial for trees to invest in horizontal root proliferation because they receive more N from the open than they export through root mortality. This result may seem trivial, but recent work (de Parseval et al., 2016) shows that in some cases, plants can get more nutrients by exploring less soil. This is actually what grasses do in the same ecosystem. Moreover, savanna palm trees extend horizontally their roots outside their canopy under tree clumps because of the higher nutrient availability (Mordelet et al., 1996) suggesting that horizontal N fluxes are widespread in savannas. This confirms results obtained in drier areas where trees tend to horizontally spread their roots (Schenk & Jackson, 2002) to overcome the scarcity of resources and the concentration of nutrients mainly located in the top soil layers (Sternberg et al., 2004). Some studies tend to explain the high soil fertility under tree canopy by high plant litter depositions (Mordelet et al., 1993), atmospheric depositions (Bernhard-Reversat, 1982; Kellman, 1979), animal dung (Belsky, 1994), termite mounds (Konaté et al., 1999) and N symbiotic fixation (Kambatuku et al., 2013). However, no study has clearly assessed the respective influence of these mechanisms on nutrient enrichment. New empirical studies are thus needed and the model we propose can be viewed as a kind of null model that allows including other mechanisms impacting N fluxes such as different mineralization rates in the open and under tree clumps, or N fixation by trees.

The observed inhibition of nitrification by grasses and stimulation of nitrification by trees suggest that grasses should prefer NH_4^+ and trees should prefer NO_3^-. This is confirmed by an ongoing experiment on *Hyparrhenia diplandra* in the Lamto savanna (S. Barot pers. comm.). Moreover, it has been found that the grass *A. gayanus* inhibits nitrification and has a clear preference for NH_4^+ (Rossiter-Rachor et al., 2009). Besides, Wang and Macko (2011) revealed that N uptake preference varies depending on climatic conditions and that grasses may change their N preference from NO_3^- in dry areas to NH_4^+ in humid areas. These findings suggest that Lamto savanna grasses prefer NH_4^+ while a preference of trees for NO_3^- is expected, at least for the roots growing below their canopy where nitrification is high (Srikanthasamy et al., 2018). However, in our model, N enrichment is higher when trees have a preference for NH_4^+ in the open (Figure 2). Even if this high N enrichment below tree clumps leads to values of tree biomass too high for the Lamto savanna (Figure 4), this suggests that a different preference of trees in the open and under their canopy can be expected because the horizontal root foraging strategy probably aims at exploiting the high NH_4^+ availability outside tree clumps.

Consequently, our model also suggests that different parts of the tree root systems have contrasting preferences for NH_4^+ versus NO_3^-. This would be possible due to the complexity of mechanisms explaining this preference and the possibility of plasticity in this preference depending on environmental and physiological conditions (Britto & Kronzucker, 2013). We studied a case without such plasticity where trees have the same preference in the open as in tree clump patch (Appendix S5) and observed qualitatively the same effects of soil exploration and tree cover on soil N pools and tree biomass. However, quantitatively, the source–sink dynamics of the Lamto savanna seem to strongly depend on grass and tree preference for NH_4^+ versus NO_3^-, confirming that plant preference has important consequences at the ecosystem scale (Boudsocq et al., 2012). Moreover, Lamto savanna grasses show a limited soil exploration (de Parseval et al., 2016), whereas grasses can compete with trees for resource acquisition by exploring horizontally the soil in other savannas (February et al., 2013). It could be interesting to study how different foraging strategies can influence source–sink dynamics in other savanna types.

4.2 | Impact of the surface occupied by tree clumps on plant biomass

Tree biomass (in kg N per ha of savanna) tends to decrease with tree cover, a rather counter-intuitive result. Indeed, increasing this cover increases NO_3^- availability through nitrification stimulation. This causes important N losses as NO_3^- is more prone to leaching than NH_4^+ and can be lost through denitrification, which accordingly decreases the quantity of N available for trees (Appendix S4) and tree biomass at the savanna scale. Numerous studies demonstrated that changes from grass and tree dominance to tree dominance lead to an increase in soil C and N contents (Blaser et al., 2014; Zhou et al., 2018). Our results suggest that, at least in some savannas, woody encroachment induces large N losses and can lead savannas towards less conservative N cycling (Srikanthasamy et al., 2018). However, changes in fire regimes following woody encroachment (Devine et al., 2017) result in less intense fires, which are not taken into account in our model and could mitigate N losses through lower rates of tree biomass and leaf litter burning.

Our model suggests that increasing the surface occupied by tree clumps may reduce tree biomass even when the amount of roots outside tree canopy increases (Figure 4b). Simulations of the effects of a continuous gradient of the surface occupied by tree clumps and the quantity of tree roots in the open on tree biomass confirmed that tree biomass per ha of savanna is generally maximized for low values of tree cover (Appendix S7). Increasing tree dominance indeed reduces the surface occupied by the open area and therefore the tree access to this NH_4^+-rich area. This is confirmed by Appendix S9 showing that it is beneficial for trees to explore horizontally the open when tree cover is low. Our model thus uncovers potential feedback mechanisms that would be influential for tree–grass and savanna dynamics: increasing tree surface may increase N losses and decrease tree access to N. Such feedbacks and their long-term consequences for the future and stability of savannas should be further studied by empirical studies and modelling. In particular, in our model, we considered the proportion of tree roots in the open, the surface occupied by tree clumps and tree biomass as independent quantities while they are actually linked. For example, when the surface of tree clumps increases, the proportion of tree roots outside tree canopy likely decreases for a fixed root foraging strategy at the individual tree scale. Including such constraints in our model will be required to better predict the impact of horizontal N fluxes on savanna dynamics and tree–grass coexistence. Our predictions on tree–grass coexistence based on a non-spatial model (Konaré et al., 2019) should be adjusted using new versions of our two-patch model.

4.3 | Effects of spatial heterogeneity on the N budget of the Lamto savanna

Our results confirm that the availability of mineral N in the Lamto savanna changes from a high NH_4^+ availability in the open to a high NO_3^- availability under tree clumps, which is largely due to the control of nitrification by plants. Nevertheless, we found that total N losses, at the savanna scale, are higher in the open patch, which can be explained by the low tree cover used in our model. This low tree cover (15%) acts on N dynamics by reducing the total N fluxes under tree clumps and by increasing total N fluxes in the open. At the patch scale, N losses per unit of area are higher under tree clumps than in the open (Appendix S3) as NO_3^- stock is higher under tree clumps and is easily lost by leaching (Srikanthasamy et al., 2018). The tree biomass found in our model in cases of N enrichment under tree clumps is much higher than the biomass observed in the Lamto savanna (Abbadie et al., 2006). This shows that the sink effect due to tree root foraging outside tree clump can be extremely strong and also confirms that other mechanisms, not considered in our model, influence tree and clump dynamics. Clearly, disturbances such as fires are critical to tree and clump dynamics in humid West African savannas (Hochberg et al., 1994).

Considering high nitrification rates in both the open and tree clump patches increases NO_3^- availability in the open. This homogeneity causes larger N losses at the savanna scale than in the case of a heterogeneous nitrification rate taking into account nitrification inhibition by grasses (Appendix S6). As a result, spatial heterogeneity in N cycling, together with nitrification inhibition by grasses, leads to a more conservative system than spatial homogeneity by decreasing N losses and largely contributing to the balance of the N budget in the Lamto savanna and its primary production (Abbadie et al., 2006; Boudsocq et al., 2009). Moreover, in both cases (heterogeneity vs. homogeneity), the horizontal extension of tree roots in the open strongly contributes to nutrient uptake by trees. This confirms the importance of horizontal N fluxes on the N budget of the Lamto savanna but also the influence of the heterogeneity in N cycling and the preference for NH_4^+ versus NO_3^- on source–sink dynamics. Moreover, Appendix S8 illustrates the N budget of the Lamto savanna for the same surface occupied by the open and the tree clump patches ($\gamma = 0.5$). While symmetrical N inputs in both patches do not influence NH_4^+ and NO_3^- pools, this increase in tree cover increases the net horizontal N flux to tree clumps and NO_3^- losses per ha of savanna through leaching and denitrification. This confirms that spatial heterogeneity in nitrification fluxes due to nitrification control by plants plays an important role in the N budget and source–sink dynamics in the Lamto savanna.

Overall, our model considers that the two types of patch are homogeneous, which is of course not realistic. Depending on the proportion of the surface covered by tree (and tree density), the spatial distribution of trees and the extension of their roots, root distribution in the open and clump patches are unlikely to be homogeneous. In turn, this should modify horizontal N fluxes. These processes would require a spatially explicit individual-based model to be fully taken into account.

5 | CONCLUSIONS

Horizontal fluxes through soil exploration by tree roots constitute an important N source and contribute to soil fertility under tree canopies. To our knowledge, this study is the first one to assess the role of horizontal soil exploration by tree roots and to show its importance for N dynamics and plant biomass in savannas. In contrast to perennial grasses for which the limitation of soil exploration by roots improves their ability to control nutrient cycling (Abbadie et al., 1992; de Parseval et al., 2016; Lata et al., 2000), our study shows that extending soil exploration in the open increases tree biomass and makes up for the higher N losses through leaching and denitrification due to the increased nitrification under trees. Taken together, trees and grasses display contrasting root foraging strategies: restricted soil exploration for grasses to locally control nutrient availability versus horizontal proliferation of tree roots to benefit from nutrients outside their canopy. Moreover, our work confirms the results of other studies (Bisson et al., 2019) parameterizing meta-ecosystem models with field data and showing that nutrient transfers between patch types are very influential for the functioning of the meta-ecosystem and its components (Gravel et al., 2010). Taken together, we have shown that considering savannas as meta-ecosystems throws new insights on their functioning. For example, our model confirms that the key features of meta-ecosystem (Gounand et al., 2018), that is, the structure of the meta-ecosystem (here the percentage of surface occupied by tree clumps), fluxes between patches (due to root foraging) and heterogeneity between patches (nitrification stimulation vs. nitrification inhibition) are influential.

Little is known about the occurrence of nitrification-inhibiting grasses and nitrification-stimulating trees outside the Lamto savanna (Rossiter-Rachor et al., 2009). However, we hypothesize that our findings would hold for all humid savannas with nitrification-inhibiting grasses and non N-fixing trees. This includes, at least, all West African Guinean and possibly Sudanian savannas (that share many grass and tree species), Northern Australian and South American savannas invaded by African grasses such as *A. gayanus* and *Brachiaria* spp. Our model can readily be used to assess the generality of our results to these savannas but other mechanisms such as N fixation by trees (that could turn tree clumps into N sources) and herbivory, negligible in the Lamto savanna, but determinant for the functioning of other savannas (Sankaran et al., 2005) should then be taken into account. Taken together, our work shows that the framework of meta-ecosystems (Gounand et al., 2018; Loreau et al., 2003) can be usefully applied to savanna dynamics as it has already been suggested for tropical forests (Menge & Levin, 2017). Finally, our work will be relevant to analyse the influence of agroforestery practices (Isaac & Borden, 2019) and the impact of tree clearing in savannas on N cycling (Schmidt & Lamblea, 2002).

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AUTHORS' CONTRIBUTIONS

S.K., S.Bo., J.G., J.-C.L., X.R. and S.Ba. conceived the ideas and designed the methodology; S.K. analysed the model and wrote the manuscript with the contribution of all co-authors. All authors contributed critically to the draft and gave final approval for publication.

DATA AVAILABILITY STATEMENT

This is a modelling paper. All information regarding the model is included in the paper.

ORCID

Sarah Konaré https://orcid.org/0000-0001-5907-1469
Sébastien Barot https://orcid.org/0000-0002-5910-538X

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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