Effet du recyclage de l'azote sur la coexistence entre les herbes et arbres en savane

Sarah Faïké Konaré

MUSÉUM NATIONAL D'HISTOIRE NATURELLE

École Doctorale 227

Sciences de la Nature et de l'Homme : évolution et écologie

Année 2020

N°attribué par la bibliothèque

|_|_|_|_|_|_|_|_|_|_|_|_|_|_|

THÈSE

pour obtenir le grade de

DOCTEUR DU MUSÉUM NATIONAL D'HISTOIRE NATURELLE

Spécialité : Ecologie

présentée et soutenue publiquement par

Sarah KONARE

le 09 Juin 2020

Effet du recyclage de l'azote sur la coexistence entre herbes et arbres en savane

sous la direction de: **Dr Jacques GIGNOUX, Directeur de recherche, CNRS, Directeur de thèse**
Dr Sébastien BAROT, Directeur de recherche, IRD, Co-directeur de thèse

devant le jury: **Pr Julien GASPARINI, Professeur, Sorbonne Université, Président de jury**
Dr Caroline LEHMANN, Senior lecturer, Université d'Edimburgh, Rapporteur
Dr Tanguy DAUFRESNE, Chargé de recherche, INRA, Rapporteur
Dr Alexia STOKES, Directrice de recherche, INRA, Examinatrice
Dr Jacques GIGNOUX, Directeur de recherche, CNRS, Directeur de thèse
Dr Sébastien BAROT, Directeur de recherche, IRD, Co-directeur de thèse

Remerciements

Je tiens à remercier les membres du Jury pour avoir accepté de juger mon travail.

Je tiens à exprimer ma gratitude à mon directeur de thèse Jacques Gignoux pour la confiance que tu m'as accordée pour ce projet. Merci également pour ta disponibilité et tes conseils lors de nos réunions qui m'ont apporté pas mal de visibilité à certains moments de ma thèse. C'était sympa de pouvoir t'embêter directement à ton bureau quand j'avais une question.

Je tiens à remercier chaleureusement Sébastien Barot mon 2ème directeur de thèse pour m'avoir fait confiance depuis mon stage de M2. Merci pour ta disponibilité, pour tous tes conseils et d'être toujours venu aux nouvelles pour savoir où j'en étais. Merci pour m'avoir encouragé et m'avoir aidé à positiver quand j'avais des doutes sur la thèse. J'ai appris beaucoup auprès de toi.

Je voudrais remercier Xavier Raynaud mon co-encadrant de thèse. Je suis ravie d'avoir pu profiter de tes conseils, de ta disponibilité et de la pertinence de tes réflexions. J'ai beaucoup appris sur R grâce à toi.

Un immense merci à Jean-Christophe Lata mon autre co-encadrant de thèse. Merci pour tes conseils et pour ta disponibilité quand j'avais besoin de toi pour calculer mes paramètres. C'était toujours très agréable de discuter avec toi et d'apprendre toujours un peu plus sur vos aventures à Lamto. Je reconnais que t'entendre râler dans le couloir va me manquer.

Un grand merci à vous 4 pour votre générosité et votre sympathie. Ce n'était pas toujours évident de faire une réunion avec 4 encadrants mais c'était toujours dans une bonne ambiance et dans la bonne humeur.

Je tiens à remercier le ministère de l'enseignement supérieur et de la recherche scientifique de Côte d'Ivoire pour ma bourse de thèse.

Je remercie profondément Simon Boudsocq qui suit mes travaux depuis le début de ma thèse et qui a toujours su apporter des remarques très constructives à mon travail.

Un immense merci à Tristan pour ses précieux conseils à la fois pour mes présentations mais aussi son expérience de chercheur. Merci pour nos discussions toujours très enrichissantes. Graĉe a toi, je fais de beaux schémas.

Un grand merci à tous les autres membres de l'équipe EMS Yvan, David, Yoan, Eric, Emmanuel et Audrey pour leur sympathie, la bonne humeur et les échanges.

Merci à mes collègues du bureau Jean-Philippe, Amara, Anicet, Fatima et Chloé et ceux

qui ont déjà soutenu Tharaniya, Fulgence, Issoufou, Raphaël, Catalina et Ludovic. J'ai passé d'agréables moments avec vous. Tout cela va beaucoup me manquer. Merci pour tous ces moments d'échange, de discussion et de rires.

Merci à Paola et Catherine pour votre disponibilité. Vous avez toujours répondu présentes quand j'étais confrontée à certains soucis administratifs. Merci Paola pour avoir tout fait pour nous permettre d'entreprendre notre séjour en Afrique du Sud.

J'adresse mes sincères remerciements aux gestionnaires de l'iEES Carole, Johana et Véronique. Merci pour avoir toujours mis tout en oeuvre pour faciliter mes participations aux conférences. Ce qui n'était pas toujours évident étant rattachée au MNHN.

Je tiens à remercier chaleureusement Clarisse pour sa sympathie et sa bonne humeur. C'était toujours très agréable de discuter avec toi.

Merci au directeur de la station de Lamto Dr Yéo Kolo pour m'avoir reçu. C'était une belle expérience de terrain en plein milieu de la savane.
Je tiens à remercier également Diego et Firmin pour leur accueil à la station de Lamto.

Merci à mes précieux amis Carine, Corinne et André d'avoir toujours été là pour moi et de m'avoir encouragé et soutenu quand j'en avais besoin. Vous avez supporté mes doutes et mes angoisses et je reconnais que je pouvais être difficile par moment. Un merci spécial à toi André pour tous les coups de main et pour ta disponibilité à toute heure malgré le décalage horaire. Merci pour tout!

Merci à ma famille mes oncles et mes tantes pour leur soutien et leurs bénédictions.

Papa, maman je n'ai pas les mots pour vous remercier. Vous avez toujours cru en moi même dans les moments de doute et de manque de confiance vous avez toujours été là. Vous êtes des parents en or et je ne peux que rendre grâce à Dieu de vous avoir comme parents.

Merci mon Dieu d'avoir veillé sur moi et de m'avoir permis d'arriver jusque là.

À mon père et ma mère

À mon oncle Abdourahamane KONARE

Résumé

Les savanes sont caractérisées par la coexistence de deux types de plantes complètement différentes, les herbes et les arbres. Bien que la coexistence de plusieurs espèces soit assez difficile à expliquer, la séparation de niche entre les herbes et les arbres et la présence de perturbations permettent d'expliquer la coexistence herbe-arbre en savane. Dans les savanes humides, la productivité est aussi élevée que dans les forêts tropicales. Dans la savane de Lamto en Côte d'Ivoire, cette productivité est due en partie à la capacité des herbes à inhiber la nitrification. Les arbres peuvent également stimuler la nitrification. Ces deux stratégies suggèrent un partage de l'azote qui pourrait faciliter l'acquisition de l'azote entre les herbes et les arbres et donc favoriser leur coexistence. J'ai tenté de répondre à cette question par l'élaboration de modèles mathématiques.

La construction et l'analyse d'un modèle mathématique champ-moyen prenant en compte la capacité des plantes à contrôler la nitrification a permis de montrer que la coexistence entre les herbes et les arbres est possible quand les plantes ont des préférences différentes pour l'ammonium et le nitrate.

Un second modèle à deux patchs a été réalisé pour prendre en compte l'hétérogenéité spatiale au niveau des flux de nitrification due à l'inhibition de la nitrification par les herbes et la stimulation par les arbres. Ce modèle spatial inclut les échanges d'azote possible entre les deux patchs grâce à l'exploration racinaire des arbres hors canopée. L'analyse de ce modèle a permis de montrer l'effet de l'hétérogénéité spatiale et de l'exploration racinaire des arbres sur les flux d'azote et le bilan d'azote de la savane de Lamto. L'exploration horizontale des arbres hors de leur canopée leur permet permet de bénéficier de la forte disponibilité de l'ammonium hors canopée lorsqu'ils ont une préférence pour le nitrate sous canopée et pour l'ammonium hors canopée. Ces flux horizontaux pourraient contribuer à l'enrichissement en nutriments sous les canopées des arbres, ce qui peut influencer le bilan d'azote dans la savane de Lamto.

Le modèle à deux patchs a permis également d'étudier l'effet de l'hétérogéneité spatiale sur la compétition entre les herbes et les arbres pour l'azote. L'analyse du modèle montre que cette hétérogéneité spatiale peut faciliter la coexistence en réduisant la compétition entre les herbes et les arbres grâce au partage de l'azote minéral. La coexistence herbe-arbre est facilitée quand les herbes préfèrent l'ammonium et les arbres le nitrate sous canopée et l'ammonium hors canopée. Ce modèle permet de confirmer que le partage de l'azote minéral en deux formes ammonium et nitrate peut être considéré comme un mécanisme de coexistence entre les herbes et les arbres dans la savane de Lamto et probablement dans d'autres savanes humides d'Afrique de l'Ouest qui ont une végétation similaire à celle de Lamto.

Abstract

Savannas are characterized by the coexistence of two different types of plants, grasses and trees. Although the coexistence of many species remains difficult to explain, tree-grass coexistence in savannas can be explained by niche separation between trees and grasses and disturbances. The primary productivity is high in humid savannas as in tropical forests. In the Lamto humid savanna, this high productivity is partly due to the capacity of grasses to inhibit nitrification. Similarly, trees can stimulate nitrification. These two strategies suggest that nitrogen partitioning could facilitate nitrogen acquisition between trees and grasses and therefore can promote their coexistence. Using mathematical models, we investigated if nitrogen partitioning can be involved in tree-grass coexistence.

First, I built a mean-field model taking into account the capacity of plants to control nitrification. This first model allows showing that coexistence between trees and grasses is possible when trees and grasses have contrasted preferences for ammonium *versus* nitrate.

A second two-patch model has been implemented to take into account the spatial heterogeneity of nitrification fluxes due to the inhibition of nitrification by grasses and the stimulation of nitrification by trees. This model also includes nitrogen transfers between these two patches through the horizontal soil exploration by tree roots in the open. Model analysis allows determining the effect of spatial heterogeneity and soil exploration by trees on nitrogen fluxes and the nitrogen budget of the Lamto savanna. The horizontal soil exploration by tree roots in the open allows trees to benefit from the high ammonium availability in the open when they have a preference for ammonium in the open and for nitrate under their canopy. These horizontal fluxes could lead to the nutrient enrichment under tree canopy, which can influence the nitrogen budget in the Lamto savanna.

The two-patch model also allows studying the effects of spatial heterogeneity on the competition of trees and grasses for nitrogen. This models shows that spatial heterogeneity can facilitate coexistence by reducing the competition between trees and grasses through nitrogen partitioning. Tree-grass coexistence is favored when grasses prefer ammonium and trees prefer nitrate under tree canopy and ammonium in the open. This model allows confirming that mineral nitrogen partitioning under two forms ammonium and nitrate can be considered as a coexistence mechanism between trees and grasses in the Lamto savanna and likely in other West african humid savannas having the same plant species as the Lamto savanna.

Table of contents

List of figures

List of tables

1 Introduction

1.1 Plant-soil feedbacks

Interactions between plants and soil organisms are important for ecosystem functioning and particularly for plant community dynamics and ecosystem processes. Through their associations with soil organisms, plants can modify the physical, chemical and biological properties of their immediate environment (Harrison and Bardgett, 2010), which feedbacks to themselves. These interactions can be positive or negative depending on their influence on plant growth (Fig. 1.1) (Bever, 2003). An individual plant can modify the soil so as to increase (positive feedback) or decrease (negative feedback) their own growth rate relative to other species (Bever et al., 1997). Plant-soil feedbacks affecting individuals of the species modifying the soil are considered as direct, while those affecting another plant species are indirect (Van der Putten et al., 2013).

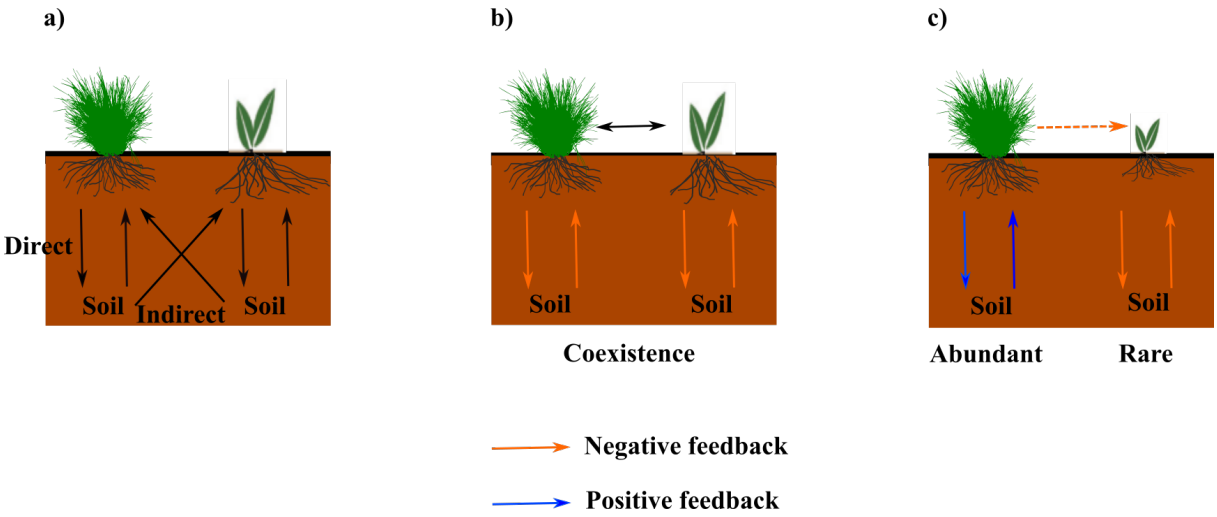

Figure 1.1 – Effects of plant-soil feedbacks on plant community organization (Adapted from Van der Putten et al. (2013)). Panel a) represents how plants can create direct and indirect feedbacks. Panel b) shows how negative feedback can influence species coexistence. Panel c) illustrates the effects of positive and negative feedbacks on plant abundance.

Most of the interactions between plants and soil microorganisms influence nutrient availability. **Positive plant-soil feedbacks** involve processes that directly stimulate soil microbial activity and hence increase the soil nutrient availability or enhance plant uptake (Klironomos, 2002). Rhizosphere microorganisms can control plant performance by influencing mineral solubilization, fixing nitrogen (N), or suppressing plant pathogens detrimental for plant growth (Bever et al., 1997). Associations between legumes and N-fixing bacteria have long been studied (Graham and Vance, 2000). Plants are able to fix atmospheric N through their symbiotic association with N-fixing bacteria rhizobia and in turn these bacteria benefit from plant carbon. Interactions between plants with mycorrhizal fungi are also important for plant acquisition by increasing the surface area of roots available to enhance nutrient capture (Hodge, 2006). By contrast, negative plant-soil feedbacks occurs through soil resource depletion (Berendse, 1994), the presence of soil pathogens and parasites (Packer and Clay, 2000) and the release of some toxic compounds (Armstrong and Armstrong,

2001). These effects can affect plant performance and can limit plant survival, growth and reproduction.

Some studies showed that plant-soil feedbacks can influence the coexistence of competitive species (Bever, 2003; Bever et al., 1997). Models developed by Bever et al. (1997) and Bever (2003) showed that positive feedbacks tend to increase dominance in plant communities and hence to reduce species diversity while negative feedbacks have been showed to enable coexistence of competing species. In the absence of negative feedbacks, the strength of interspecific competition increases. However, when negative feedbacks become more important, the negative effects on conspecific growth can favor the establishment of the competitor, which ultimately leads to an indirect reciprocal positive interaction between competing species (Bonanomi et al., 2005).Taken together, plant-soil feedbacks have important impacts on plant diversity and plant spatial distributions but can also affect ecosystem processes such as nitrogen cycling.

1.2 Nitrogen cycle

Nitrogen (N) is one of the most limiting factors of plant productivity in agricultural as well as in natural ecosystems (Miller and Cramer, 2004; Tilman, 1985; Vitousek and Howarth, 1991). The availability of N in ecosystems is strongly influenced by mineralization, nitrification and denitrification processes, besides other inputs and losses of N (Fig. 1.2).

1.2.1 Nitrogen inputs

Atmospheric depositions

Dry and wet depositions provide N inputs in both organic and mineral N (ammonium, NH_4^+ and nitrate, NO_3^-) forms. Plants can intercept the small particles contained in rains, fogs and dust depositions. The importance of atmospheric depositions in ecosystem N availability varies according to ecosystems and seasonality. N inputs by rains depend on rain frequency, rain intensity and N content in rain (Abbadie, 2006).

Biological fixation of nitrogen

N is incredibly abundant in the atmosphere, being its principal constituent, and virtually absent from the lithosphere. As a result, all N in soils originates from atmospheric N through N fixation: fixation is the entry point of N into the biosphere from its biggest natural pool. All other processes then appear as N recycling. N fixation can be achieved directly by (often rhizospheric) bacteria and archaea (non-symbiotic fixation) or in associations with plants (symbiotic N fixation). Non symbiotic fixation can contribute to the input of N to ecosystems. It mainly occurs in the rhizosphere (near of plant roots) where they can benefit from root exudates as energy source. Many studies show that the association of plants with N-fixing

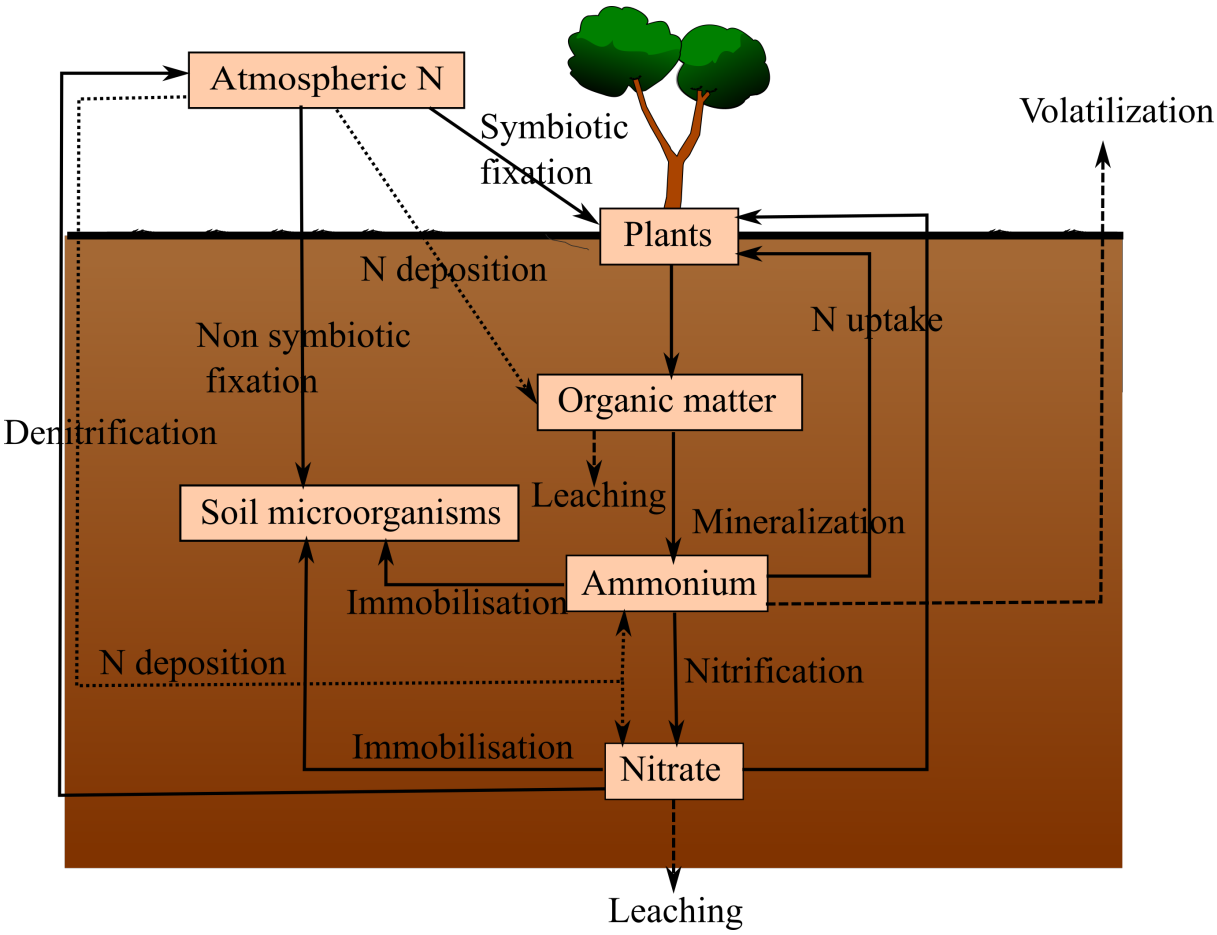

Figure 1.2 – Representation of N cycle. Dotted lines correspond to N inputs through atmospheric depositions and dashed arrows represent N losses

bacteria provides high N inputs in terrestrial ecosystems (Menge et al., 2009). This strategy allows to overcome N limitation in some ecosystems and can reduce competition for N between plants.

1.2.2 Nitrogen inputs through nitrogen transformations

Nitrogen mineralization

Mineralization is defined as the biological transformation of organic N into inorganic N in its dominant forms NH_4^+ and NO_3^- mainly by microorganisms. NH_4^+ is released from organic N through the action of microbial enzymes. The input of organic matter in the soil through plant litter (and to some extent root exudation) and dead animals provides both carbon and energy to microbial biomass to produce mineral N. Once produced, NH_4^+ can be assimilated by microorganisms (immobilization), transformed into NO_3^- by nitrifying organisms (nitrification) or directly absorbed by plants (Fig. 1.2). Mineralization can control N availability for plants (Binkley and Hart, 1989; Mengel, 1996; Powlson and Barraclough, 1993). Reich et al. (2001) through their study showed that the annual primary production in oak savanna stands is positively linked to soil net N mineralization.

Many factors positively influence the net N mineralization: soil temperature and humidity (Joshi et al., 2003), organic N content (Vervaet et al., 2002), plant biomass and soil pH (Falkengren-Grerup et al., 1998). In contrast, the lignin content of the litter (Joshi et al., 2003) as well as the soil C/N ratio (Côté et al., 2000; Janssen, 1996) negatively impact N mineralization.

Nitrification

Nitrification is the transformation of NH_4^+ into nitrite (NO_2^-) and then into nitrate (NO_3^-) by nitrifying microorganims (autotrophic bacteria or archaea). It is mainly controlled by the NH_4^+ availability and therefore tends to be correlated with N mineralization (Booth et al., 2005; Hart et al., 1997). In some cases, the uptake of NH_4^+ by microorganisms and plants can decrease the NH_4^+ availability for nitrifying organisms. Some studies showed that nitrification decreases with the soil C/N ratio or the lignin/N ratio of plant litter (Joshi et al., 2003). Other factors can influence nitrification such as soil temperature (Haynes, 1986), soil humidity and soil pH (Falkengren-Grerup et al., 1998; Li et al., 2007). The activity of nitrifying organisms also increases with oxygen concentration.

The nitrification process can be inhibited by specific molecules contained in plant organs (Kraus et al., 2003, 2004; Subbarao et al., 2007). These compounds tend to block the activity of at least the ammonia oxidisers, and thus prevent the oxydation of NH_4^+ into nitrite (Subbarao et al., 2007; Ward et al., 1997).

1.2.3 Nitrogen outputs

Fire

In fire-prone ecosystems (e.g. savannas, meditteranean shrublands, dry forests, etc.), fire contributes to losses of N by burning dry aboveground plant biomass and plant litter (Abbadie, 2006). These losses by volatilization strongly decrease the quantity of N that was supposed to enter the soil. Fire impacts on the N cycle depend on its intensity, itself dependent on the date of burning and of the amount of fuel (dry plant biomass).

A part of the nutrients contained in the burned biomass comes back to the soil through ash depositions (Abbadie, 2006). These depositions can have a positive effect on microorganisms by providing immediately available nutrients. This N supply acts as priming effect, i.e., an increase of the decomposition rate of soil organic matter after an input of easily available organic matter (Fontaine et al., 2003), and stimulates the activity of soil microorganisms and thus the regrowth of vegetation.

Herbivory

The uptake of plants by herbivores influence plant abundance, which can feedback on N cycling. An experiment of Belovsky and Slade (2000) showed that the density of grasshopers can increase the N availability for plants and thus increase plant biomass but their effects depend on the intensity of the insect herbivory. Some mammals spend a part of their time in or under tree canopy as they benefit from nesting sites, shade and food. By absorbing plant leaves, herbivores also absorb the N contained in these plants. A part of this N ingested by herbivores comes back to the soil through their dungs/urine, which can affect N cycling.

Nitrogen leaching

N leaching constitutes an important N loss from the soil. It occurs in the form of dissolved organic compounds (Van Breemen, 2002) or in the form of mineral N. As NH_4^+ is easily adsorbed by clay-organic matter complex (overall negatively charged), it is less mobile in the soil than NO_3^- (Marschner, 2008). This increases N losses through NO_3^- leaching (Jussy et al., 2004, 2000). Losses by leaching depend on the quantity of atmospheric inputs and the C/N ratio of humus (Gundersen et al., 1998), soil structure, the intensity of the mineralization, nitrification and microbial immobilization, and plant N uptake (Jussy et al., 2000).

Denitrification

In the absence or depletion of oxygen (anoxic conditions), nitrifying organisms can use NO_3^- for cellular respiration. This process, called denitrification, constitutes an important loss of NO_3^- in the gaseous form. Moreover, as in the nitrification process, an incomplete denitrification can also lead to the release of NO and N_2O in the atmosphere. Some studies showed that many parameters affect the activity of denitrifying bacteria, especially NO_3^- concentration (Fillery, 1983; Sigunga et al., 2002), the organic matter content of the soil (Brettar and Höfle, 2002), humidity, soil temperature, oxygen concentration and soil pH (Dannenmann et al., 2008).

Besides denitrification, N can be lost through the volatilization of ammoniac (NH_3), specifically in conditions of basic soil pH (Zia et al., 1999).

1.2.4 Plant preference for nitrogen forms

Plant preference for the different forms of N available in the soil is strongly influenced by many environmental and physiological conditions (Fig. 1.3) (Britto and Kronzucker, 2013).

The preference of plants for NH_4^+ versus NO_3^- depends on the plant species. N is generally absorbed in mineral form by plants. Some studies showed that the biomass of plants can increase depending on the mineral N form absorbed, which suggests a certain preference for one form compared to another one. Plants can directly assimilate NH_4^+, but a high NH_4^+ absorption can be toxic for some plants (Britto and Kronzucker, 2002). Indeed, NH_4^+ uptake

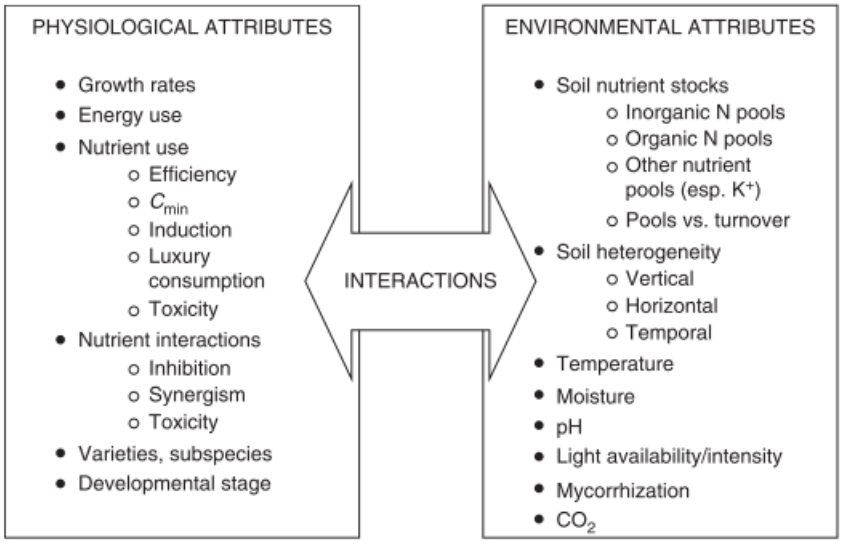

Figure 1.3 – Factors influencing plant N preference (From (Britto and Kronzucker, 2013))

induces the release of H^+ leading to soil acidification and reducing the availability of other nutrients such as Ca^{2+}, K^+ and Mg^{2+} (Britto and Kronzucker, 2002; Salsac et al., 1987). Moreover, because of its positive charge, NH_4^+ is easily adsorbed by clays and soil organic matter (Marschner, 2008; Subbarao et al., 2015), which can make it less mobile within the soil and unavailable to plants in dry soils. In contrast, as NO_3^- needs to be reduced before being assimilated by plants, NO_3^- uptake can be energically costly for plants (Konnerup and Brix, 2010). Compared toNH_4^++, the negative charge of NO_3^- makes it more mobile within the soil and therefore readily available for plants (Marschner, 2008) but also more prone to leaching. Because plants have different root transport systems for NH_4^+ and NO_3^-, NH_4^+ specialists can have atrophied NO_3^- uptake systems (Britto and Kronzucker, 2002) or atrophied NH_4^+ uptake systems for NO_3^- specialists (Kronzucker et al., 1997). For most plants, the mixture of both NH_4^+ and NO_3^- increases their growth compared to an uptake of only NH_4^+ or only NO_3^- (Britto and Kronzucker, 2002; Britto et al., 2001).

Some studies also showed that in areas where the mineralization of N is low, plants are able to absorb organic N (Chapin et al., 1993; Kielland, 1994; Schimel and Chapin, 1996). This has been observed in alpine (Ashton et al., 2010), boreal (Jones and Kielland, 2002) and tundra (McKane et al., 2002) plants. However, even if the proportion of organic and inorganic N forms absorbed by plants differ between plants, few studies tried to quantify it (Leadley et al., 1997). Some experimental studies showed that plants having preferences for different chemical N forms (organic and inorganic N) can coexist (Ashton et al., 2010; Kahmen et al., 2006; McKane et al., 2002). Plants can change their preference depending on the most available N form (Britto and Kronzucker, 2013). An empirical study of Houlton et al. (2007) showed that plants can change their N form by absorbing NO_3^- in dry sites and NH_4^+ in humid sites.

1.2.5 Effects of plant-soil feedbacks on nitrogen availability

Plant productivity is linearly correlated with soil N supply and N mineralization (Reich et al., 2001). Plants can influence soil N cycling by controlling N inputs and outputs. Indeed, plant architecture plays a major role in the interception of atmospheric N deposition, and hence on the input of this nutrient in the system (Lovett, 1991). Symbiotic fixation also contributes to N supply, and some studies show that its importance is dependent on plant biomass (Maron and Jefferies, 1999).

Plants can also exert a strong influence on the availability of soil N through the depletion of water and nutrients as well as the secretion of root exudates in the rhizosphere. N mineralization tends to be higher in the rhizosphere than in global soil (Colin-Belgrand et al., 2003; Priha and Smolander, 1999). Moreover, root exudates may also contain substances that inhibit the activity of nitrifying organisms (Subbarao et al., 2006, 2007). Plants roots can also influence nitrification by the absorption of NH_4^+, which indirectly decreases its availability for nitrifying microorganisms.

Some studies on forest species showed that mineralization and nitrification processes are influenced by plants (Augusto et al., 2002; Compton et al., 1998). The quantity and quality of litterfall vary according to plant species (Augusto et al., 2002; Nugroho et al., 2006), which can alter the rate of litter decomposition by microbial community and thus the rate of N mineralization and nitrification (Persson et al., 2000; Scott and Binkley, 1997). But these feedbacks on N availability strongly depend on microbial N loop as plant-available N is determined by what is released by soil microorganisms after microbial immobilization (Knops et al., 2002). Indeed, soil microorganisms have often been shown to be more competitive than plants for mineral N in the soil (Jackson et al., 1989). Plant litter inputs affect mineralization process by providing an easily degradable source of carbon for microorganisms.

Plants can also facilitate N recycling. In nutrient-limited ecosystems such as savannas, Abbadie et al. (1992) showed that grasses directly take up nutrients produced through mineralization of their own dead roots, which results in a very efficient recycling system. Taken together, plants can exert direct and indirect feedbacks on soil N cycling.

1.2.6 Effects of N recycling on ecosystem processes

The N availability strongly influence plant biomass and plant productivity at equilibrium (Knops et al., 2002; Menge et al., 2009) in N-limited ecosystems. Plant productivity largely depends on the balance between the N inputs and outputs, as well as on the recycling efficiency of the latter (Barot et al., 2007; De Mazancourt et al., 1998). Plant-soil feedbacks involve different mechanisms impacting the availability of soil N. The efficiency of nutrient recycling strongly influences primary production by limiting nutrient losses through leaching.

Barot et al. (2007) studied the effect of earthworms on N cycling through trophic and non trophic activities, and found that their long-term effects on plants and earthworm compartments depended on N recycling efficiency. The relative intensity of nutrient transformation processes of a limiting nutrient, such as mineralization and nitrification, plays a major role in its distribution within the different ecosystem compartments (Knops et al., 2002, 1997). The higher the recycling efficiency, the higher the proportion of nutrients conserved within the ecosystem along a complete N recycling loop.

Moreover, some organisms may impact N cycling by controlling N inputs and outputs (Knops et al., 2002). These effects can influence the efficiency of recycling of limiting nutrient, and the size of the different compartments involved in N cycling (plants, microorganisms, soil organic matter, etc.) as well as the plant productivity. Models of De Mazancourt et al. (1998) and de Mazancourt et al. (1999) suggest that the intensity of herbivory can increase the primary production through their influence on N cycling. This likely occurs in ecosystems frequently disturbed, such as savannas (De Mazancourt et al., 1998) where fires leads to the volatilization of N contained in the litter and in the aboveground herbaceous biomass through biomass burning. The assimilation of N by the herbivores is protected from fire and then returned to the soil in the forms of dung or when animals die, which allows a part of the N to be kept in the ecosystem.

Another model of Boudsocq et al. (2009) shows that plants may increase the primary production through their influence on N cycling. They found that nitrification inhibition induced by plants can increase primary production and the size of all ecosystem compartments. This particularly occurs when the recycling efficiency of NH_4^+ is higher than that of NO_3^-, i.e., when plant uptake is higher than N losses. This shows that plants can improve N conservation through their control of nitrification. **This study also suggested that N recycling through nitrification by plants could be one of the reasons explaining the high primary production in humid savannas**.

1.3 Savannas

Savannas are defined as ecosystems dominated by a dense layer of C_4 grasses and C_3 trees and are geographically present in both temperate or tropical areas (Fig. 1.4) (Scholes and Archer, 1997). They cover at least 12% of total land cover (Rutten et al., 2016). Savannas occupy areas with mean annual precipitations ranging between 300 and 1800 mm (Accatino et al., 2010), which influences the biomass of trees and grasses and leads to different types of savannas: dry savannas for rainfall approximately lower than 650-700 mm/yr and humid savannas for higher rainfall (Sankaran et al., 2005). Savannas can also be classified according to their tree-grass ratio from grassy savannas to savanna woodlands. Tropical savannas are considered as one of the most important biomes in tropical regions (Scholes and Archer,

1997) and represent about one half of Africa. Moreover, savannas provide many services very important for the often dense populations living in these areas: food supply, pasture for cattle, soils for agriculture, fuel wood.... They also host an important biodiversity that contributes to the economic development of some countries through hunting and tourism.

1.3.1 Coexistence mechanisms between trees and grasses in savannas

Several studies have tried to explain the coexistence of species on the same resources. Although widely debated in literature, the coexistence of species on the same resources is still difficult to explain (Barot and Gignoux, 2004) because of the principle of competitive exclusion that limits the number of competitive species to the number of limiting resources (Hardin, 1960). Indeed, this principle stipulates that coexistence of species on the same resources is not possible because the best competitor (the one which maintains at lowest level of resource availability) will exclude all the others on the long-term. The coexistence of plant species seems particularly more difficult to explain as they rely on the same resources (water, light, nutrients).

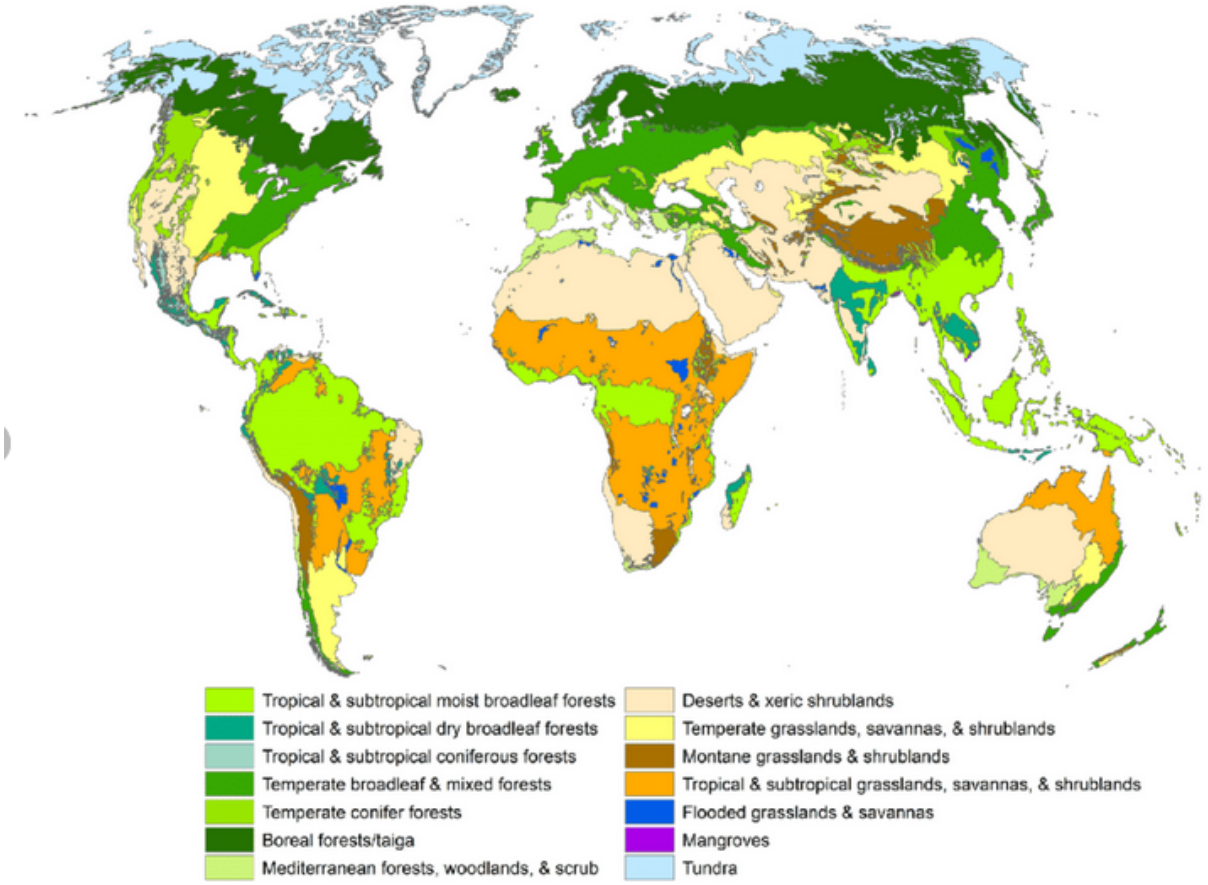

Figure 1.4 – Map of biome distribution showing savanna distribution over the world in orange (adapted from Olson et al. (2001))

However, although the theoretical importance of plant coexistence has raised and still generates numerous studies, the question of tree-grass coexistence and the stability of sa-

vannas is very important in the context of climate and land-use changes. The maintenance of savannas partly depends on the coexistence between trees and grasses. But this coexistence seems difficult to understand as trees tend to be more competitive for light than grasses. **Two theories are proposed to explain the coexistence between grasses and trees: resource-based mechanisms due to competition for water (Walker and Noy-Meir, 1982; Walter, 1971), and disturbance-based mechanisms affecting the demography of grasses and trees (Bond, 2005; Higgins et al., 2010; Jeltsch et al., 2000)**

Resource partitioning

Some studies suggest that resource partitioning through different root profiles between trees and grasses leads to long-term coexistence between them (Van Langevelde et al., 2003; Walker and Noy-Meir, 1982; Walter, 1971). Because of their high root density in the top soil layers, grass roots are more competitive than trees for surface water acquisition. Contrary to grasses, trees have the ability to reach deeper soil layers to increase their water acquisition (Schenk and Jackson, 2002). This niche separation through different root depths can enable coexistence between trees and grasses (Fig. 1.5) specially in dry savannas where water is the main limiting factor (Ward et al., 2013). Indeed, water partitioning reduces niche overlap and hence promotes the competition between trees and grasses. Water availability seems to be the main driver of woody cover structure in arid and semi-arid savannas (Sankaran et al., 2008). Indeed, in savannas where mean annual precipitation ranges between 150 and 650 mm, woody cover increases with rainfall. Some studies questioned the vertical root separation proposed by Walter (1971) and found that grass and tree roots can overlap in the same soil horizons (February and Higgins, 2010; Hipondoka et al., 2003), which can on the contrary increase the competition for resources.

Plants can influence soil water availability through water uptake and water infiltration. Some studies investigated the effects of the interactions between water and vegetation on plant dynamics and coexistence in savannas through spatially-explicit models (Baudena and Rietkerk, 2013; Gilad et al., 2007). While Gilad et al. (2007) assume that grasses and trees can increase water infiltration and evaporation in their model, Baudena and Rietkerk (2013) consider that only grasses increase water infiltration and tree shading favors water evaporation. The latter found that the infiltration feedback can lead to stable coexistence in arid savannas even without disturbances.

Other resources such as N and phosphorus (P) can be involved in competitive interactions between trees and grasses in savannas (Cramer et al., 2007; Okin et al., 2008). February and Higgins (2010) studied the distribution of tree and grass roots according to soil N and water availability in both in an arid (rainfall 547 mm/yr) and a humid (rainfall 737 mm/yr) savanna. They found that root distribution is positively correlated with soil N content but negatively correlated with soil moisture. Moreover, because most studies have focused on the

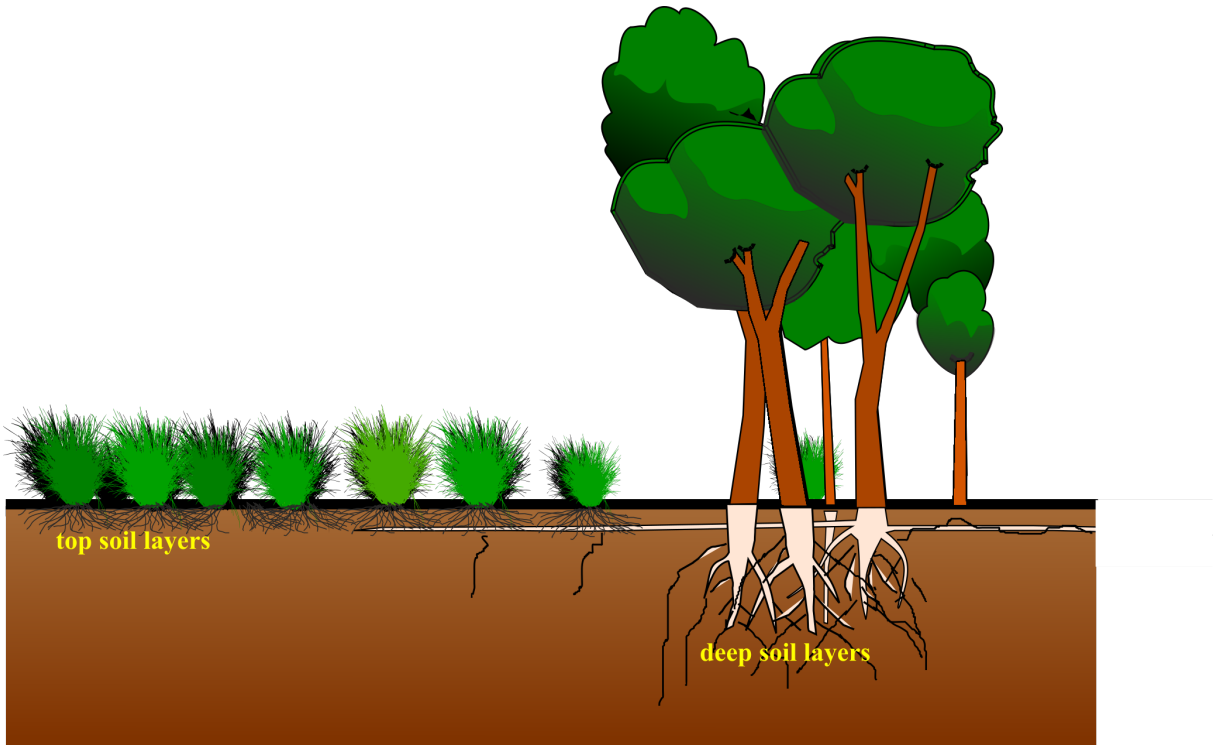

Figure 1.5 – Vertical root partitioning between trees and grasses

competition between trees and grasses for water, Donzelli et al. (2013) through a theoretical approach studied the conditions of coexistence between trees and grasses for soil water and mineral N in dry savannas (400-1000 mm/yr). They found that while grasses are more competitive than trees for water acquisition, trees are more competitive than grasses for N. This induces a coexistence between trees and grasses resulting from a balanced competition for water and N.

Disturbances

Savannas have long been considered as transition states between systems only dominated by grasses (grasslands) and systems completely dominated by trees (forests) considered as stable states (Higgins et al., 2000; Jeltsch et al., 2000; Sankaran et al., 2004). At low values of rainfall (< 700 mm), maintenance of savannas seem to be water-dependent as trees strongly increase with rainfall (Bond et al., 2003; Sankaran et al., 2008). But at intermediate values of rainfall (1000-2500 mm), Staver et al. (2011b) showed that two alternative stable states are possible: forests and savannas. But the presence of disturbances (Fig. 1.6), and particularly fire, tend to maintain savannas and thereby prevent forest establishment (Staver et al., 2011a,b). Experiments of long-term fire exclusion between burned and unburned sites in arid and humid areas led to an increase of tree cover and biomass in humid savannas (Bond et al., 2003). In contrast, the increase of tree cover observed after exclusion in arid savannas confirms that other mechanisms such as water competition explain tree-grass coexistence. Savannas are thus viewed as unstable systems in which disturbances allow to regulate the tree-grass ratio and thus promote tree-grass coexistence (Higgins et al., 2000; Jeltsch et al.,

1998). Fire is considered as one of the main drivers of savanna structure (Bond et al., 2003; Higgins et al., 2000; Sankaran et al., 2005). It acts as a bottleneck in tree demography as it increases the mortality of tree seedlings and saplings, which reduces their chance of recruitment into the adult stage (Gignoux et al., 2009; Higgins et al., 2000; Jeltsch et al., 2000). Fire intensity partly depends on the biomass of flammable grasses used as fuel loads (Archibald et al., 2012).

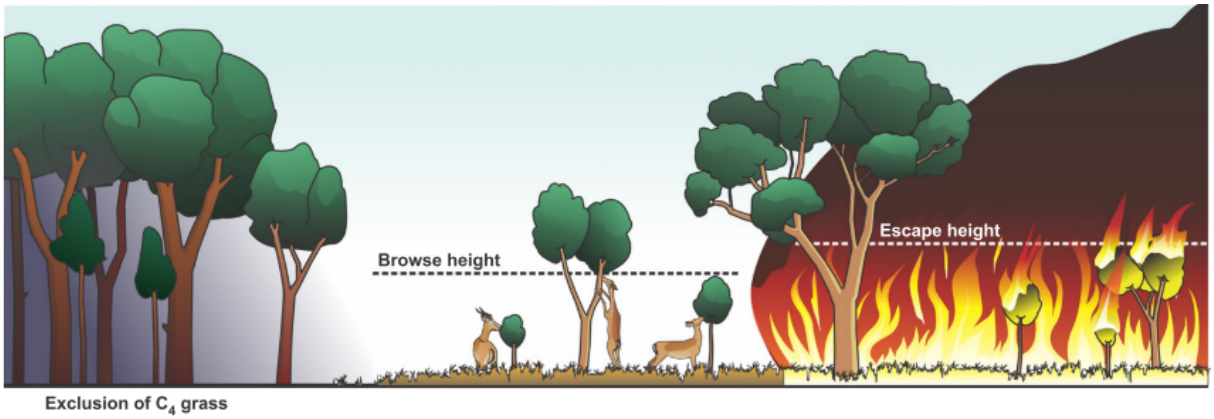

Figure 1.6 – Disturbance-based mechanisms of tree-grass coexistence: fire and browsing (from Osborne et al. (2018))

Similarly, herbivores such as grazers and browsers respectively reduce grass and tree biomass. Grazers (i.e., eating grasses) decrease grass biomass, which in turn decreases fire intensity and results in an increase of woody plants (Sankaran et al., 2008). In the same way, large mammals browsing (i.e., eating tree leaves) and trampling can reduce tree biomass (Osborne et al., 2018), which can favor a more open savanna state dominated by grasses. The effects of herbivores on the density of grasses and trees can directly reduce competition or indirectly induce feedbacks with fire (Sankaran et al., 2008; Van Langevelde et al., 2003).

Many savanna models have explicitly studied the effects of fire (in which fire intensity depends on flammable grasses) (Beckage et al., 2009; D'Odorico et al., 2006; Hochberg et al., 1994) or fire and herbivory on savanna dynamics (Van Langevelde et al., 2003). Savanna trees are characterized by their capacity to resprout after aboveground biomass removal because of their stored resources in belowground compartments (Gignoux et al., 2009). This allows some trees to produce a sufficient aboveground biomass to escape the fire and browsing traps (Higgins et al., 2007, 2000). Dynamic global vegetation models (DGVM) based on ecophysiological processes are also considered as interesting tools to study the effects of fire and herbivory on tree and grass dynamics (Scheiter and Higgins, 2009, 2012). Although plant competition for light and water is taken into account to predict tree-grass dynamics in these models, the effects of soil nutrients in plant growth are so far neglected (Baudena et al., 2014). DGVM are also used to predict vegetation structure in response to elevated concentrations of CO_2 and land use change (Scheiter and Savadogo, 2016).

Compared to studies that considered only resource-based mechanisms (Walter, 1971) or disturbance-based mechanisms (D'Odorico et al., 2006), other studies highlight the necessity to take into account both resource competition and disturbances to understand tree-grass coexistence (Sankaran et al., 2004). Van Langevelde et al. (2003) and Accatino et al. (2010) modelled the savanna vegetation through system of equations to study the influence of the vertical niche separation and disturbances. Van Langevelde et al. (2003) showed that interactions between fire and herbivores strongly influence tree-grass dynamics and are involved in the occurrence of alternative stable states. Accatino et al. (2010) suggest that both niche separation and disturbances simultaneously affect tree-grass coexistence but the dominance of each mechanism in tree-grass coexistence varies between dry and wet savannas. In particular, competition for water seems more relevant in dry savannas while in humid savannas high level of fire or herbivory is necessary to maintain them. By using a deterministic model, (Scheiter and Higgins, 2007) partition aboveground and belowground compartments and show how competition between trees and grasses for resources interacts with fire and herbivores. They found that depending on the intensity of root competition for soil resources, coexistence can be possible in the absence of disturbances and light competition. Bond (2005) classified the determinants of vegetation in three categories: the green world (the vegetation is driven by climate), the brown world (vegetation is controlled by herbivores) and the black world (fire is the main driver of vegetation distribution). However, nutrient availability is also important for plant growth.

1.4 The Lamto savanna

The Lamto savanna is one of the most studied ecosystems in the world (Abbadie et al., 2006). The Lamto Natural Reserve is located in Côte d'Ivoire, particularly 180 km north of Abidjan (6°13 N, 5° 02W) (Fig. 1.7). The Lamto ecological station was created in 1961 and covers approximately 2.500 ha (Fig. 1.8). Besides, this site is located in a transition zone between a forest zone (south) and the savanna (north).

1.4.1 Climate

The Lamto climate is tropical wet with a mean annual temperature of 29°C and the precipitation averages 1200 mm/ yr (Fig. 1.9). The climate is divided in four seasons: a long dry season from December to February, a long rainy season from March to July, a short dry season in August and a short rainy season from September to November (Abbadie et al., 2006).

1.4.2 Soil

Because of their low availability of organic matter and nutrients (N, P, K^+), the soils of the Lamto savanna are often viewed as soils with a low agronomic value (Abbadie et al., 2006). Four main types of soils can be distinguished in the Lamto savanna:

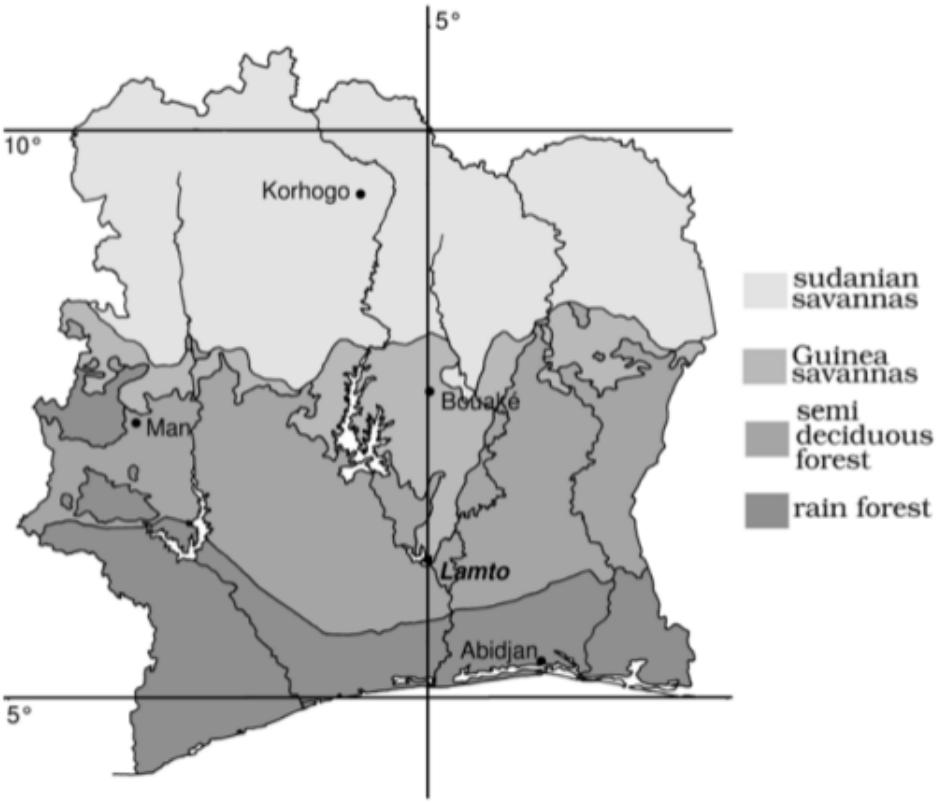

Figure 1.7 – Location of the Lamto savanna (from Abbadie et al. (2006))

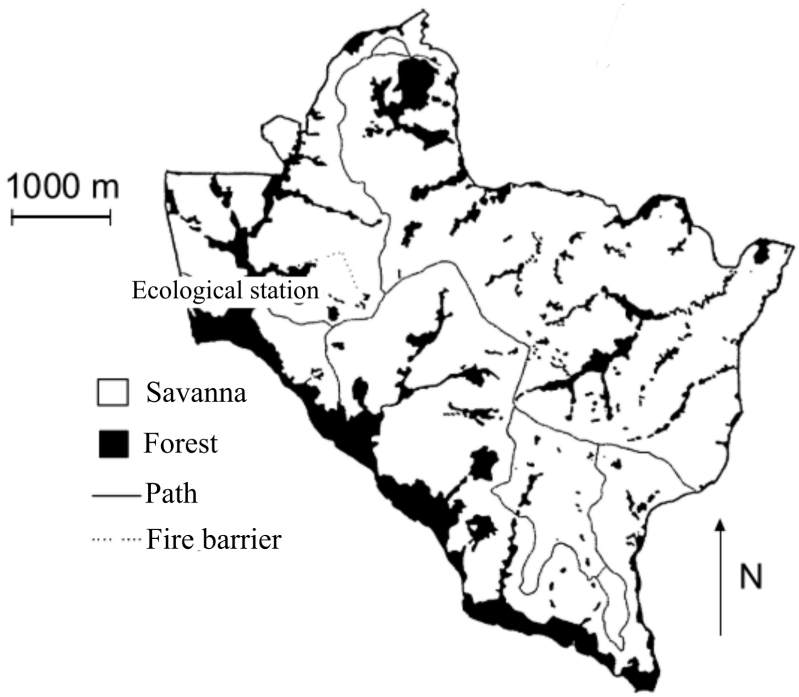

Figure 1.8 – Map of the Lamto savanna (from Gautier (1990))

- leached tropical ferruginous soils characterized by their high proportion of sand (from 40 to 60% of coarse sand and from 20 to 30% of fine sand), the low amount and quality of clays (illite and kaolinite), very poor in Ca^{2+}, K^{+}, P and humus.
- tropical ferruginous soils: they differ in greater impermeability and a higher content of

silt. They are more prone to erosion.

- hydromorphic soils: These soils contains surface horizons rich in silt while deep horizons are sandy. They are regularly waterlogged.
- Vertisols on amphibolites: compared to ferruginous soils, they are rather clay-silty, rich in organic matter (from 3 to 6%) up to 20 cm depth and have a high proportion of clays (from 18 to 25% in the surface horizons, mainly montmorillonites).

1.4.3 Vegetation

The Lamto vegetation is a mosaic of savannas and gallery forests (Abbadie et al., 2006). The vegetation in this site is composed of perennial grasses (Poaceae) intermiwed with small trees and tall palm trees. It is defined by three strata: an herbaceous stratum, a shrubby stratum and a tree stratum (Abbadie et al., 2006) (Fig. 1.10). Grasses mainly grow in tussocks separated by bare soil. Trees are often clumped as the low biomass of grasses due to tree shading increases their resistance to fire (Fig. 1.11).

The herbaceous stratum is largely composed of perennial grasses such as *Andropogon canaliculatus*, *Andropogon schirensis*, *Hyparrhenia diplandra* and *Loudetia simplex*. The dominant tree species (90% of the woody layer) in the Lamto savanna are *Crossopteryx febrifuga*, *Cussonia arborea*, *Bridelia ferruginea* and *Piliostigma thonningii*.

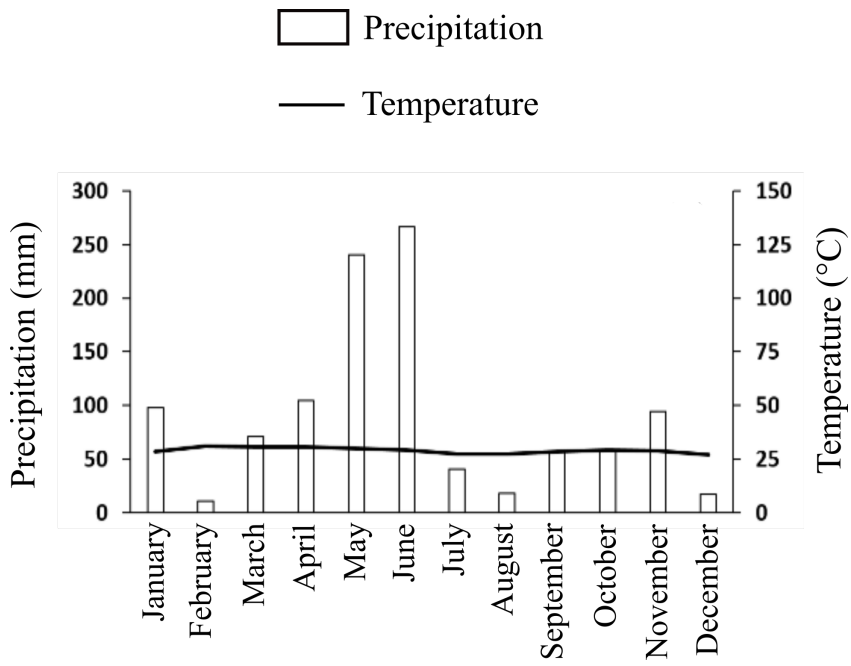

Figure 1.9 – Diagram of mean annual precipitation and mean annual temperature in 2017 (data from geophysical station of Lamto)

Figure 1.10 – Lamto savanna landscape showing the different strata herbaceaous, shrubs and Palm trees (photo Sébastien Barot)

1.4.4 Fire

Fire strongly contributes to the structure of the Lamto savanna. It is set by technicians and students of the reserve and generally occurs in mid-January (Fig. 1.12). It burns a large part of aboveground herbaceous vegetation (about 80%) and a part of tree seedlings and saplings (Abbadie et al., 2006). In the Lamto savanna, the rapid regrowth of grasses is due to their perennial root system (Fig. 1.13).

Figure 1.11 – Aerial view showing the structure of the Lamto savanna (photo Sébastien Barot)

Figure 1.12 – Fire in the Lamto savanna (photo Sébastien Barot)

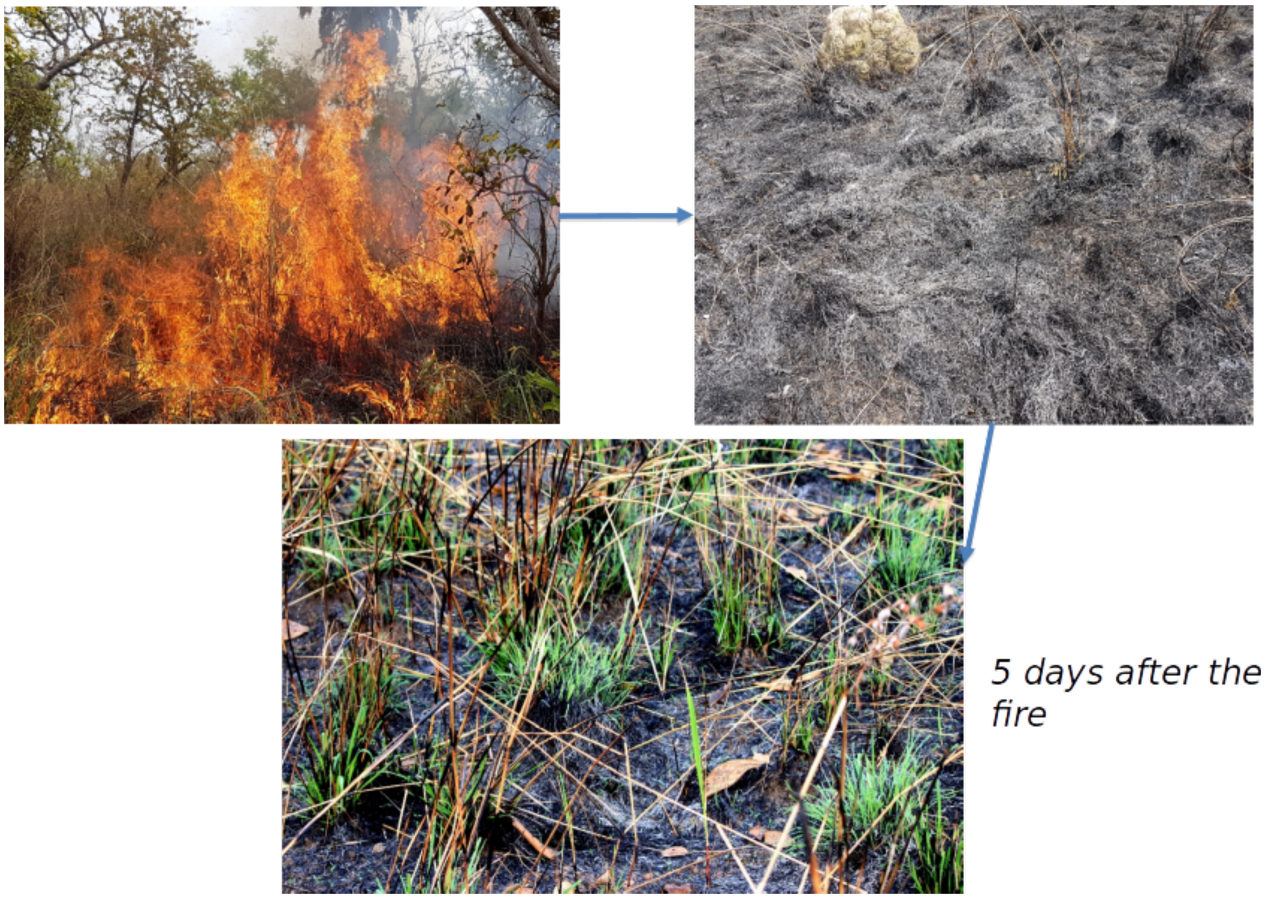

Figure 1.13 – Regrowth of grasses after fire (photo Jean-Christophe Lata 2017)

1.5 Nitrogen cycle in the Lamto savanna

As many savannas, the Lamto savanna is strongly constrained by fire, rainfall seasonality and nutrient-poor soils but the total primary production is about 30 $t\ ha^{-1}\ yr^{-1}$ (Abbadie et al., 2006, 1992). This high primary production is linked to N cycle.

1.5.1 Nitrogen inputs

In the Lamto savanna, wet depositions are estimated between 6.5 and 6.6 kgN $ha^{-1}\ yr^{-1}$ for NH_4^+ and 1.4 and 2.4 kgN $ha^{-1}\ yr^{-1}$ for NO_3^- (Abbadie, 2006). A large part of N inputs through wet deposition is in the form of organic N (14 kgN $ha^{-1}\ yr^{-1}$). The quantity of NH_4^+ and NO_3^- provided by dusts (dry depositions) is about 10 kgN $ha^{-1}\ yr^{-1}$ for NH_4^+ and 4 kgN $ha^{-1}\ yr^{-1}$ for NO_3^-. (Abbadie, 2006).

Furthermore, the biological fixation of N constitutes an important source of N in the Lamto savanna through the fixation by cyanobacteria that develop algal crusts between grass tussocks and asymbiotic fixation by free N-fixing bacteria (Abbadie, 2006; Abbadie et al., 1992). In some savannas, the presence of *Acacias* species can contribute to N inputs through symbiotic N fixation (Cramer et al., 2010). But in the Lamto savanna, symbiotic N fixation is negligible in the budget of the Lamto savanna as the biomass of legumes is very low (because of the annual fire) and the absence of N-fixing tree species (Abbadie, 2006).

1.5.2 Nitrogen inputs through nitrogen transformations

In the Lamto savanna, (Mordelet, 1993) and Srikanthasamy et al. (2018) showed that mineralization rates and soil organic N content are higher under tree canopy than in the open. The effects of trees on soil humidity and temperature and the high organic N content improve the soil mineralization rate under tree canopy, which can influence microbial activity and can consequently create small-scale heterogeneity. Moreover, grass roots under tufts directly take up mineral N coming from the decomposition of dead roots spatially close to living roots. This strategy induces an efficient nutrient recycling that minimizes N losses and therefore makes the Lamto savanna functioning particularly conservative (Abbadie, 2006; Abbadie et al., 1992).

The dominant grass species of the Lamto savanna are able to inhibit nitrification (Lata et al., 2004; Srikanthasamy et al., 2018). This capacity is viewed as a strategy to use N efficiently and to reduce N losses. In contrast, the nitrification activity is higher under tree canopy than under grasses. Srikanthasamy et al. (2018) showed that archaea are more involved in the nitrification process than bacteria. Experiments comparing bare soil and soil under trees suggest a stimulation of nitrification by trees (Srikanthasamy et al., 2018). This leads to a local heterogeneity in nitrification with low nitrification under grasses and high nitrification under trees.

1.5.3 Nitrogen losses

In the Lamto savanna, fire occurs during the dry season and about 80% of the total surface is burned (Abbadie, 2006). Early fires occurring at the beginning of the dry season when aboveground biomass is not dry induce a low N volatilization. In the same way, late fires occurring at the beginning of the growing season can favor higher N losses (Abbadie et al., 2006). Although a part of the N present in the leaves is transferred in perennial tissues of plants during the dry season, fire represents a large N loss on the long-term. Losses by fire are estimated between 9 and 24 kg N/ha/yr for grasses and between 7.3 and 12.6 kg N/ha/yr for trees.

A high pressure of herbivores can be stressful for plants. Some plants have developed defense strategies such as spines to limit herbivore uptake (Charles-Dominique et al., 2016). Other plants tend to tolerate grazing and attract herbivores by investing more in their highly palatable leaves. This creates nutrient-rich areas called grazing lawns (Bonanomi et al., 2008; Hempson et al., 2015). However, in the Lamto savanna, the density of large herbivores is low, which reduces the impacts of herbivory on N cycling (Le Roux et al., 2006).

Leaching also contributes to N losses. The inhibition of nitrification by grasses induces a low availability of NO_3^-, which reduces NO_3^- losses. But the high nitrification under trees and the sandy soil of Lamto savanna can increase losses by leaching under tree clumps. Contrary to NH_4^+ that is easily adsorbed by soil and less prone to leaching, a part of soil organic N can be lost through leaching.

The low availability of NO_3^- under grasses in the Lamto savanna reduces the NO_3^- availability for denitrifying organisms. Denitrification is 9 times higher under tree canopy than under grasses as trees can stimulate nitrification (Srikanthasamy et al., 2018).NH_4^+ volatilization is a potential N loss but it is negligible in Lamto soils because of the slightly acid soil pH (Abbadie, 2006).

1.6 Research problematic and questions

The aim of my PhD was to determine the role of the competition for the N resource in the functioning of savannas. The coexistence between trees and grasses in savannas is still not perfectly understood as trees and grasses are two completely different types of plants. In the Lamto savanna, a humid savanna in Côte d'Ivoire (Abbadie et al., 2006), the high primary productivity is partly due to the biological nitrification inhibition (BNI) by dominant grass species. This BNI by grasses occurs through the release of root exudates that impedes nitrifying organisms activity (Lata et al., 2004, 2000; Srikanthasamy et al., 2018; Subbarao et al., 2007). This strategy reduces NO_3^- availability and thus N losses as keeping N in NH_4^+ form decreases NO_3^- losses by leaching and denitrification. In the same way, it has been

shown that trees can stimulate nitrification (Srikanthasamy et al., 2018).

Taken together, these strategies developed by plants induce a spatial partitioning of N into two mineral forms NH_4^+ and NO_3^-. This spatial partitioning suggests different plant preference for NH_4^+ versus NO_3^- in order to promote their coexistence. A model developed by Boudsocq et al. (2012) showed that different plant preferences for NH_4^+ and NO_3^- can influence coexistence of two plant species but that this influence depends on their impact on nitrification. This result is particularly interesting in our case as different plant preference for NH_4^+ versus NO_3^- could be influential for tree-grass coexistence. **By using a modeling approach, the objective of my PhD is to apply this mechanism of coexistence to tree-grass competition in savannas. More specifically, I have tried to determine whether mineral N partitioning between trees and grasses can facilitate their coexistence, and how nitrification inhibition by grasses and stimulation by trees impact this effect.**

The first step of my study is to determine under which conditions the capacity of grasses to inhibit nitrification and different preferences for NH_4^+ and NO_3^- between trees and grasses can contribute to tree-grass coexistence. To do so, I developed a non-spatialized mean-field model based on Boudsocq et al. (2012) model to test the impact of competitive interactions between trees and grasses on N acquisition. In this model, the resource is shared by the two plants types and compared different mathematical formalisms to describe nitrification. I also compared a first case where nitrification is independent from plant biomass and a second case where nitrification depends on plant biomass.

As nitrification inhibition by grasses and nitrification stimulation by trees induce a spatial heterogeneity in the relative availability of NH_4^+ and NO_3^-, the second step of my study was to build a two-patch model taking into account this spatial heterogeneity in nitrification. This model considers a patch of open area characterized by a low nitrification rate and a patch of tree clump characterized by a high nitrification rate. I also included in the model the ability of savannas trees to extend their root in the surrounding open area (Belsky, 1994). This can lead to horizontal N fluxes between both patches that could impact N dynamics. **The objectives of this model are two-fold**: to test **(1)** the effects of spatial heterogeneity of nitrification on N fluxes and the budget of the Lamto savanna and **(2)** the effects of this spatial heterogeneity on tree-grass coexistence. By controlling nitrification, plants can influence the availability of NH_4^+ and NO_3^-, which can subsequently develop their capacity to absorb NH_4^+ and NO_3^-. These different plant preference for NH_4^+ and NO_3^- can influence ecosystem properties by increasing plant productivity and biomass and minimizing mineral N losses (Boudsocq et al., 2012). Besides, the heterogeneity of nitrification can locally create nutrient-rich patches, which can influence soil fertility and allow for plants to overcome nutrient limitation. All these parameters should influence N dynamics at the patch and at the savanna scales.

The manuscript thesis is presented in the form of articles. The different chapters are therefore organized and formatted in the form of research articles that are or will be published in scientific journals. Besides the introduction part, I present my results in three sections:

- A chapter on the results of the mean-field model (published in Ecosystems, Konaré et al. (2019)),
- A chapter presenting the results of the two-patch model on N fluxes (submitted to Functional Ecology, in revision),
- A last chapter on the results of the two-patch model on tree-grass coexistence.

Finally, we propose a general discussion of all results and the perspectives of the study.

Bibliography

Abbadie, L. (2006). Nitrogen inputs to and outputs from the soil-plant system. In *Lamto: structure, functioning, and dynamics of a savanna ecosystem*, pages 255–275. New York: Springer.

Abbadie, L., Gignoux, J., Le Roux, X., and Lepage, M. (2006). *Lamto: structure, functioning, and dynamics of a savanna ecosystem*. New York: Springer.

Abbadie, L., Mariotti, A., and Menaut, J.-C. (1992). Independence of savanna grasses from soil organic matter for their nitrogen supply. *Ecology*, 73(2):608–613.

Accatino, F., De Michele, C., Vezzoli, R., Donzelli, D., and Scholes, R. J. (2010). Tree–grass coexistence in savanna: interactions of rain and fire. *Journal of theoretical biology*, 267(2):235–242.

Archibald, S., Staver, A. C., and Levin, S. A. (2012). Evolution of human-driven fire regimes in africa. *Proceedings of the National Academy of Sciences*, 109(3):847–852.

Armstrong, J. and Armstrong, W. (2001). An overview of the effects of phytotoxins on *Phragmites australis* in relation to die-back. *Aquatic Botany*, 69(2-4):251–268.

Ashton, I. W., Miller, A. E., Bowman, W. D., and Suding, K. N. (2010). Niche complementarity due to plasticity in resource use: plant partitioning of chemical n forms. *Ecology*, 91(11):3252–3260.

Augusto, L., Ranger, J., Binkley, D., and Rothe, A. (2002). Impact of several common tree species of european temperate forests on soil fertility. *Annals of forest science*, 59(3):233–253.

Barot, S. and Gignoux, J. (2004). Mechanisms promoting plant coexistence: can all the proposed processes be reconciled? *Oikos*, 106(1):185–192.

Barot, S., Ugolini, A., and Brikci, F. B. (2007). Nutrient cycling efficiency explains the long-term effect of ecosystem engineers on primary production. *Functional Ecology*, 21:1–10.

Baudena, M., Dekker, S. C., van Bodegom, P. M., Cuesta, B., Higgins, S. I., Lehsten, V., Reick, C. H., Rietkerk, M., Scheiter, S., Yin, Z., et al. (2014). Forests, savannas and grasslands: bridging the knowledge gap between ecology and dynamic global vegetation models. *Biogeosciences Discussions*, 11(6):9471–9510.

Baudena, M. and Rietkerk, M. (2013). Complexity and coexistence in a simple spatial model for arid savanna ecosystems. *Theoretical Ecology*, 6(2):131–141.

Beckage, B., Platt, W. J., and Gross, L. J. (2009). Vegetation, fire, and feedbacks: a disturbance-mediated model of savannas. *The American Naturalist*, 174(6):805–818.

Belovsky, G. and Slade, J. (2000). Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences*, 97(26):14412–14417.

Belsky, A. J. (1994). Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology*, 75(4):922–932.

Berendse, F. (1994). Ecosystem stability, competition, and nutrient cycling. In *Biodiversity and ecosystem function*, pages 409–431. Springer.

Bever, J. D. (2003). Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New phytologist*, 157(3):465–473.

Bever, J. D., Westover, K. M., and Antonovics, J. (1997). Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology*, 85(5):561–573.

Binkley, D. and Hart, S. C. (1989). The components of nitrogen availability assessments in forest soils. In *Advances in soil science*, pages 57–112. Springer.

Bonanomi, G., Giannino, F., and Mazzoleni, S. (2005). Negative plant–soil feedback and species coexistence. *Oikos*, 111(2):311–321.

Bonanomi, G., Rietkerk, M., Dekker, S. C., and Mazzoleni, S. (2008). Islands of fertility induce co-occurring negative and positive plant-soil feedbacks promoting coexistence. *Plant Ecology*, 197(2):207–218.

Bond, W., Midgley, G., and Woodward, F. (2003). The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology*, 9(7):973–982.

Bond, W. J. (2005). Large parts of the world are brown or black: a different view on the 'green world'hypothesis. *Journal of Vegetation Science*, 16(3):261–266.

Booth, M. S., Stark, J. M., and Rastetter, E. (2005). Controls on nitrogen cycling in terrestrial ecosystems: a synthetic analysis of literature data. *Ecological monographs*, 75(2):139–157.

Boudsocq, S., Lata, J.-C., Mathieu, J., Abbadie, L., and Barot, S. (2009). Modelling approach to analyse the effects of nitrification inhibition on primary production. *Functional Ecology*, 23(1):220–230.

Boudsocq, S., Niboyet, A., Lata, J. C., Raynaud, X., Loeuille, N., Mathieu, J., Blouin, M., Abbadie, L., and Barot, S. (2012). Plant preference for ammonium versus nitrate: a neglected determinant of ecosystem functioning? *The American Naturalist*, 180(1):60–69.

Brettar, I. and Höfle, M. G. (2002). Close correlation between the nitrate elimination rate by denitrification and the organic matter content in hardwood forest soils of the upper rhine floodplain (france). *Wetlands*, 22(2):214–224.

Britto, D. T. and Kronzucker, H. J. (2002). NH_4^+ toxicity in higher plants: a critical review. *Journal of plant physiology*, 159(6):567–584.

Britto, D. T. and Kronzucker, H. J. (2013). Ecological significance and complexity of N-source preference in plants. *Annals of botany*, 112(6):957–963.

Britto, D. T., Siddiqi, M. Y., Glass, A. D., and Kronzucker, H. J. (2001). Futile transmembrane NH_4^+ cycling: a cellular hypothesis to explain ammonium toxicity in plants. *Proceedings of the National Academy of Sciences*, 98(7):4255–4258.

Chapin, F. S., Moilanen, L., and Kielland, K. (1993). Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge. *Nature*, 361(6408):150–153.

Charles-Dominique, T., Davies, T. J., Hempson, G. P., Bezeng, B. S., Daru, B. H., Kabongo, R. M., Maurin, O., Muasya, A. M., Van der Bank, M., and Bond, W. J. (2016). Spiny plants, mammal browsers, and the origin of african savannas. *Proceedings of the National Academy of Sciences*, 113(38):E5572–E5579.

Colin-Belgrand, M., Dambrine, E., Bienaimé, S., Nys, C., and Turpault, M.-p. (2003). Influence of tree roots on nitrogen mineralization. *Scandinavian journal of forest research*, 18(3):260–268.

Compton, J. E., Boone, R. D., Motzkin, G., and Foster, D. R. (1998). Soil carbon and nitrogen in a pine-oak sand plain in central massachusetts: role of vegetation and land-use history. *Oecologia*, 116(4):536–542.

Côté, L., Brown, S., Paré, D., Fyles, J., and Bauhus, J. (2000). Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixedwood. *Soil Biology and Biochemistry*, 32(8-9):1079–1090.

Cramer, M. D., Chimphango, S. B., Van Cauter, A., Waldram, M., and Bond, W. (2007). Grass competition induces N_2 fixation in some species of african acacia. *Journal of Ecology*, 95(5):1123–1133.

Cramer, M. D., Van Cauter, A., and Bond, W. J. (2010). Growth of n2-fixing african savanna acacia species is constrained by below-ground competition with grass. *Journal of Ecology*, 98(1):156–167.

Dannenmann, M., Butterbach-Bahl, K., Gasche, R., Willibald, G., and Papen, H. (2008). Dinitrogen emissions and the N_2: N_2O emission ratio of a rendzic leptosol as influenced by ph and forest thinning. *Soil Biology and Biochemistry*, 40(9):2317–2323.

De Mazancourt, C., Loreau, M., and Abbadie, L. (1998). Grazing optimization and nutrient cycling: when do herbivores enhance plant production? *Ecology*, 79(7):2242–2252.

de Mazancourt, C., Loreau, M., and Abbadie, L. (1999). Grazing optimization and nutrient cycling: potential impact of large herbivores in a savanna system. *Ecological Applications*, 9(3):784–797.

Donzelli, D., De Michele, C., and Scholes, R. (2013). Competition between trees and grasses for both soil water and mineral nitrogen in dry savannas. *Journal of theoretical biology*, 332:181–190.

D'Odorico, P., Laio, F., and Ridolfi, L. (2006). A probabilistic analysis of fire-induced tree-grass coexistence in savannas. *The American Naturalist*, 167(3):E79–E87.

Falkengren-Grerup, U., Brunet, J., and Diekmann, M. (1998). Nitrogen mineralisation in deciduous forest soils in south sweden in gradients of soil acidity and deposition. *Environmental Pollution*, 102(1):415–420.

February, E. C. and Higgins, S. (2010). The distribution of tree and grass roots in savannas in relation to soil nitrogen and water. *South African Journal of Botany*, 76(3):517–523.

Fillery, I. (1983). Biological denitrification. In *Gaseous loss of nitrogen from plant-soil systems*, pages 33–64. Springer.

Fontaine, S., Mariotti, A., and Abbadie, L. (2003). The priming effect of organic matter: a question of microbial competition? *Soil biology and biochemistry*, 35(6):837–843.

Gautier, L. (1990). Contact forêt-savane en côte-d'ivoire centrale: évolution du recouvrement ligneux des savanes de la réserve de lamto (sud du v-baoulé). *Candollea*, 45(2):627–641.

Gignoux, J., Lahoreau, G., Julliard, R., and Barot, S. (2009). Establishment and early persistence of tree seedlings in an annually burned savanna. *Journal of Ecology*, 97(3):484–495.

Gilad, E., von Hardenberg, J., Provenzale, A., Shachak, M., and Meron, E. (2007). A mathematical model of plants as ecosystem engineers. *Journal of Theoretical Biology*, 244(4):680–691.

Graham, P. H. and Vance, C. P. (2000). Nitrogen fixation in perspective: an overview of research and extension needs. *Field crops research*, 65:93–106.

Gundersen, P., Callesen, I., and De Vries, W. (1998). Nitrate leaching in forest ecosystems is related to forest floor cn ratios. *Environmental pollution*, 102(1):403–407.

Hardin, G. (1960). The competitive exclusion principle. *science*, 131(3409):1292–1297.

Harrison, K. A. and Bardgett, R. D. (2010). Influence of plant species and soil conditions on plant–soil feedback in mixed grassland communities. *Journal of Ecology*, 98(2):384–395.

Hart, S. C., Binkley, D., and Perry, D. A. (1997). Influence of red alder on soil nitrogen transformations in two conifer forests of contrasting productivity. *Soil Biology and Biochemistry*, 29(7):1111–1123.

Haynes, R. (1986). Uptake and assimilation of mineral nitrogen by plants. *Mineral nitrogen in the plant-soil system*, pages 303–378.

Hempson, G. P., Archibald, S., and Bond, W. J. (2015). A continent-wide assessment of the form and intensity of large mammal herbivory in africa. *Science*, 350(6264):1056–1061.

Higgins, S. I., Bond, W. J., February, E. C., Bronn, A., Euston-Brown, D. I., Enslin, B., Govender, N., Rademan, L., O'Regan, S., Potgieter, A. L., et al. (2007). Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology*, 88(5):1119–1125.

Higgins, S. I., Bond, W. J., and Trollope, W. S. (2000). Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology*, 88(2):213–229.

Higgins, S. I., Scheiter, S., and Sankaran, M. (2010). The stability of african savannas: insights from the indirect estimation of the parameters of a dynamic model. *Ecology*, 91(6):1682–1692.

Hipondoka, M., Aranibar, J., Chirara, C., Lihavha, M., and Macko, S. (2003). Vertical distribution of grass and tree roots in arid ecosystems of southern africa: niche differentiation or competition? *Journal of Arid Environments*, 54(2):319–325.

Hochberg, M. E., Menaut, J. C., and Gignoux, J. (1994). The influences of tree biology and fire in the spatial structure of the west african savannah. *Journal of Ecology*, 82:217–226.

Hodge, A. (2006). Plastic plants and patchy soils. *Journal of experimental botany*, 57(2):401–411.

Houlton, B. Z., Sigman, D. M., Schuur, E. A., and Hedin, L. O. (2007). A climate-driven switch in plant nitrogen acquisition within tropical forest communities. *Proceedings of the National Academy of Sciences*, 104(21):8902–8906.

Jackson, L. E., Schimel, J. P., and Firestone, M. K. (1989). Short-term partitioning of ammonium and nitrate between plants and microbes in an annual grassland. *Soil Biology and Biochemistry*, 21(3):409–415.

Janssen, B. (1996). Nitrogen mineralization in relation to C: N ratio and decomposability of organic materials. *Plant and Soil*, 181:39–45.

Jeltsch, F., Milton, S., Dean, W., Van Rooyen, N., and Moloney, K. (1998). Modelling the impact of small-scale heterogeneities on tree—grass coexistence in semi-arid savannas. *Journal of Ecology*, 86(5):780–793.

Jeltsch, F., Weber, G. E., and Grimm, V. (2000). Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology*, 150(1-2):161–171.

Jones, D. L. and Kielland, K. (2002). Soil amino acid turnover dominates the nitrogen flux in permafrost-dominated taiga forest soils. *Soil Biology and Biochemistry*, 34(2):209–219.

Joshi, A. B., Vann, D. R., Johnson, A. H., and Miller, E. K. (2003). Nitrogen availability and forest productivity along a climosequence on whiteface mountain, new york. *Canadian Journal of Forest Research*, 33(10):1880–1891.

Jussy, J., Colin-Belgrand, M., Dambrine, E., Ranger, J., Zeller, B., and Bienaime, S. (2004). N deposition, N transformation and N leaching in acid forest soils. *Biogeochemistry*, 69(2):241–262.

Jussy, J.-H., Colin-Belgrand, M., and Ranger, J. (2000). Production and root uptake of mineral nitrogen in a chronosequence of douglas-fir (*Pseudotsuga menziesii*) in the beaujolais mounts. *Forest ecology and management*, 128(3):197–209.

Kahmen, A., Renker, C., Unsicker, S. B., and Buchmann, N. (2006). Niche complementarity for nitrogen: an explanation for the biodiversity and ecosystem functioning relationship? *Ecology*, 87(5):1244–1255.

Kielland, K. (1994). Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. *Ecology*, 75(8):2373–2383.

Klironomos, J. N. (2002). Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, 417(6884):67–70.

Knops, J., Bradley, K., and Wedin, D. (2002). Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecology Letters*, 5(3):454–466.

Knops, J. M., Koenig, W. D., and Nash III, T. H. (1997). On the relationship between nutrient use efficiency and fertility in forest ecosystems. *Oecologia*, 110(4):550–556.

Konaré, S., Boudsocq, S., Gignoux, J., Lata, J.-C., Raynaud, X., and Barot, S. (2019). Effects of mineral nitrogen partitioning on tree–grass coexistence in west african savannas. *Ecosystems*, 22(7):1676–1690.

Konnerup, D. and Brix, H. (2010). Nitrogen nutrition of *Canna indica*: effects of ammonium versus nitrate on growth, biomass allocation, photosynthesis, nitrate reductase activity and n uptake rates. *Aquatic Botany*, 92(2):142–148.

Kraus, T. E., Dahlgren, R. A., and Zasoski, R. J. (2003). Tannins in nutrient dynamics of forest ecosystems-a review. *Plant and soil*, 256(1):41–66.

Kraus, T. E., Zasoski, R. J., Dahlgren, R. A., Horwath, W. R., and Preston, C. M. (2004). Carbon and nitrogen dynamics in a forest soil amended with purified tannins from different plant species. *Soil Biology and Biochemistry*, 36(2):309–321.

Kronzucker, H. J., Siddiqi, M. Y., and Glass, A. D. (1997). Conifer root discrimination against soil nitrate and the ecology of forest succession. *Nature*, 385(6611):59–61.

Lata, J.-C., Degrange, V., Raynaud, X., Maron, P.-A., Lensi, R., and Abbadie, L. (2004). Grass populations control nitrification in savanna soils. *Functional Ecology*, 18(4):605–611.

Lata, J.-C., Guillaume, K., Degrange, V., Abbadie, L., and Lensi, R. (2000). Relationships between root density of the african grass *Hyparrhenia diplandra* and nitrification at the decimetric scale: an inhibition–stimulation balance hypothesis. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1443):595–600.

Le Roux, X., Abbadie, L., Fritz, H., and Leriche, H. (2006). Modifications of the savanna functioning by herbivores. In *Lamto: structure, functioning, and dynamics of a savanna ecosystem*, pages 185–198. New York: Springer.

Leadley, P. W., Reynolds, J. F., and Chapin, F. S. (1997). A model of nitrogen uptake by eriophorum vaginatum roots in the field: ecological implications. *Ecological monographs*, 67(1):1–22.

Li, X.-G., Rengel, Z., Mapfumo, E., et al. (2007). Increase in pH stimulates mineralization of 'native'organic carbon and nitrogen in naturally salt-affected sandy soils. *Plant and soil*, 290(1-2):269–282.

Maron, J. L. and Jefferies, R. L. (1999). Bush lupine mortality, altered resource availability, and alternative vegetation states. *Ecology*, 80(2):443–454.

Marschner, H. (2008). *Mineral nutrition of higher plants*. London:Academic Press.

McKane, R. B., Johnson, L. C., Shaver, G. R., Nadelhoffer, K. J., Rastetter, E. B., Fry, B., Giblin, A. E., Kielland, K., Kwiatkowski, B. L., Laundre, J. A., et al. (2002). Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, 415(6867):68–71.

Menge, D. N., Levin, S. A., and Hedin, L. O. (2009). Facultative versus obligate nitrogen fixation strategies and their ecosystem consequences. *The American Naturalist*, 174(4):465–477.

Mengel, K. (1996). Turnover of organic nitrogen in soils and its availability to crops. *Plant and Soil*, 181(1):83–93.

Miller, A. J. and Cramer, M. D. (2004). Root nitrogen acquisition and assimilation. *Plant and Soil*, 274:1–36.

Mordelet, P. (1993). *Influence des arbres sur la strate herbacée d'une savane humide (Lamto, Côte d'Ivoire)*. PhD thesis, Paris 6.

Nugroho, R. A., Röling, W., Laverman, A., and Verhoef, H. (2006). Net nitrification rate and presence of nitrosospira cluster 2 in acid coniferous forest soils appear to be tree species specific. *Soil Biology and Biochemistry*, 38(5):1166–1171.

Okin, G., Mladenov, N., Wang, L., Cassel, D., Caylor, K., Ringrose, S., and Macko, S. (2008). Spatial patterns of soil nutrients in two southern african savannas. *Journal of Geophysical Research: Biogeosciences*, 113(G02011).

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., et al. (2001). Terrestrial ecoregions of the world: A new map of life on eartha new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, 51(11):933–938.

Osborne, C. P., Charles-Dominique, T., Stevens, N., Bond, W. J., Midgley, G., and Lehmann, C. (2018). Human impacts in african savannas are mediated by plant functional traits. *New Phytologist*, 220(1):10–24.

Packer, A. and Clay, K. (2000). Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature*, 404(6775):278–281.

Persson, T., Rudebeck, A., Jussy, J., Colin-Belgrand, M., Priemé, A., Dambrine, E., Karlsson, P., and Sjöberg, R. (2000). Soil nitrogen turnover—mineralisation, nitrification and denitrification in european forest soils. In *Carbon and nitrogen cycling in European forest ecosystems*, pages 297–311. Springer.

Powlson, D. and Barraclough, D. (1993). Mineralization and assimilation in soil-plant systems. In *In 'Nitrogen isotope techniques'.(Eds R Knowles, TH Blackburn)*, pages 209–242. Academic Press: San Diego.

Priha, O. and Smolander, A. (1999). Nitrogen transformations in soil under pinus sylvestris, picea abies and betula pendula at two forest sites. *Soil Biology and Biochemistry*, 31(7):965–977.

Reich, P. B., Peterson, D. W., Wedin, D. A., and Wrage, K. (2001). Fire and vegetation effects on productivity and nitrogen cycling accross a forest-grassland continuum. *Ecology*, 82:1703–1719.

Rutten, G., Prati, D., Hemp, A., and Fischer, M. (2016). Plant-soil feedback in east-african savanna trees. *Ecology*, 97(2):294–301.

Salsac, L., Chaillou, S., Morot-Gaudry, J.-F., Lesaint, C., and Jolivet, E. (1987). Nitrate and ammonium nutrition in plants. *Plant physiology and biochemistry (Paris)*, 25(6):805–812.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., Gignoux, J., Higgins, S. I., Le Roux, X., Ludwig, F., et al. (2005). Determinants of woody cover in african savannas. *Nature*, 438(7069):846–849.

Sankaran, M., Ratnam, J., and Hanan, N. (2008). Woody cover in african savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography*, 17(2):236–245.

Sankaran, M., Ratnam, J., and Hanan, N. P. (2004). Tree–grass coexistence in savannas revisited–insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology letters*, 7(6):480–490.

Scheiter, S. and Higgins, S. I. (2007). Partitioning of Root and Shoot Competition and the Stability of Savannas. *The American Naturalist*, 170(4):587–601.

Scheiter, S. and Higgins, S. I. (2009). Impacts of climate change on the vegetation of africa: an adaptive dynamic vegetation modelling approach. *Global Change Biology*, 15(9):2224–2246.

Scheiter, S. and Higgins, S. I. (2012). How many elephants can you fit into a conservation area. *Conservation Letters*, 5(3):176–185.

Scheiter, S. and Savadogo, P. (2016). Ecosystem management can mitigate vegetation shifts induced by climate change in west africa. *Ecological modelling*, 332:19–27.

Schenk, H. J. and Jackson, R. B. (2002). Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, 90(3):480–494.

Schimel, J. P. and Chapin, F. S. (1996). Tundra plant uptake of amino acid and NH_4^+ nitrogen in situ: plants complete well for amino acid N. *Ecology*, 77(7):2142–2147.

Scholes, R. and Archer, S. (1997). Tree-grass interactions in savannas. *Annual review of Ecology and Systematics*, 28(1):517–544.

Scott, N. A. and Binkley, D. (1997). Foliage litter quality and annual net n mineralization: comparison across north american forest sites. *Oecologia*, 111(2):151–159.

Sigunga, D., Janssen, B., and Oenema, O. (2002). Effects of improved drainage and nitrogen source on yields, nutrient uptake and utilization efficiencies by maize (zea mays l.) on vertisols in sub-humid environments. *Nutrient Cycling in Agroecosystems*, 62(3):263–275.

Srikanthasamy, T., Leloup, J., N'Dri, A. B., Barot, S., Gervaix, J., Koné, A. W., Koffi, K. F., Le Roux, X., Raynaud, X., and Lata, J.-C. (2018). Contrasting effects of grasses and trees on microbial n-cycling in an african humid savanna. *Soil Biology and Biochemistry*, 117:153–163.

Staver, A. C., Archibald, S., and Levin, S. (2011a). Tree cover in sub-saharan africa: rainfall and fire constrain forest and savanna as alternative stable states. *Ecology*, 92(5):1063–1072.

Staver, A. C., Archibald, S., and Levin, S. A. (2011b). The global extent and determinants of savanna and forest as alternative biome states. *Science*, 334(6053):230–232.

Subbarao, G., Ito, O., Sahrawat, K., Berry, W., Nakahara, K., Ishikawa, T., Watanabe, T., Suenaga, K., Rondon, M., and Rao, I. M. (2006). Scope and strategies for regulation of nitrification in agricultural systems—challenges and opportunities. *Critical Reviews in Plant Sciences*, 25(4):303–335.

Subbarao, G., Rondon, M., Ito, O., Ishikawa, T., Rao, I. M., Nakahara, K., Lascano, C., and Berry, W. (2007). Biological nitrification inhibition (BNI)—is it a widespread phenomenon? *Plant and Soil*, 294(1-2):5–18.

Subbarao, G. V., Yoshihashi, T., Worthington, M., Nakahara, K., Ando, Y., Sahrawat, K. L., Rao, I. M., Lata, J.-C., Kishii, M., and Braun, H.-J. (2015). Suppression of soil nitrification by plants. *Plant Science*, 233:155–164.

Tilman, D. (1985). The resource-ratio hypothesis of plant succession. *The American Naturalist*, 125(6):827–852.

Van Breemen, N. (2002). Natural organic tendency. *Nature*, 415(6870):381–382.

Van der Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., Kardol, P., Klironomos, J. N., Kulmatiski, A., Schweitzer, J. A., et al. (2013). Plant–soil feedbacks: the past, the present and future challenges. *Journal of Ecology*, 101(2):265–276.

Van Langevelde, F., Van De Vijver, C. A., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A. K., Hearne, J. W., Stroosnijder, L., Bond, W. J., et al. (2003). Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, 84(2):337–350.

Vervaet, H., Massart, B., Boeckx, P., Van Cleemput, O., and Hofman, G. (2002). Use of principal component analysis to assess factors controlling net N mineralization in deciduous and coniferous forest soils. *Biology and Fertility of Soils*, 36(2):93–101.

Vitousek, P. M. and Howarth, R. W. (1991). Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry*, 13(2):87–115.

Walker, B. H. and Noy-Meir, I. (1982). Aspects of the stability and resilience of savanna ecosystems. In *Ecology of tropical savannas*, pages 556–590. Springer.

Walter, H. (1971). *Ecology of tropical and subtropical vegetation*. Edinburgh: Oliver Boyd.

Ward, B., Courtney, K., and Langenheim, J. (1997). Inhibition of nitrosomonas europaea by monoterpenes from coastal redwood (*Sequoia sempervirens*) in whole-cell studies. *Journal of Chemical Ecology*, 23(11):2583–2598.

Ward, D., Wiegand, K., and Getzin, S. (2013). Walter's two-layer hypothesis revisited: back to the roots! *Oecologia*, 172(3):617–630.

Zia, M., Aslam, M., Arshad, M., and Ahmed, T. (1999). Ammonia volatilization from nitrogen fertilizers with and without gypsum. *Soil use and management*, 15(2):133–135.

2

Effects of mineral nitrogen partitioning on tree-grass coexistence in West African savannas

Effects of mineral nitrogen partitioning on tree-grass coexistence in West African savannas

S Konaré [1] *, S Boudsocq [2], J Gignoux [1], J-C Lata [1,3], X Raynaud [1] and S Barot [1]

[1] Sorbonne Université, IRD, CNRS, INRA, UPEC, Univ Paris Diderot, Institute of Ecology and Environmental Sciences, iEES Paris, 75005 Paris, France; [2] Eco&Sols, INRA, CIRAD, IRD, Montpellier SupaAgro, Univ Montpellier, Montpellier, France; [3] Department of Geoecology and Geochemistry, Institute of Natural Resources, Tomsk Polytechnic University, 30, Lenin Street, Tomsk 634050, Russia

Abstract

Coexistence between trees and grasses in savannas is generally assumed to be due to a combination of partial niche separation for water acquisition and disturbances impacting the demography of trees and grasses. We propose a mechanism of coexistence solely based on the partitioning of the two dominant forms of mineral nitrogen (N), ammonium (NH_4^+) and nitrate (NO_3^-). We built a mean-field model taking into account the capacity of grasses and trees to alter nitrification fluxes as well as their relative preferences for NH_4^+ *versus* NO_3^-. Two models were studied and parameterized for the Lamto savanna (Côte d'Ivoire): a first where nitrification only depends on the quantity of available NH_4^+ and a second where nitrification rate is also controlled by tree and grass biomass. Consistent with coexistence theories, our results show that taking these two forms of mineral N into account can allow coexistence when trees and grasses have contrasting preferences for NH_4^+ and NO_3^-. Moreover, coexistence is more likely to occur for intermediate nitrification rates. Assuming that grasses are able to inhibit nitrification while trees can stimulate it, as observed in the Lamto savanna, the most likely case of coexistence would be when grasses prefer NH_4^+ and trees NO_3^-. We propose that mineral N partitioning is a stabilizing coexistence mechanism that occurs in interaction with already described mechanisms based on disturbances by fire and herbivores. This mechanism is likely relevant in many N-limited African savannas with vegetation composition similar to the one at the Lamto site, but should be thoroughly tested through empirical studies and new models taking into account spatio-temporal heterogeneity in nitrification rates.

Keywords: ammonium, nitrate, nitrification control, resource partitioning, savanna, tree-grass coexistence

2.1 Introduction

Savannas cover about 20% of Earth's land surface and are characterized by the coexistence of trees and grasses (Sankaran et al., 2004; Scholes and Archer, 1997). Coexistence mechanisms among plant species have been much debated, in particular because of the competitive exclusion principle stating that two species using the same resource cannot coexist over the long term (Hardin, 1960; Rastetter et al., 2002). Many theories have thus been proposed to explain coexistence among plants (Barot and Gignoux, 2004) but two main ideas emerged to explain coexistence between trees and grasses in savannas: (1) Niche separation through different rooting depths between trees and grasses could foster their coexistence (Walker and Noy-Meir, 1982; Walter, 1971; Ward et al., 2013). (2) Disturbances such as fire and herbivory (browsing and grazing) prevent the ecosystem from reaching a forest or grassland state (Accatino et al., 2010; Higgins et al., 2000; Jeltsch et al., 2000; Sankaran et al., 2004).

In particular, the partitioning of soil resources by vertical separation can favor coexistence between trees and grasses (Walter, 1971). Grasses are often considered as better competitors for water in the top soil layer because of their superficial high root density while trees have access to water from deeper soil layers (Schenk and Jackson, 2002). Such rooting niche separation could therefore reduce competition between trees and grasses (Walker and Noy-Meir, 1982; Walter, 1971). However, resource partitioning is not supported by all studies (February et al., 2013; Higgins et al., 2000; Holdo et al., 2018; Jeltsch et al., 2000) and disturbances can constitute an important coexistence mechanism especially in areas where the mean annual precipitation is high enough to allow the existence of forest (Sankaran et al., 2005; Staver et al., 2011a). Fire, by limiting tree recruitment and establishment, influences savanna structure (Accatino et al., 2010; Gignoux et al., 2009; Van Langevelde et al., 2003). Similarly, through the selective effects of browsers and grazers on tree and grass biomass, herbivores can maintain the open state of savannas (Van Langevelde et al., 2003).

Here, we focus on a newly proposed coexistence mechanism based on the partitioning of mineral nitrogen (N) (Boudsocq et al., 2012; McKane et al., 2002; Miller and Bowman, 2002). In the Lamto humid savanna in Côte d'Ivoire (Abbadie et al., 2006), one of the factors explaining the high plant productivity is biological nitrification inhibition (BNI) by the dominant perennial grasses (Boudsocq et al., 2009; Lata et al., 2004, 2000; Srikanthasamy et al., 2018). The other perennial species of this savanna have not been tested for BNI capabilities and this savanna virtually hosts no annual grass. Nevertheless, all perennial grasses of the Lamto savanna seem to have the same ecological behavior. Therefore, we expect them to inhibit nitrification while annual grasses are less likely to inhibit nitrification because of their lower root densities. BNI has also been described outside the Lamto site in other African perennial grass species (*Brachiaria humidicola* and *Andropogon gayanus*) (Rossiter-Rachor et al., 2009; Subbarao et al., 2009). Nitrification allows the presence of two forms of mineral N (ammonium, nitrate) that are jointly exploited by plants. As shown in other perennial grass species, BNI is due to the release of allelopathic compounds from their root systems that impede nitrifying activity (Rossiter-Rachor et al., 2009). By maintaining most mineral N in the ammonium (NH_4^+) form, BNI reduces N losses due to nitrate (NO_3^-) leaching and denitrification and consequently increases N conservation and primary production (Boudsocq et al., 2009). NH_4^+ is directly assimilated by plants, but an excess of NH_4^+ uptake can be toxic for plants (Britto and

Kronzucker, 2002). In particular, NH_4^+ uptake favors the release of H^+ that causes soil acidification and reduces the availability of other nutrients such as Ca^{2+}, K^+ and Mg^{2+} important for plant growth (Britto and Kronzucker, 2002; Salsac et al., 1987). Moreover, because of its positive charge, NH_4^+ is adsorbed by clays and soil organic matter (Marschner, 2011; Subbarao et al., 2015) and can become unavailable to plants in dry soils. By contrast, NO_3^- uptake is energetically more costly because it needs to be reduced before being assimilated (Konnerup and Brix, 2010) and its mobility within the soil makes it more available for plants but also more prone to leaching (Marschner, 2011). NO_3^- can also be lost from ecosystems through denitrification taking place in water-saturated pore spaces. Although the relative proportion of NO_3^- and NH_4^+ used by plant species is not documented for many plant species and soil conditions (Boudsocq et al., 2012), some studies suggest that plant species differ in their preferences for NH_4^+ *versus* NO_3^- (Falkengren-Grerup and Lakkenborg-Kristensen, 1994; Huangfu et al., 2016; Konnerup and Brix, 2010) and that these preferences depend on a variety of physiological and environmental factors (Britto and Kronzucker, 2013). The existence of a trade-off between root uptake capacity for NH_4^+ and NO_3^- has been explicitly demonstrated in one case (Maire et al., 2009). This trade-off is likely to arise because (1) NH_4^+ and NO_3^- are not taken up through the same transporters (Maire et al., 2009; Nacry et al., 2013) and (2) their spatial distribution can be heterogeneous within the soil profile, leading to different uptake strategies (rooting depth, root densities) (Jumpponen et al., 2002; Maire et al., 2009). For example, the assimilation of more NO_3^- requires spending energy for its reduction, while the assimilation of more NH_4^+ requires investing in fine root biomass with a high turnover because of the low mobility of NH_4^+, which probably leads to a trade-off in terms of resource allocation.

Some studies have shown that the preference for one form of mineral N can influence ecological dynamics and species distribution (Boudsocq et al., 2012; Britto and Kronzucker, 2013) and favor species coexistence. Indeed, resource partitioning can allow coexistence if the use of existing resources is sufficiently different among species (Harrison et al., 2007; Holt, 2008). By using a modelling approach, Boudsocq et al. (2012) studied the conditions of coexistence between two plant species having the same N uptake rate but different preferences for NH_4^+ and NO_3^- and found that coexistence was possible if plants' preference for NH_4^+ and NO_3^- was different enough. In the Lamto savanna, grass species can inhibit nitrification (Lata et al., 2004, 2000; Srikanthasamy et al., 2018) while trees can stimulate it through an unidentified mechanism (Srikanthasamy et al., 2018). This increase of nitrification could be due to (1) some specific root exudates that stimulate nitrifying activity or (2) to an increase of dead organic matter below tree canopy that stimulates microbial activity and nitrification. It would thus make sense that grasses prefer NH_4^+ and trees prefer NO_3^-, which is in accordance with some preliminary data (Tavernier, 2003). Besides, Rossiter-Rachor et al. (2009) studied the impact of the invasion of an African grass *Andropogon gayanus* on Australian savanna functioning and found that this grass strongly affects N dynamics through BNI capacity and has a strong preference for NH_4^+.

Our main objective was to test whether tree and grass capacity to control nitrification and their respective preferences for NH_4^+ and NO_3^- could facilitate tree-grass coexistence in the Lamto savanna. To reach this goal, we used a modified version of the model of Boudsocq et al. (2012). While Boudsocq et al. (2012) studied the coexistence of theoretical species having the same overall rate of mineral N uptake, we precisely parameterize our model for trees and grasses in the Lamto savanna taking

into account their respective impact on nitrification, the likely consequences of their preferences for NH_4^+ and NO_3^- and their different uptake rates of mineral N. Because it is not easy to find in the literature a comprehensive set of parameters for N cycling (rate of leaching, inputs through dry and wet deposits...), Boudsocq et al. (2012) used N cycling parameters from the Lamto savanna and we used the same parameter values.

First, we used a simple formula for nitrification that only depends on the availability of NH_4^+. Then, to identify whether nitrification inhibition and stimulation could influence tree-grass coexistence in the Lamto savanna, we used a second model in which nitrification also depended on the biomass of both types of plants. This second formula is supported by results on the impact of trees and grasses on nitrification (Lata et al., 2004, 2000; Srikanthasamy et al., 2018). Five hypotheses were tested for the Lamto savanna: (**1**) The existence of two forms of mineral N influences tree and grass biomass and allows the coexistence of both plant types. (**2**) This coexistence is facilitated when grasses prefer NH_4^+ and trees prefer NO_3^-. (**3**) Nitrification rate influences coexistence and intermediate values should increase the chances of coexistence. (**4**) Nitrification inhibition by grasses and its stimulation by trees increase the possibilities of coexistence. (**5**) Coexistence is possible even when trees and grasses have not the same overall uptake capacity for mineral N.

2.2 Materials and methods

2.2.1 Model definition

We used a mean-field model, i.e. taking into account no spatial heterogeneity, adapted from the model by Boudsocq et al. (2012) to explore competitive interactions between trees and grasses for NO_3^- and NH_4^+ acquisition. Our model describes N dynamics among five compartments: Grass biomass (G), Tree biomass (T), Soil organic matter (O) and the two mineral N forms, NH_4^+ (N_A) and NO_3^- (N_N) (Fig. 2.1), where the use of the term "plant biomass" in the context of this study is used to refer to "plant N pool size".

These compartments correspond to N stocks and are expressed as a quantity of N per unit surface, considering a soil depth of a 30 cm, that hosts the majority of grass and tree fine roots in this ecosystem (Mordelet et al., 1997). Nutrient fluxes are expressed in kilograms N per hectare per year. All the parameters describing N fluxes among these compartments are considered as constant (see Table 1). The preference for NH_4^+ *versus* NO_3^- is described in the model through the parameter β that ranges between 0 and 1 and corresponds to the preference for NH_4^+ . The higher the β, the higher the preference for NH_4^+ . Total N uptake is represented by a rate u (ha/kg N/yr) so that βu represents the intake rate of NH_4^+ while (1-β)u is the intake rate of NO_3^- . Fluxes of N uptake are "linearly donor-recipient controlled" i.e., they are proportional to the sizes of both the donor (mineral N) and receiver (plants) compartments. All other fluxes are modeled as "linearly donor controlled" (e.g. the flux due to mortality d_G G is only proportional to the Grasses compartment).
Uptake of mineral N, U(N) is expressed as follows (e.g. for grasses):
$U(NH_4^+) = u_G\ \beta_G\ N_A\ G$
$U(NO_3^-) = u_G\ (1-\beta_G)\ N_N\ G$

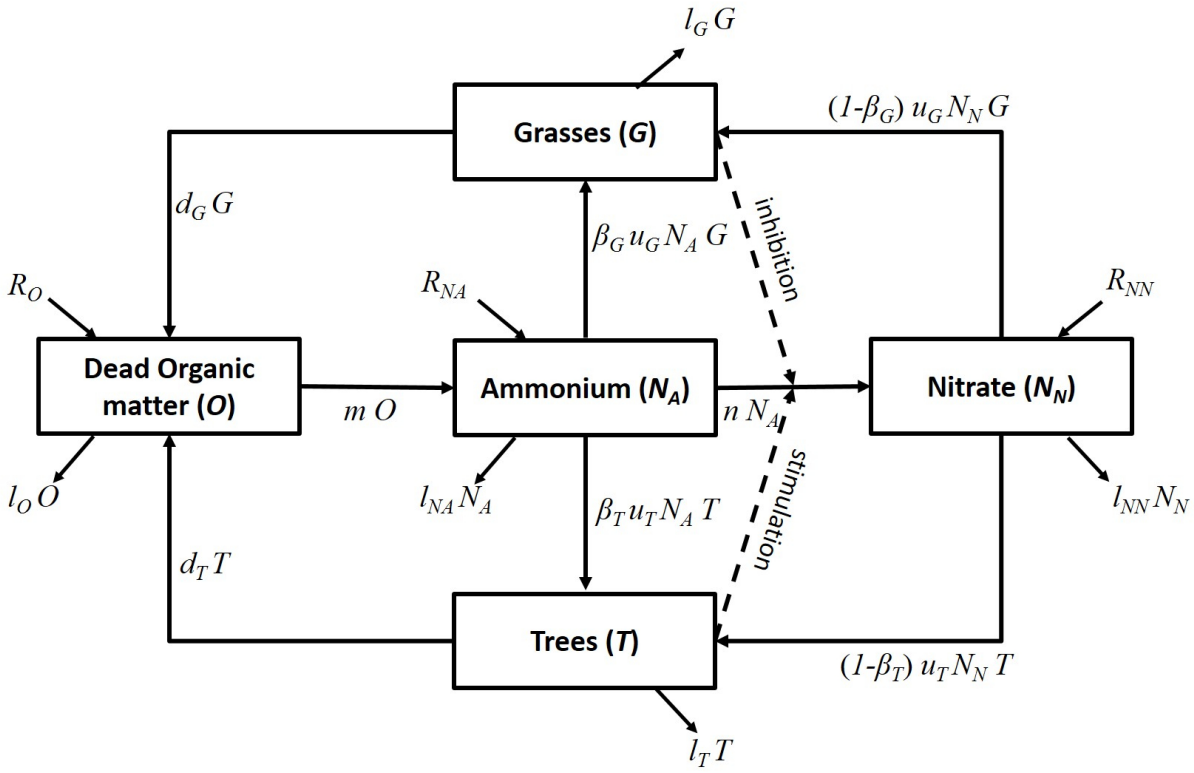

Figure 2.1 – General model of the N cycle in savanna ecosystem. Arrows indicate fluxes linking compartments, while dashed arrows correspond to the influence of plants on nitrification (inhibition and stimulation). In model 1, plant influence on nitrification (dashed arrows) is implemented by imposing different nitrification rates. In model 2, this influence is modeled using Eqs 2.6 and 2.7

The turnover of plant biomass leads to an input of organic N to the soil (compartment *O*) at rate d (yr^{-1}). Organic matter is then mineralized into NH_4^+ (compartment N_A) at rate m (yr^{-1}). Nitrification transforms NH_4^+ into NO_3^- (compartment N_N) at rate n (yr^{-1}). The model also takes into account inputs to the different compartments. Wet and dry depositions provide constant N inputs to the organic (R_O) and inorganic (R_{NA} , R_{NN}) nutrient pools, independently of their size. We consider that non-symbiotic fixation can also exist and is included in the R_O term. The model does not include any symbiotic N fixation because none of the dominant tree species are N fixing and only a few negligible forbs are N fixing (Abbadie, 2006). Losses from the different compartments are represented by parameters l_G , l_T , l_O , l_{NA} and l_{NN} , respectively, for the *G*, *T*, *O*, N_A and N_N compartments. In savannas, N losses from the plant compartment (l_G , l_T) are mainly due to fire. Soil organic matter can be lost through fire, soil erosion and leaching (l_O). Losses from the N_A compartment (l_{NA}) are caused by leaching and volatilization, while losses from the N_N compartment (l_{NN}) are due to leaching and denitrification. We used two different formulas for nitrification that are detailed in the following: (1) Nitrification flux only depends on the availability of NH_4^+ and (2) nitrification flux depends on both tree and grass biomass to allow simulating their respective influence on nitrification.

Model 1: Nitrification Independent from Plant Biomass

Nitrification only depends on the availability of NH_4^+ in the soil, that is, the nitrification flux is proportional to the stock of NH_4^+ ($n N_A$) (Eqs. 2.4).

$$\frac{dG}{dt} = \beta_G\ u_G\ N_A\ G + (1-\beta_G) u_G N_N\ G - (d_G + l_G)\ G \tag{2.1}$$

$$\frac{dT}{dt} = \beta_T\ u_T\ N_A\ T + (1-\beta_T) u_T N_N T - (d_T + l_T)\ T \tag{2.2}$$

$$\frac{dO}{dt} = R_O + d_G\ G + d_T\ T - (m + l_O)\ O \tag{2.3}$$

$$\frac{dN_A}{dt} = R_{NA} + m\ O - (\beta_G u_G\ G + \beta_T u_T T + n + l_{NA})\ N_A \tag{2.4}$$

$$\frac{dN_N}{dt} = R_{NN} + n\ N_A - ((1-\beta_G)\ u_G\ G + (1-\beta_T) u_T\ T) + l_{NN})\ N_N \tag{2.5}$$

Model 2: Nitrification Dependent on Plant Biomass

To study the influence of trees and grasses on nitrification (Lata et al., 2004, 2000; Srikanthasamy et al., 2018) and to take into account the likely influence of their biomass, a second scheme was used for nitrification. In this case, nitrification also depends on the biomass of grasses and trees. At least, nitrification inhibition has been shown to increase with grass root density (Lata et al., 2000). This control of nitrification is expressed by a coefficient of nitrification inhibition by grasses (i_G) and a coefficient of nitrification stimulation by trees (s_T). Thus, the flux of nitrification is modeled as $n\ N_A e^{-(i_G G - s_T T)}$, with $i_G > 0$ and $s_T > 0$. In this case, Eqs. 2.4 and 2.5 of model 1 are replaced by Eqs.2.6 and 2.7 in model 2.

$$\frac{dN_A}{dt} = R_{NA} + m\ O - (\beta_G\ u_G\ G + \beta_T\ u_T\ T + n\ e^{-(i_G G - s_T T)} + l_{NA})\ N_A \tag{2.6}$$

$$\frac{dN_N}{dt} = R_{NN} + n\ N_A\ e^{-(i_G G - s_T T)} - ((1-\beta_G)\ u_G\ G + (1-\beta_T)\ u_T\ T + l_{NN})\ N_N \tag{2.7}$$

2.2.2 Analytical and Numerical Analysis

Model 1 was analytically solved using Mathematica 10 to find equilibria (Wolfram Research, 2017). As model 2 could not be analytically solved, we used the deSolve package (Soetaert et al., 2010) available in R (R Core Team, 2019) to run numerical simulations. All simulations were run for 1000 time steps (years) to allow the model to reach equilibrium. We checked that after 1000 years there was virtually no-longer any variation in the variables. Simulations were performed for the two models to study the impact of preference for NH_4^+ *versus* NO_3^- on tree and grass biomass and under which conditions of preference they can coexist. Tree–grass coexistence was determined using the mutual invasibility criterion. This criterion, which stipulates that when two species can mutually invade each other starting from a very low biomass,coexistence is necessarily stable (Chesson, 2000). We first considered

a resident plant type (10 kgN ha^{-1}), for example trees, and an invading plant (0.01 kgN ha^{-1}), for example grasses, and then reversed their respective roles. To study the effect of nitrification on the conditions of coexistence of plants, we tested different values of nitrification rate in the first model. The parameterization (see below) of the model for the Lamto savanna led to N uptake rates much lower for trees than for grasses (Table 2.1). This increases grass competitive ability. We tested for the two the robustness of our coexistence results towards the relative grass and tree competitive ability for N, by progressively increasing the N uptake rate by trees. As no available data allows assessing with certainty the tree preference for NH_4^+ (β_T) and the grass preference for NH_4^+ (β_G), we made simulations scanning all possible combinations of these two parameters varying from 0 to 1 with an increment of 0.005.

2.2.3 Parameterization

For numerical analysis, the model was parameterized from data collected in the Lamto research station by different researchers (see Table 2.1 for parameter values and origin of parameters). Lamto research station is located in a tropical humid savanna in Côte d'Ivoire (06°13'N, 05°02'W). Mean annual temperature is about 27°C and rainfall averages 1200 mm divided in four seasons: two wet seasons (a long wet season from March to July and a short from September to November) and two dry seasons (a long dry season from December to February and a short dry season in August). The herbaceous layer is mainly composed of perennial grasses such as *Andropogon canaliculatus*, *Andropogon schirensis*, *Hyparrhenia diplandra* and *Loudetia simplex*. The dominant tree species in the Lamto savanna are *Crossopteryx febrifuga*, *Cussonia arborea*, *Bridelia ferruginea*, *Piliostigma thonningii*. We used the values of parameters calculated by Boudsocq et al. (2012) except for tree parameters. As no empirical results from the Lamto site allows to directly assess the uptake of N by trees, we constructed a simple model without grasses and estimated their uptake rate u_T by numerical simulations so as to get a realistic N stock (86.1 kgN ha^{-1}) and primary productivity for trees (16.4 kgN ha^{-1} yr^{-1}) (Menaut and Cesar, 1979). The resulting much lower uptake parameter for trees (u_T) than for grasses (u_G) does not only reflect their strategy for the acquisition of mineral N. It also depends on many other factors, such as the fire regime indirectly influencing tree and grass capacities to take up mineral N at the scale of a few hectares.

Turnover and loss rates of trees were determined by dividing the N fluxes by the N stocks considered, assuming that the available data correspond to the Lamto savanna at equilibrium. These rates depend on plant capacity to resorb a part of their N from leaves before leaf fall (Aerts, 1996; Van Heerwaarden et al., 2003). This process permits plants to better conserve their nutrients. To calculate the turnover rate, we thus considered a resorption rate of 1/3 from leaves back to storage compartments prior to leaf shedding (Bernhard-Reversat and Poupon, 1980). Furthermore, N losses by herbivory are not considered in the model because the density of larger herbivores is very low in the Lamto savanna (Le Roux et al., 2006).

The nitrification rate for the first model was obtained by dividing the nitrification flux by the NH_4^+ stock at equilibrium (Boudsocq et al., 2009). We used a low nitrification rate as default value ($n = 2.7$ yr^{-1}) for the two models. In model 2 (Eq. 2.6), the rate of nitrification stimulation by trees (s_T) was

determined by assuming that the biomass of grasses was zero. Then, the rate s_T was calculated, with the second expression of nitrification ($n\,N_A e^{s_T T}$), considering that the nitrification flux under a tree canopy (150 kgN $ha^{-1}\ yr^{-1}$) is fifty times higher than under grasses (3 kgN $ha^{-1}\ yr^{-1}$) (Lata, 1999).

Table 2.1 – Parameters of the mean-field model

Parameters	Definition	Value	Unit	References
Tree parameters				
d_T	Turnover rate of tree biomass	0.0988	yr^{-1}	Menaut and César (1979)
l_T	Rate of N losses from the tree compartment	0.1098	yr^{-1}	Menaut and César (1979)
u_T	N uptake rate by trees	0.018	ha kg N^{-1} yr^{-1}	Estimated
β_T	Preference of tree for NH_4^+	[0,1]	No unit	
s_T	Nitrification stimulation rate	0.05	ha kg N^{-1}	Estimated
Grass parameters				
d_G	Turnover rate of grass biomass	0.6	yr^{-1}	Lata (1999)
l_G	Rate of N losses from the grass compartment	0.4	yr^{-1}	Lata (1999)
u_G	N uptake rate by grasses	0.14186	ha kg N^{-1} yr^{-1}	Boudsocq et al. (2012)
β_G	Preference of grass for NH_4^+	[0,1]	No unit	
i_G	Nitrification inhibition rate	0.02	ha kg N^{-1}	Boudsocq et al. (2012)
Soil parameters				
R_O	N organic input to the savanna	16.5	kg N ha^{-1} yr^{-1}	Villecourt and Roose (1978)
m	N mineralization rate	0.025	yr^{-1}	Abbadie et al (2006)
l_O	Rate of N losses from the organic matter compartment	0.0027	yr^{-1}	Abbadie et al (2006)
R_{NA}	NH_4^+ inputs to the savanna	23	kg N ha^{-1} yr^{-1}	Villecourt and Roose (1978)
l_{NA}	NH_4^+ loss rate	0.0133	yr^{-1}	Villecourt and Roose (1978)
R_{NN}	NO_3^- inputs to the savanna	4.1	kg N ha^{-1} yr^{-1}	Villecourt and Roose (1978)
l_{NN}	NO_3^- loss rate	2.7	yr^{-1}	Boudsocq et al (2009)
n	Nitrification rate	2.7	yr^{-1}	Boudsocq et al (2009)

2.3 Results

2.3.1 Equilibria and stability conditions in the two models

Analysis of model 1 (Eqs 3.1-3.5) reveals six equilibria: one trivial equilibrium, two where only trees are present, two where only grasses are present and one where trees and grasses coexist. Only four equilibria have exclusively positive compartment sizes and thus are biologically relevant. Stability of equilibria was evaluated (using Mathematica) from the sign of the eigenvalues of the Jacobian matrix at these equilibria (Appendix 1). Together with numerical simulations, these calculations revealed that the model always converges to a single stable positive equilibrium.

Model 2 being more complex and non-linear, it was not possible to analytically determine the stability of equilibria. However, numerical simulations were performed for values of β_G and β_T corresponding to the different cases observed (no invasion but residents maintain themselves, grasses invade and exclude trees, trees and grasses coexist). These simulations were run for 1000 time steps to reach equilibrium.

2.3.2 Effects of NH_4^+ and NO_3^- preference on coexistence

Under the baseline conditions for nitrification and N uptake by trees ($n = 2.7\ yr^{-1}$; $u_T = 0.018\ ha\ kg^{-1}$ N yr^{-1}), model 1 predicts only two outcomes of tree-grass competition in relation to NH_4^+ and NO_3^- preference (Fig. 2.2a): (1) If trees prefer NH_4^+ and grasses prefer NO_3^-, trees and grasses coexist (Fig. 2.2a, zone 3) and (2) if grass preference for NH_4^+ (β_G) is sufficiently higher than tree preference for NH_4^+ (β_T), grasses successfully invade and exclude trees (Fig. 2.2a, zone 1).

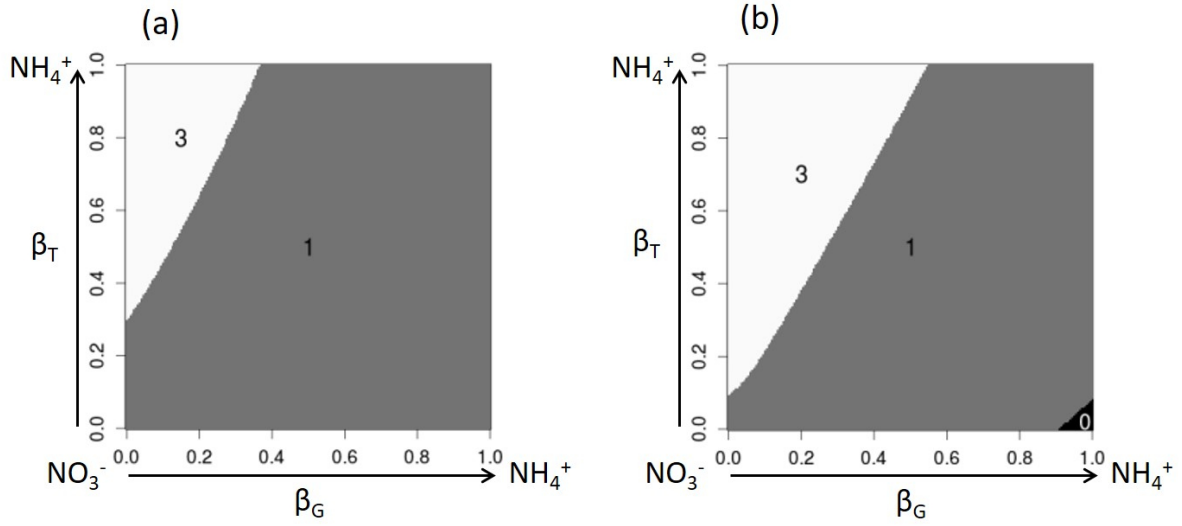

Figure 2.2 – Diagrams of mutual invasion between trees and grasses. In panel **a**, nitrification is independent from tree and grass biomass. In panel **b**, nitrification depends on the biomass of trees and grasses. Invasion zones: 0, no invasion but residents persist; 1, grasses invade and exclude trees; 3, trees and grasses coexist.

In model 2, when nitrification depends both on the availability of NH_4^+ and plant biomass (Fig. 2.2b), the overall pattern is similar but the region of coexistence is larger than for model 1. Moreover,

residents can persist and prevent invaders from establishing when trees strongly prefer NO_3^- and grasses prefer NH_4^+ (Fig. 2.2b, zone 0). In this case, the influence of plants on nitrification can also prevent the invasion but allows resident grasses or trees to persist. This leads to the presence of two alternative stable states for the same set of parameters with either only trees or only grasses (see Appendix 4). Taken together, with both formulas, coexistence is possible when trees and grasses exhibit contrasting N preferences.

Besides their influence on coexistence, tree and grass preferences for NH_4^+ and NO_3^- also determine tree and grass biomass (Fig. 2.3). In the case where nitrification only depends on the availability of NH_4^+ (model 1), total biomass is high in the region of coexistence (Fig. 2.3c). Within the region of coexistence, tree biomass increases as their preference for NH_4^+ increases and as grass preference for NH_4^+ decreases (Fig. 2.3a). Within this same region, grass biomass decreases as tree biomass increases (Fig. 2.3b). With model 2 where nitrification also depends on plant biomass, coexistence does not necessarily result in higher total plant biomass (Appendix 2).

2.3.3 Coexistence and nitrification rate

Nitrification significantly influences the conditions of coexistence whatever the nitrification rate. As discussed above, when nitrification is low ($n = 2.7\ yr^{-1}$), coexistence is favored if grasses have a high preference for NO_3^- and trees have a high preference for NH_4^+ (Fig. 2.4a). Grasses exclude trees for any other combinations of β_G and β_T. With increasing nitrification rate ($n = 5\ yr^{-1}$), a second zone of coexistence appears when grasses and trees prefer NH_4^+ and NO_3^-, respectively (Fig. 2.4b, zone 3). When nitrification increases further ($n = 6\ yr^{-1}$), two new zones appear (Fig. 2.4c, zones 2 and 4): a zone where trees completely exclude grasses and a zone where neither trees nor grasses can persist. Zone 4 is ecologically not realistic and corresponds to cases where the preference for NH_4^+ of both trees and grasses is too high for the nitrification rate. In such cases, trees and grasses can only lose N. The region in which grasses and trees coexist corresponds to cases where grasses prefer NH_4^+ ($0.78 < \beta_G < 1$) and trees prefer NO_3^- ($\beta_T < 0.4$). When nitrification is very high (i.e. close to values observed under tree canopy at Lamto), the size of the region of coexistence strongly decreases while the sizes of the zones of invasion by trees and of exclusion of both trees and grasses increase (Fig. 2.4d).

These results show that coexistence is possible whatever the nitrification rate. When nitrification is low, coexistence occurs if grasses prefer NO_3^- and trees prefer NH_4^+, and the reverse for high nitrification rates.

2.3.4 Coexistence and N uptake by trees

Fig. 2.5 illustrates the outcomes of the mutual invasion of trees and grasses for different tree capacities to take up N (u_T). When nitrification only depends on the availability of NH_4^+ (model 1), the variations of u_T always lead to two distinct zones: a zone of coexistence and a zone of exclusion (in which either trees or grasses are excluded). As described above, when N uptake rate by trees is low ($u_T = 0.018\ ha\ kg^{-1}$ N yr^{-1}), coexistence occurs when grasses prefer NO_3^- and trees prefer NH_4^+ (Fig. 2.5a). When N uptake rate by trees increases (Figure 5b, $u_T = 0.058\ ha\ kg^{-1}$ N yr^{-1}), trees become able to invade and exclude grasses. With high N uptake by trees, coexistence becomes possible when grasses prefer

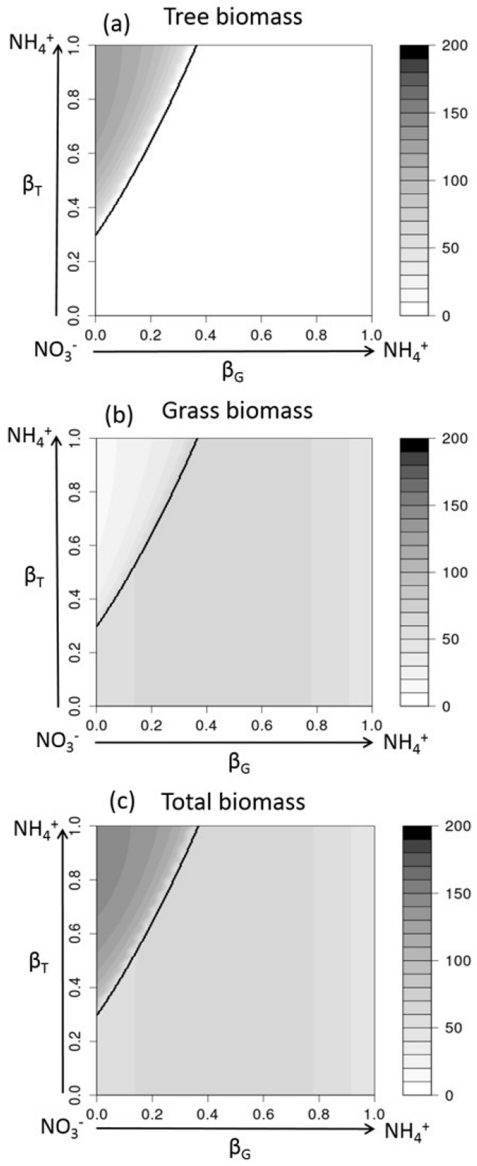

Figure 2.3 – Diagrams of tree biomass (a), grass biomass (b) and total biomass (c) when nitrification only depends on the availability of NH_4^+. Biomass values are equilibrium biomass resulting from the mutual invasion between trees and grasses. The solid line delimits the zone of tree-grass coexistence and the zone of invasion by grasses (above this line trees and grasses coexist and below this line grasses exclude trees). The color gradient is expressed in kgN ha^{-1}.

NH_4^+ and trees prefer NO_3^-. When grasses and trees have the same N uptake rate (Fig. 2.5c), trees tend to exclude grasses for all combinations of β_G and β_T except for a small zone of coexistence when trees have a high preference for NO_3^- and grasses for NH_4^+.

In contrast to model 1, preferences corresponding to the zone of coexistence in model 2 do not change when N uptake rate increases. Coexistence occurs nearly under the same condition as in model 1 (Fig. 2.5d, zone 3) when the rate of N uptake is low. Unlike with model 1, there is a small zone where no invasion is possible (but residents persist) (Fig. 2.5d, zone 0). When N uptake by trees increases (Fig. 2.5e, $u_T = 0.058$ $ha\ kg^{-1}$N yr^{-1}), this zone increases (intermediate β_G values and low β_T values). When N uptake by trees becomes equal to the uptake by grasses (Fig. 2.5f), the size of the zone of coexistence decreases, the size of the zone of exclusion of grasses increases, and the zone where no

invasion is possible disappears.

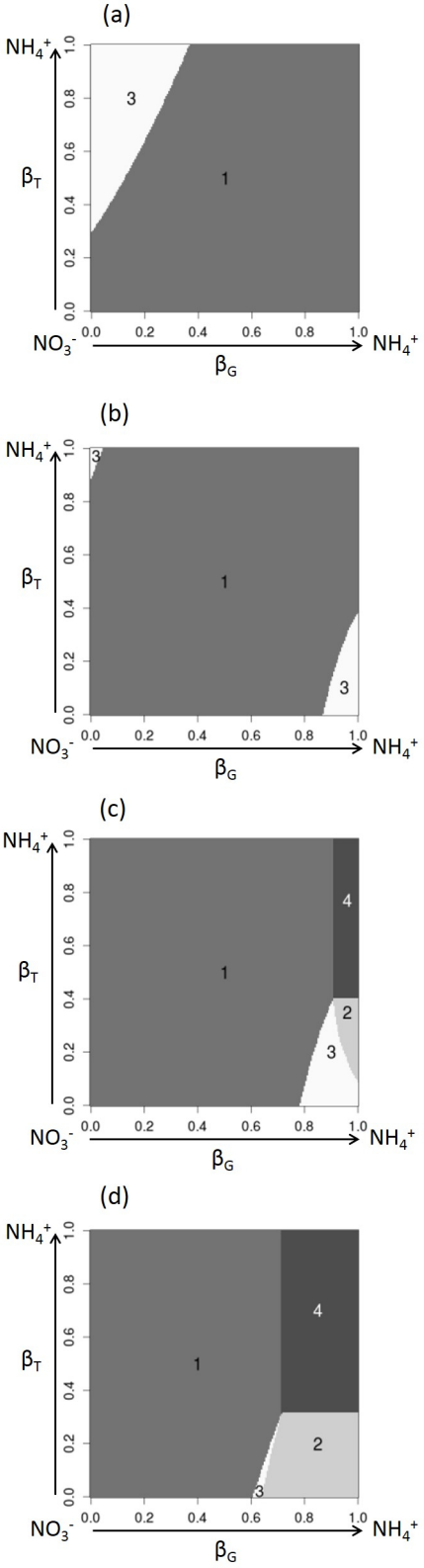

Figure 2.4 – Diagrams of mutual invasion between trees and grasses of model 1 according to different nitrification rates. Nitrification rate increases from the top to the bottom (a): $n = 2.7\ yr^{-1}$, (b): $n = 5\ yr^{-1}$, (c): $n = 6\ yr^{-1}$, (d): $n = 10\ yr^{-1}$. Invasion zones: 1, grasses invade and exclude trees; 2, trees invade and exclude grasses; 3, trees and grasses coexist and 4, no invasion and exclusion of residents.

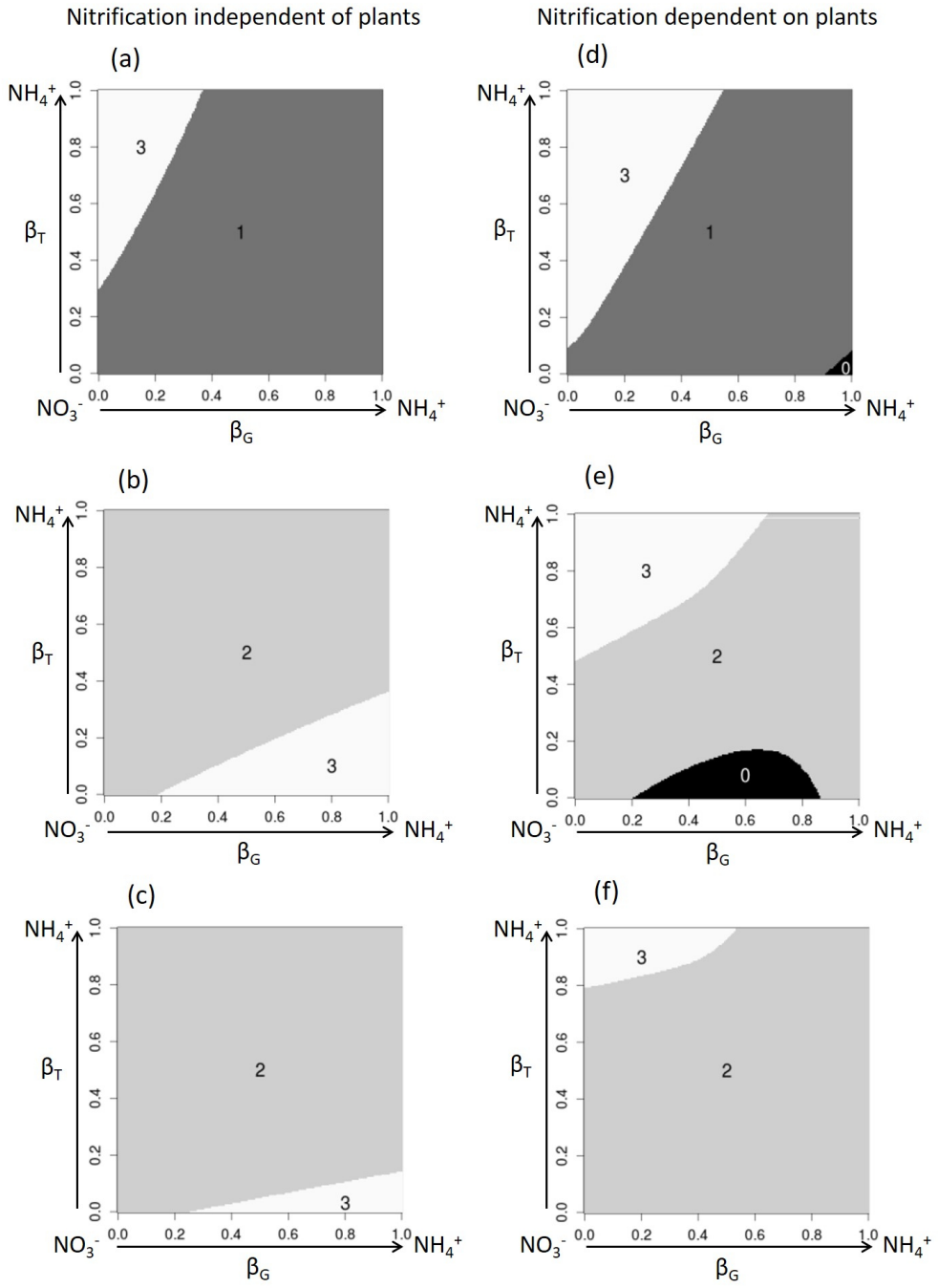

Figure 2.5 – Diagrams of mutual invasion between trees and grasses according to different values of N uptake by trees. Panels (a), (b) and (c) correspond to cases where nitrification is independent from the biomass of trees and grasses. Panels (d), (e) and (f) correspond to cases where nitrification depends on the biomass of trees and grasses. The uptake of mineral N by trees increases from the top to the bottom (a and d: $u_T = 0.018\ ha\ kg^{-1}\text{N}\ yr^{-1}$, b and e: $u_T = 0.058\ ha\ kg^{-1}\text{N}\ yr^{-1}$, c and f: $u_T = 0.14186\ ha\ kg^{-1}\text{N}\ yr^{-1}$). Invasion zones: 0, no invasion but residents persist; 1, grasses invade and exclude trees; 2, trees invade and exclude grasses; 3, trees and grasses coexist.

2.4 Discussion

2.4.1 Partitioning of mineral N may explain coexistence

Both models suggest that the partitioning of the two forms of mineral N can allow coexistence. This is consistent with theories suggesting that the use of different resources allows the coexistence among

different species through a stabilizing mechanism (Armstrong and McGehee, 1980; Chesson, 2000). Such coexistence by resource partitioning is a particular case of niche complementarity (Barot and Gignoux, 2004; Silvertown, 2004). Our results are supported by empirical studies on niche partitioning for different chemical forms of N (NH_4^+, NO_3^- and amino acids) that show that plant species differ in their preferences for various N forms and suggest that this can allow them to coexist (Ashton et al., 2010; Harrison et al., 2007; Kahmen et al., 2006; McKane et al., 2002).

In our models, the partitioning of mineral N only enables the coexistence of species having contrasting preferences for NH_4^+ and NO_3^- (Fig. 2.2) as in Boudsocq et al. (2012). Indeed, the case for which plants prefer the same mineral N form is similar to competition for a single resource and coexistence is not possible because the best competitor for this mineral form excludes the other species given that the resource is limiting enough (Hardin, 1960). In accordance with Boudsocq et al. (2012), we found that the inhibition or stimulation of nitrification could influence coexistence. Nitrification and the factors controlling it modify the availability of NH_4^+ relative to NO_3^-. If nitrification is very strong, only NO_3^- is available; if it is low, only NH_4^+ is available. In either case, the species preferring the unavailable N form is excluded because N tends to be available under a single form and becomes a single resource. Chances of coexistence are thus maximized for intermediate rates of nitrification. In contrast to the model of Boudsocq et al. (2012) that considered two species having the same N uptake rate (independently of their preference for NH_4^+ *versus* NO_3^-), we show that species having different N uptake rates can also coexist. This strongly increases the likelihood that the emphasized coexistence mechanism influences real plant communities where plants differ in their ecological and physiological characteristics.

2.4.2 Model limitations

Our model is a mean-field model where trees and grasses have access to the same mineral N compartments. But savannas are spatially structured ecosystems with tree clumps and patches of grasses (Barot et al., 1999). It would thus be more realistic to build a model taking into account the spatial heterogeneity of nitrification fluxes with zones of low nitrification under grasses (Lata et al., 2004, 2000; Srikanthasamy et al., 2018) and zones of high nitrification under tree canopy (Srikanthasamy et al., 2018). This model would also allow taking into account competition for light and the fact that under trees, the growth of grasses is limited by tree shading (leading to a spatially heterogeneous rate of mineral N uptake for grasses).

We acknowledge that plant preference for NH_4^+ *versus* NO_3^- is a multifactorial complex process (Britto and Kronzucker, 2013) . At the root scale, this parameter depends on physiological properties of roots (at least NH_4^+ and NO_3^- transporters). At the plant scale, it also depends on plant capacity to reduce and metabolize NO_3^-, which is a costly process (Konnerup and Brix, 2010). However, at the plant or ecosystem scale, it should also depend on the spatial-temporal distribution of the two forms of mineral N within the soil profile and on root distribution (Ashton et al., 2010; Fang et al., 1999; Houlton et al., 2007). We assumed a fixed value for the preference for NH_4^+ *versus* NO_3^- that does not take into account the plasticity of plants in the uptake of mineral N according to environmental and physiological conditions. This means that fully testing our hypotheses and determining the

consequences of N recycling on the tree-grass dynamics should involve: (1) assessing the preference for NH_4^+ *versus* NO_3^- of trees and grasses of the Lamto savanna, (2) assessing the plasticity in this preference, (3) including this plasticity in new models. In the same vein, our models do not explicitly include many additional important processes such as water fluxes and temporal variations of N cycle. Model parameters are averaged values concealing the spatio-temporal variability in N fluxes. In particular, mineralization, nitrification and denitrification depend on soil humidity and the seasonality in rainfall. Implementing such a temporal variability would allow answering new questions about the influence of the synchronization and desynchronization of N fluxes.

2.4.3 Case of savannas: influence of nitrification on coexistence

Many mechanisms have been suggested to explain tree-grass coexistence in savannas (Sankaran et al., 2004). So far, studies on resource partitioning between trees and grasses have only dealt with the spatial and temporal separation of the water resource (Walker and Noy-Meir, 1982; Walter, 1971). Competition for mineral N between trees and grasses has been modelled in savannas, but N has been considered as a single resource (Donzelli et al., 2013), whereas the models developed in this study take into account two different pools of mineral N (NH_4^+ and NO_3^-).

Our models suggest that, for a low nitrification rate, grasses and trees coexist when grasses prefer NO_3^- and trees prefer NH_4^+ (Fig. 2.4a). This case is not consistent with our hypothesis that coexistence is facilitated when grasses prefer NH_4^+ and trees prefer NO_3^-. Lamto perennial grasses are known to inhibit nitrification (Lata et al., 2004, 2000; Srikanthasamy et al., 2018) while trees stimulate it (Srikanthasamy et al., 2018), which suggests that grasses should preferNH_4^++ and trees NO_3^- ($\beta_G > 0.7$; $\beta_T < 0.3$). When nitrification rate increases and reaches an intermediate value, coexistence becomes possible if grasses prefer NH_4^+ and trees prefer NO_3^- (Fig. 2.4b). The latter case is consistent with our hypothesis and seems more realistic. This suggests that nitrification inhibition can be viewed as an adaptation of some savanna grasses to increase N availability (Lata et al., 2004; Subbarao et al., 2007) and nitrification stimulation may be interpreted as a response of trees to limit competition with grasses for NH_4^+. Although there is some evidence that nitrification-inhibiting grasses prefer NH_4^+ (Rossiter-Rachor et al., 2009) (Tavernier, 2003), further empirical studies are needed to test tree and grass preferences for NH_4^+ *versus* NO_3^- in the Lamto savanna and in savannas with different pedoclimatic conditions. In any case, we do not expect a strict preference for one form or the other (tree being only able to take up NO_3^- and grasses, NH_4^+) because taking up one form of mineral N does not prevent the uptake of the other form. Moreover, some studies showed that plant growth is maximized when plants take up a mixture of NH_4^+ and NO_3^- (Britto and Kronzucker, 2002; Forde and Clarkson, 1999; Konnerup and Brix, 2010). It must be noticed that tree and grass preferences for NH_4^+ *versus* NO_3^- also influence tree and grass biomass (Fig. 2.3) and that coexistence through N partitioning does not necessarily maximize total biomass (Appendix 3). This suggests that further studies should focus on the way tree and grass preferences for NH_4^+ *versus* NO_3^- and nitrification influence the plant biomass of savannas and their primary production. Finally, the existence of zones where both trees and grasses simultaneously have a clear preference for NH_4^+ and cannot persist because nitrification is too high (zone 4 in Fig. 2.4) confirms that evolution should select complementary strategies linking the preference for NH_4^+ and NO_3^- and the ability to inhibit or stimulate nitrification.

2.4.4 Alternative stable states in tree-grass dynamics

The analysis of the second model where nitrification depends on the availability of NH_4^+ and plant biomass shows that the control of nitrification can lead to bistability (Appendix 4) when trees and grasses have a high preference respectively for NO_3^- ($\beta_T < 0.1$) and NH_4^+ ($\beta_G > 0.93$). Depending on the initial biomass of trees and grasses, only trees or grasses persist. This is a kind of founder control effect (Perry et al., 2003) where initially present trees impede any invasion by grass and vice versa, by increasing the availability of their preferred form of mineral N. The low density of invaders prevents them from influencing the availability of NH_4^+ or NO_3^- and thus to increase the availability of their preferred N form (Boudsocq et al., 2012). The possibility of such scenarios and the required preferences for NH_4^+ and NO_3^- would need to be tested empirically.

Determining whether savannas are bistable systems is important to predict their dynamics (Staver et al., 2011a; Van Langevelde et al., 2003). Baudena and Rietkerk (2013) showed that depending on the initial density of trees and grasses, multiple states could be observed, leading to the tree-grass coexistence or the exclusion of either trees or grasses, or even the exclusion of both. In African savannas, intermediate values of precipitation may lead to the presence of two alternative stable states, i.e., savannas and forests (Sankaran et al., 2008). In this case, fire and herbivores become a determinant factor of the savanna structure because they prevent the establishment of a forest by reducing woody cover and thus allow grasses to persist (Higgins et al., 2010; Staver et al., 2011a,b). While fire and herbivory are usually mentioned as factors responsible for savanna bistability, our model suggests that plant-soil feedbacks and the partitioning of the N resource could also be involved in such a bistability.

2.5 Conclusion and perspectives

We have shown that mineral N partitioning can be involved in tree-grass coexistence in the Lamto savanna and that this mechanism should be more efficient when grasses inhibit nitrification and trees stimulate nitrification. Adjustments and new parameterization are required to test whether the partitioning of the mineral N resource is likely to facilitate tree-grass coexistence in other types of savannas. There are some hints that the capacity to inhibit nitrification is a general phenomenon in African perennial grasses (Lata et al., 2004; Rossiter-Rachor et al., 2009; Subbarao et al., 2007). This inhibition suggests that mineral N partitioning could be involved in tree-grass coexistence of many African savannas, especially of West African savannas that share many tree and grass species with the Lamto savanna. However, grass BNI capacity has so far never been tested on a large geographical and taxonomic scale and needs to be studied in other savannas. This should be achieved to assess the generality of our model results testing BNI abilities in more African savanna grasses and in Australian and South American native savanna grasses. Because of the success of African perennial grasses in South America and Australia (D'Antonio and Vitousek, 1992; Rossiter-Rachor et al., 2017), we hypothesize that savanna grasses non-native from Africa do not have BNI capacities and that the mechanism we emphasize would not hold outside African savannas. Furthermore, our model does not take into account two important features, absent from the Lamto savanna, but important in other savannas: high herbivore pressures and N fixing trees (e.g. *Acacias*) that can lead to an N limited system under grasses and a P-limited system under trees (Ludwig et al., 2001). These two features impact N

cycling and should be included in future models to test the influence of our proposed nutrient-related coexistence mechanism in these savannas. Different coexistence mechanisms often interact with one another (Ellner et al., 2019; Van Langevelde et al., 2003,?). In our case, mineral N partitioning very likely interacts with fire-induced mortality reported for trees in the Lamto savanna (Hochberg et al., 1994). These mechanisms involve tree and grass demography (Higgins et al., 2000), while our models only focus on the role of N fluxes. Future studies on interaction mechanisms determining tree-grass coexistence and their relative influence should therefore involve individual-based models that allow to take into account both tree and grass demography and N fluxes. Coexistence may also depend on mechanisms leading to more complex uptake functions (i.e., saturating with the availability of the N pool and plant biomass) (Rastetter et al., 2002). New simulations (Appendix 5) show that such mechanisms interact with the partition of the mineral N resource to determine the possibility of tree-grass coexistence and could, depending on parameters values, increase the possibilities of coexistence, or lead the same pattern of coexistence found with the linear donor-recipient function.

In summary, our modeling study emphasizes that mineral N partitioning could be a highly relevant mechanism determining coexistence of savanna trees and grasses aside from other commonly suggested mechanisms. Partitioning of mineral N forms should be also studied further because it may influence the total biomass and its repartition between trees and grasses.

Besides, as our models are rather theoretical, it will be necessary to test their results using empirical approaches, for example by manipulating N limitation and the relative availability of NH_4^+ and NO_3^- (by the addition of N fertilizer), or by assessing N fluxes in the field using in situ labeling of N. Finally, the partitioning of mineral N forms between trees and grasses could also be involved in the currently observed global trend of woody encroachment in savannas (Ward, 2005). This encroachment is likely due to a combination of factors (increase in atmospheric CO_2, changes in fire regimes and herbivore pressures), but our model results suggest that N cycling and the current global eutrophication of terrestrial ecosystems could also be influential, especially when atmospheric deposits of N add more NH_4^+ than NO_3^-, as it is the case at the Lamto site (Abbadie, 2006).

Bibliography

Abbadie, L. (2006). Nitrogen inputs to and outputs from the soil-plant system. In *Lamto: structure, functioning, and dynamics of a savanna ecosystem*, pages 255–275. New York: Springer.

Abbadie, L., Gignoux, J., Le Roux, X., and Lepage, M. (2006). *Lamto: structure, functioning, and dynamics of a savanna ecosystem*. New York: Springer.

Accatino, F., De Michele, C., Vezzoli, R., Donzelli, D., and Scholes, R. J. (2010). Tree–grass co-existence in savanna: interactions of rain and fire. *Journal of theoretical biology*, 267(2):235–242.

Aerts, R. (1996). Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology*, 84:597–608.

Armstrong, R. A. and McGehee, R. (1980). Competitive exclusion. *The American Naturalist*, 115(2):151–170.

Ashton, I. W., Miller, A. E., Bowman, W. D., and Suding, K. N. (2010). Niche complementarity due to plasticity in resource use: plant partitioning of chemical n forms. *Ecology*, 91(11):3252–3260.

Barot, S. and Gignoux, J. (2004). Mechanisms promoting plant coexistence: can all the proposed processes be reconciled? *Oikos*, 106(1):185–192.

Barot, S., Gignoux, J., and Menaut, J.-C. (1999). Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. *Ecology*, 80(6):1987–2005.

Baudena, M. and Rietkerk, M. (2013). Complexity and coexistence in a simple spatial model for arid savanna ecosystems. *Theoretical Ecology*, 6(2):131–141.

Bernhard-Reversat, F. and Poupon, H. (1980). Nitrogen cycling in a soil-tree system in a sahelian savanna: example of *Acacia senegal*. In *Proceedings of a workshop arranged by the SCOPE/UNEP*, pages 363–9.

Boudsocq, S., Lata, J.-C., Mathieu, J., Abbadie, L., and Barot, S. (2009). Modelling approach to analyse the effects of nitrification inhibition on primary production. *Functional Ecology*, 23(1):220–230.

Boudsocq, S., Niboyet, A., Lata, J. C., Raynaud, X., Loeuille, N., Mathieu, J., Blouin, M., Abbadie, L., and Barot, S. (2012). Plant preference for ammonium versus nitrate: a neglected determinant of ecosystem functioning? *The American Naturalist*, 180(1):60–69.

Britto, D. T. and Kronzucker, H. J. (2002). NH_4^+ toxicity in higher plants: a critical review. *Journal of plant physiology*, 159(6):567–584.

Britto, D. T. and Kronzucker, H. J. (2013). Ecological significance and complexity of N-source preference in plants. *Annals of botany*, 112(6):957–963.

Chesson, P. (2000). General theory of competitive coexistence in spatially-varying environments. *Theoretical population biology*, 58(3):211–237.

D'Antonio, C. M. and Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual review of ecology and systematics*, 23(1):63–87.

Donzelli, D., De Michele, C., and Scholes, R. (2013). Competition between trees and grasses for both soil water and mineral nitrogen in dry savannas. *Journal of theoretical biology*, 332:181–190.

Ellner, S. P., Snyder, R. E., Adler, P. B., and Hooker, G. (2019). An expanded modern coexistence theory for empirical applications. *Ecology letters*, 22(1):3–18.

Falkengren-Grerup, U. and Lakkenborg-Kristensen, H. (1994). Importance of ammonium and nitrate to the performance of herb-layer species from deciduous forests in southern sweden. *Environmental and Experimental Botany*, 34(1):31–38.

Fang, Y., Babourina, O., Rengel, Z., Yang, X., and Pu, M. (1999). Ammonium and nitrate uptake by the floating plant landoltia punctata. *Annals of Botany*, 99:365–370.

February, E. C., Higgins, S. I., Bond, W. J., and Swemmer, L. (2013). Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology*, 94(5):1155–1164.

Forde, B. G. and Clarkson, D. T. (1999). Nitrate and ammonium nutrition of plants: physiological and molecular perspectives. *Advances in botanical research*, 30:1–90.

Gignoux, J., Lahoreau, G., Julliard, R., and Barot, S. (2009). Establishment and early persistence of tree seedlings in an annually burned savanna. *Journal of Ecology*, 97(3):484–495.

Hardin, G. (1960). The competitive exclusion principle. *science*, 131(3409):1292–1297.

Harrison, K. A., Bol, R., and Bardgett, R. D. (2007). Preferences for different nitrogen forms by coexisting plant species and soil microbes. *Ecology*, 88(4):989–999.

Higgins, S. I., Bond, W. J., and Trollope, W. S. (2000). Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology*, 88(2):213–229.

Higgins, S. I., Scheiter, S., and Sankaran, M. (2010). The stability of african savannas: insights from the indirect estimation of the parameters of a dynamic model. *Ecology*, 91(6):1682–1692.

Hochberg, M. E., Menaut, J. C., and Gignoux, J. (1994). The influences of tree biology and fire in the spatial structure of the west african savannah. *Journal of Ecology*, 82:217–226.

Holdo, R. M., Nippert, J. B., and Mack, M. C. (2018). Rooting depth varies differentially in trees and grasses as a function of mean annual rainfall in an african savanna. *Oecologia*, 186(1):269–280.

Holt, R. D. (2008). Theoretical perspectives on resource pulses. *Ecology*, 89(3):671–681.

Houlton, B. Z., Sigman, D. M., Schuur, E. A., and Hedin, L. O. (2007). A climate-driven switch in plant nitrogen acquisition within tropical forest communities. *Proceedings of the National Academy of Sciences*, 104(21):8902–8906.

Huangfu, C., Li, H., Chen, X., Liu, H., Wang, H., and Yang, D. (2016). Response of an invasive plant, *Flaveria bidentis*, to nitrogen addition: a test of form-preference uptake. *Biological invasions*, 18(11):3365–3380.

Jeltsch, F., Weber, G. E., and Grimm, V. (2000). Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology*, 150(1-2):161–171.

Jumpponen, A., Högberg, P., Huss-Danell, K., and Mulder, C. (2002). Interspecific and spatial differences in nitrogen uptake in monocultures and two-species mixtures in north European grasslands. *Functional Ecology*, 16(4):454–461.

Kahmen, A., Renker, C., Unsicker, S. B., and Buchmann, N. (2006). Niche complementarity for nitrogen: an explanation for the biodiversity and ecosystem functioning relationship? *Ecology*, 87(5):1244–1255.

Konnerup, D. and Brix, H. (2010). Nitrogen nutrition of *Canna indica*: effects of ammonium versus nitrate on growth, biomass allocation, photosynthesis, nitrate reductase activity and n uptake rates. *Aquatic Botany*, 92(2):142–148.

Lata, J.-C. (1999). *Interactions entre processus microbiens, cycle des nutriments et fonctionnement du couvert herbacé: cas de la nitrification dans les sols d'une savane humide de Côte d'Ivoire sous couvert à Hyparrhenia diplandra*. PhD thesis, Paris 6.

Lata, J.-C., Degrange, V., Raynaud, X., Maron, P.-A., Lensi, R., and Abbadie, L. (2004). Grass populations control nitrification in savanna soils. *Functional Ecology*, 18(4):605–611.

Lata, J.-C., Guillaume, K., Degrange, V., Abbadie, L., and Lensi, R. (2000). Relationships between root density of the african grass *Hyparrhenia diplandra* and nitrification at the decimetric scale: an inhibition–stimulation balance hypothesis. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1443):595–600.

Le Roux, X., Abbadie, L., Fritz, H., and Leriche, H. (2006). Modifications of the savanna functioning by herbivores. In *Lamto: structure, functioning, and dynamics of a savanna ecosystem*, pages 185–198. New York: Springer.

Ludwig, F., de Kroon, H., Prins, H. H., and Berendse, F. (2001). Effects of nutrients and shade on tree-grass interactions in an east african savanna. *Journal of Vegetation Science*, 12(4):579–588.

Maire, V., Gross, N., da Silveira Pontes, L., Picon-Cochard, C., and Soussana, J.-F. (2009). Trade-off between root nitrogen acquisition and shoot nitrogen utilization across 13 co-occurring pasture grass species. *Functional Ecology*, 23(4):668–679.

Marschner, H. (2011). *Marschner's mineral nutrition of higher plants*. Academic press.

McKane, R. B., Johnson, L. C., Shaver, G. R., Nadelhoffer, K. J., Rastetter, E. B., Fry, B., Giblin, A. E., Kielland, K., Kwiatkowski, B. L., Laundre, J. A., et al. (2002). Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, 415(6867):68–71.

Menaut, J. and Cesar, J. (1979). Structure and primary productivty of lamto savannas, ivory coast. *Ecology*, 60(6):1197–1210.

Miller, A. E. and Bowman, W. D. (2002). Variation in nitrogen-15 natural abundance and nitrogen uptake traits among co-occurring alpine species: do species partition by nitrogen form? *Oecologia*, 130(4):609–616.

Mordelet, P., Menaut, J.-C., and Mariotti, A. (1997). Tree and grass rooting patterns in an african humid savanna. *Journal of Vegetation Science*, 8(1):65–70.

Nacry, P., Bouguyon, E., and Gojon, A. (2013). Nitrogen acquisition by roots: physiological and developmental mechanisms ensuring plant adaptation to a fluctuating resource. *Plant and Soil*, 370(1-2):1–29.

Perry, L. G., Neuhauser, C., and Galatowitsch, S. M. (2003). Founder control and coexistence in a simple model of asymmetric competition for light. *Journal of Theoretical Biology*, 222(4):425–436.

R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rastetter, E. B. et al. (2002). Changes in individual allometry can lead to species coexistence without niche separation. *Ecosystems*, 5(8):0789–0801.

Rossiter-Rachor, N., Setterfield, S., Douglas, M., Hutley, L. B., Cook, G., and Schmidt, S. (2009). Invasive *Andropogon gayanus* (gamba grass) is an ecosystem transformer of nitrogen relations in australian savanna. *Ecological Applications*, 19(6):1546–1560.

Rossiter-Rachor, N. A., Setterfield, S. A., Hutley, L., McMaster, D., Schmidt, S., and Douglas, M. M. (2017). Invasive *Andropogon gayanus* (gamba grass) alters decomposition and nitrogen fluxes in an australian tropical savanna. *Scientific reports*, 7:11705.

Salsac, L., Chaillou, S., Morot-Gaudry, J.-F., Lesaint, C., and Jolivet, E. (1987). Nitrate and ammonium nutrition in plants. *Plant physiology and biochemistry (Paris)*, 25(6):805–812.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., Gignoux, J., Higgins, S. I., Le Roux, X., Ludwig, F., et al. (2005). Determinants of woody cover in african savannas. *Nature*, 438(7069):846–849.

Sankaran, M., Ratnam, J., and Hanan, N. (2008). Woody cover in african savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography*, 17(2):236–245.

Sankaran, M., Ratnam, J., and Hanan, N. P. (2004). Tree–grass coexistence in savannas revisited–insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology letters*, 7(6):480–490.

Schenk, H. J. and Jackson, R. B. (2002). Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, 90(3):480–494.

Scholes, R. and Archer, S. (1997). Tree-grass interactions in savannas. *Annual review of Ecology and Systematics*, 28(1):517–544.

Silvertown, J. (2004). Plant coexistence and the niche. *Trends in Ecology & evolution*, 19(11):605–611.

Soetaert, K. E., Petzoldt, T., and Setzer, R. W. (2010). Solving differential equations in R: package desolve. *Journal of Statistical Software*, 33.

Srikanthasamy, T., Leloup, J., N'Dri, A. B., Barot, S., Gervaix, J., Koné, A. W., Koffi, K. F., Le Roux, X., Raynaud, X., and Lata, J.-C. (2018). Contrasting effects of grasses and trees on microbial n-cycling in an african humid savanna. *Soil Biology and Biochemistry*, 117:153–163.

Staver, A. C., Archibald, S., and Levin, S. (2011a). Tree cover in sub-saharan africa: rainfall and fire constrain forest and savanna as alternative stable states. *Ecology*, 92(5):1063–1072.

Staver, A. C., Archibald, S., and Levin, S. A. (2011b). The global extent and determinants of savanna and forest as alternative biome states. *Science*, 334(6053):230–232.

Subbarao, G., Nakahara, K., Hurtado, M. d. P., Ono, H., Moreta, D., Salcedo, A. F., Yoshihashi, A., Ishikawa, T., Ishitani, M., Ohnishi-Kameyama, M., et al. (2009). Evidence for biological nitrification inhibition in brachiaria pastures. *Proceedings of the National Academy of Sciences*, 106(41):17302–17307.

Subbarao, G., Rondon, M., Ito, O., Ishikawa, T., Rao, I. M., Nakahara, K., Lascano, C., and Berry, W. (2007). Biological nitrification inhibition (BNI)—is it a widespread phenomenon? *Plant and Soil*, 294(1-2):5–18.

Subbarao, G. V., Yoshihashi, T., Worthington, M., Nakahara, K., Ando, Y., Sahrawat, K. L., Rao, I. M., Lata, J.-C., Kishii, M., and Braun, H.-J. (2015). Suppression of soil nitrification by plants. *Plant Science*, 233:155–164.

Tavernier, V. A. M. (2003). *Interactions entre structures racinaires et cycle de l'azote en zone de savane africaine*. PhD thesis, Paris, Institut national d'agronomie de Paris Grignon.

Van Heerwaarden, L., Toet, S., and Aerts, R. (2003). Current measures of nutrient resorption efficiency lead to a substantial underestimation of real resorption efficiency: facts and solutions. *Oikos*, 101(3):664–669.

Van Langevelde, F., Van De Vijver, C. A., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A. K., Hearne, J. W., Stroosnijder, L., Bond, W. J., et al. (2003). Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, 84(2):337–350.

Walker, B. H. and Noy-Meir, I. (1982). Aspects of the stability and resilience of savanna ecosystems. In *Ecology of tropical savannas*, pages 556–590. Springer.

Walter, H. (1971). *Ecology of tropical and subtropical vegetation*. Edinburgh: Oliver Boyd.

Ward, D. (2005). Do we understand the causes of bush encroachment in african savannas? *African Journal of Range and Forage Science*, 22(2):101–105.

Ward, D., Wiegand, K., and Getzin, S. (2013). Walter's two-layer hypothesis revisited: back to the roots! *Oecologia*, 172(3):617–630.

Wolfram Research (2017). *Mathematica, Version 10.0*. Wolfram Research Champaign IL.

2.6 Appendix

2.6.1 Appendix 1: Equations and jacobian matrix of model 1

Model 1 corresponds to the case where nitrification only depends on the availability of NH_4^+ and is represented by the following equations:

$$\frac{dG}{dt} = \beta_G u_G N_A G + (1-\beta_G) u_G N_N G - (d_G + l_G) G \tag{2.8}$$

$$\frac{dT}{dt} = \beta_T u_T \, N_A \, T + (1-\beta_T) \, u_T N_N \, T - (d_T + l_T) \, T \tag{2.9}$$

$$\frac{dO}{dt} = R_O + d_T T + d_G \, G - (m + l_O) \, O \tag{2.10}$$

$$\frac{dN_A}{dt} = R_{NA} + m \, O - (\beta_G u_G \, G + \beta_{T1} u_T \, T + n + l_{NA}) \, N_A \tag{2.11}$$

$$\frac{dN_N}{dt} = R_{NN} + n \, N_A - ((1-\beta_G) u_G \, G + (1-\beta_T) u_T \, T + l_{NN}) \, N_N \tag{2.12}$$

Solving of model 1 leads to six equilibria. We calculate the jacobian matrix to determine their stability.

$$J(G,T,O,N_A,N_N) = 1 \begin{bmatrix} -d_G - l_G + \alpha_G N_A + (1-\beta_G) N_N & 0 & 0 & \alpha_G G & c_G G \\ 0 & -d_T - l_T + \alpha_T N_A + (1-\beta_T) N_N & 0 & \alpha_T T & c_T T \\ d_G & d_T & -l_0 - m & 0 & 0 \\ -\alpha_G N_A & -\alpha_T N_A & m & -lNA - n - \alpha_G G - \alpha_T T & 0 \\ -c_G n_N & -c_T n_N & 0 & n & -l_{NN} - c_G - c_T T \end{bmatrix}$$

with $a_G = u_G \, \beta_G$; $a_T = u_T \, \beta_T$; $c_G = u_G \, (1\text{-}\beta_G)$ and $c_T = u_T \, (1\text{-}\beta_T)$

2.6.2 Appendix 2: Plant biomass and coexistence

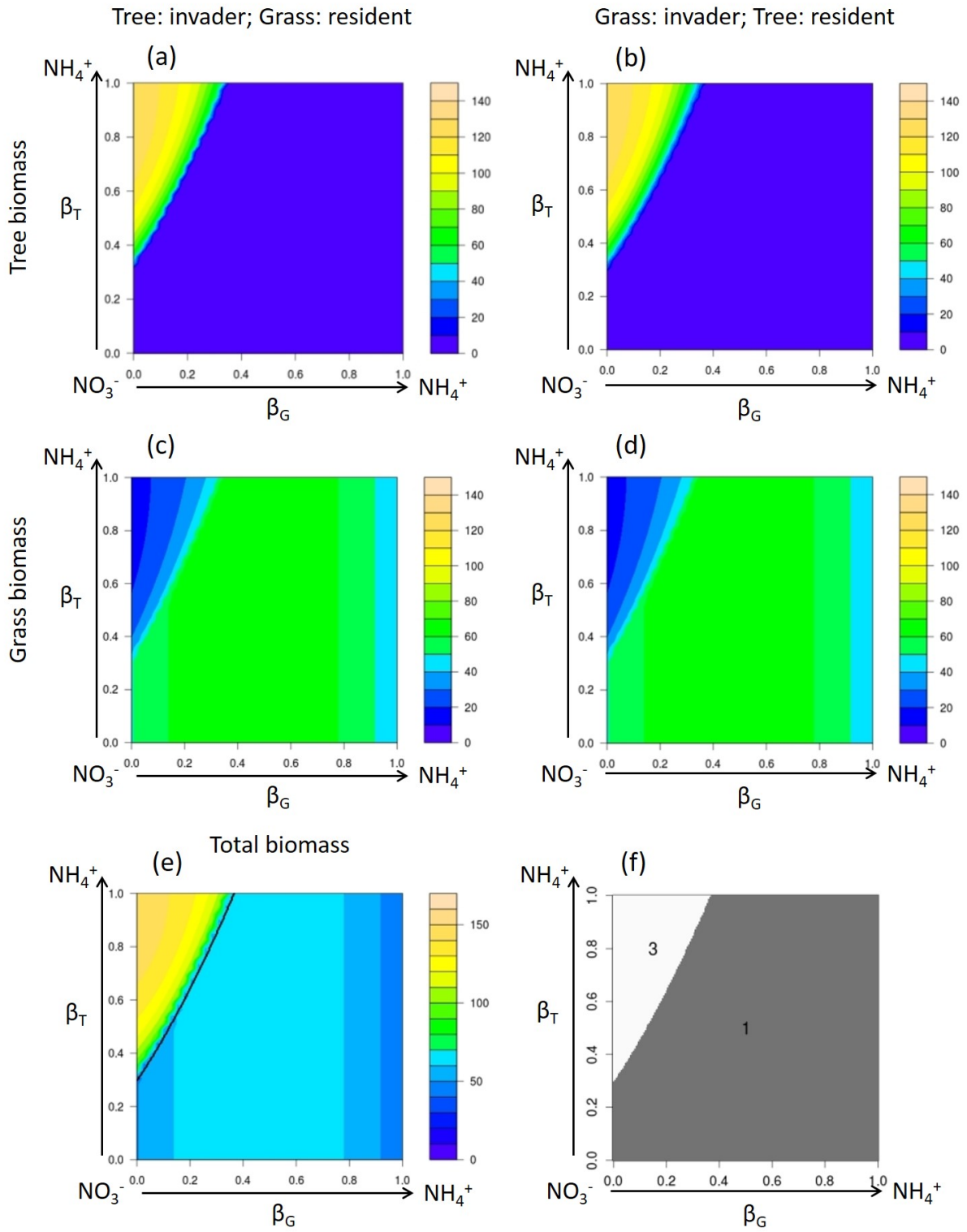

Figure 2.6 – Diagrams of tree biomass (a) and (b), grass biomass (c) and (d), total biomass (e) and coexistence/invasion (f) when nitrification only depends on the availability of NH_4^+. Invasion zones: 1, grasses exclude trees; 3, trees and grasses coexist. The color gradient is expressed in kg N/ha.

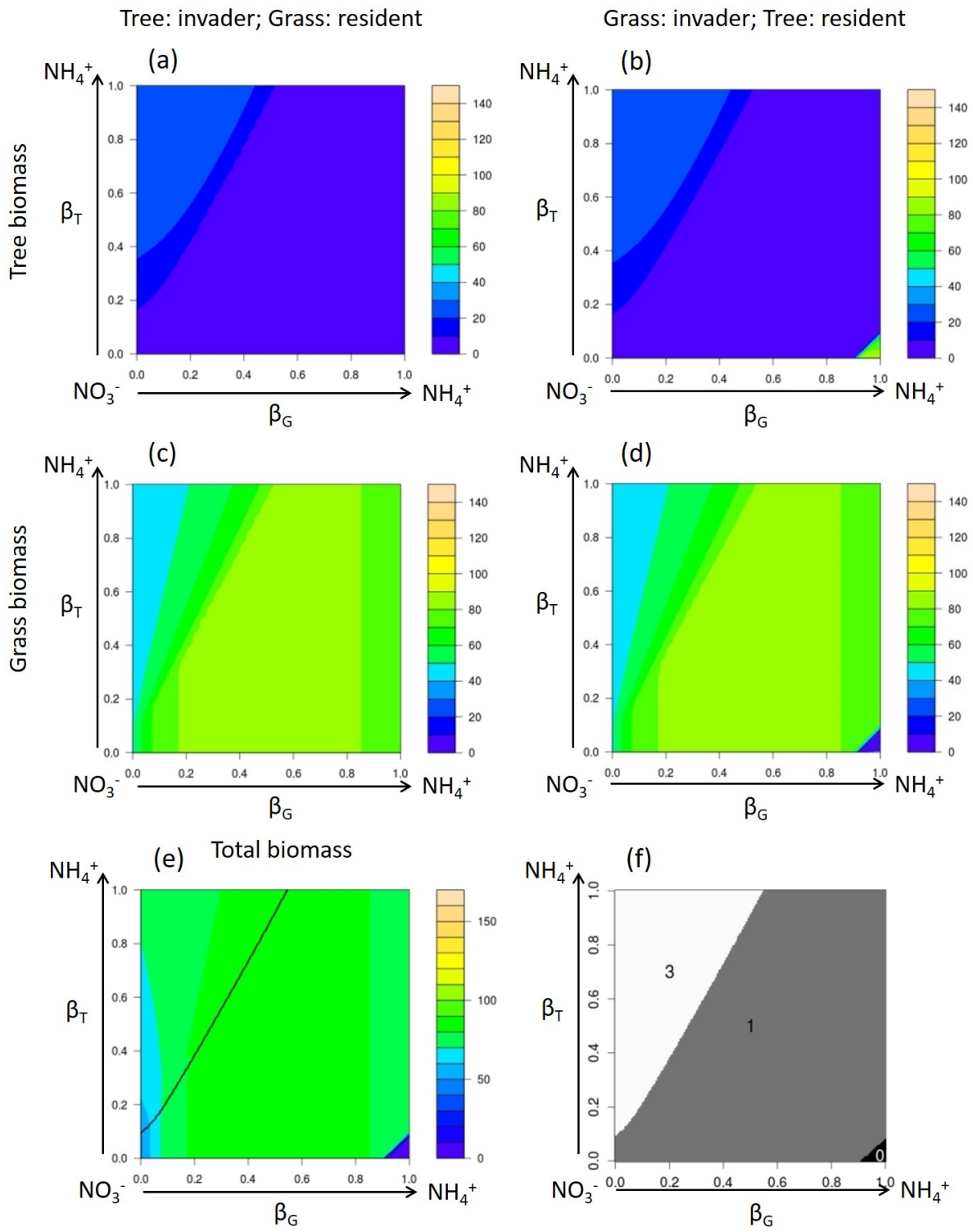

Figure 2.7 – Diagrams of tree biomass (a) and (b), grass biomass (c) and (d), total biomass (e) and coexistence/invasion (f) when nitrification depends on both the availability of NH_4^+ and the influence of tree and grass biomass. Invasion zones: 0, no invasion but residents persist; 1, grasses exclude trees; 3, trees and grasses coexist. The color gradient is expressed in kg N/ha.

2.6.3 Appendix 3: Link between coexistence and total biomass of trees and grasses

We focus on the case where coexistence is possible when trees prefer nitrate and grasses prefer ammonium ($n = 5\ yr^{-1}$). This case seems more realistic when we consider the inhibition of nitrification by grasses and stimulation of nitrification by trees in the Lamto savanna. We ran simulations of mutual invasion (grasses are the invading plant and trees are the resident species and the reverse).

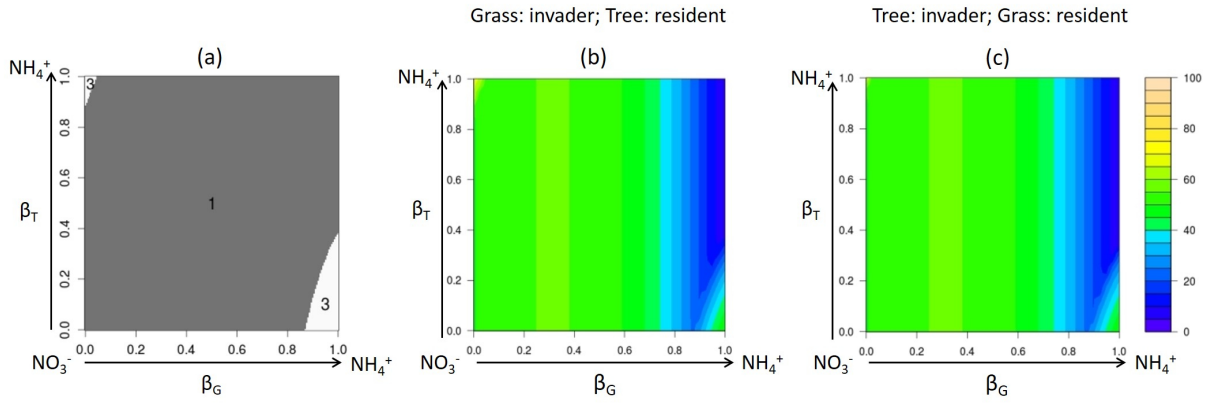

Figure 2.8 – Diagram of mutual invasion between trees and grasses of model 1 ($n = 5\ yr^{-1}$), total biomass corresponding to the diagram of mutual invasion when grasses invade (b) and trees invade (c). Invasion zones: 1, grasses exclude trees; 3, trees and grasses coexist. The color gradient is expressed in kg N/ha.

2.6.4 Appendix 4: Study of bistability

In the case where nitrification depends on the availability of NH_4^+ and the tree and grass biomass (model 2), we observe the presence of two alternative stable states. When trees prefer NO_3^- ($\beta_T = 0.005$) and grasses prefer NH_4^+ ($\beta_G > 0.9$), two different situations can be observed according to the initial grass biomass. If grasses are the resident species and trees are the invading species, grasses maintain a high biomass and trees are not able to invade. However, if grasses are the invading species and trees the resident species, grasses cannot invade and trees maintain a high biomass.

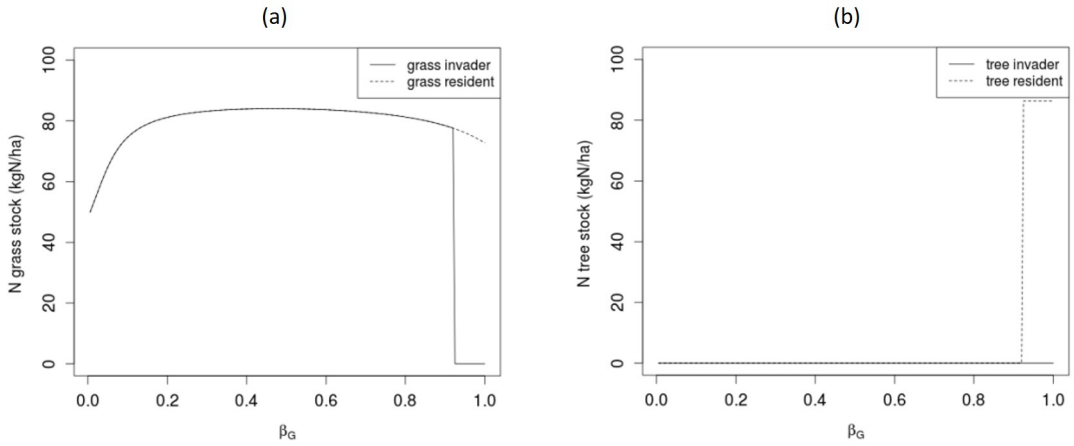

Figure 2.9 – Effects of grass preference for NH_4^+ on: (a) grass N stock and (b) tree N stock ($\beta_T = 0.005$)

2.6.5 Appendix 5: Sensitivity of tree-grass coexistence to nitrogen uptake function

In the main text of the article, we used "linearly donor-recipient" fluxes to model N uptake by plants. Rastetter et al. (2002) suggested that a linear growth function proportional to the population biomass limits the coexistence of species to the number of limiting resources in the ecosystem. Besides, they demonstrated that the coexistence of species limited by only one resource is possible if the growth function leads to a concave downward function that is not linearly proportional to the biomass. Hence, we tested the impact of the mathematical formula proposed by Rastetter et al. (2002) on tree-grass coexistence using the version of our model where nitrification is independent from plant biomass. More specifically, we tested whether this formula increases the possibilities of coexistence in our case where mineral resources is represented under two forms. We also tested how this formula changes the coexistence pattern found with the linearly donor-recipient formula. This new formula includes new parameters such as the reduction of N availability per unit of plant biomass (α_G for grasses and α_T for trees) and the N concentration when the plant achieves the half of its maximum growth (k_{NA} for NH_4^+ and k_{NN} for NO_3^-). For example, the NH_4^+ uptake flux becomes (e.g. for grasses):

$$G\frac{\alpha_G\, G+1}{\gamma_G\, G+1}\frac{u_G\beta_G\, N_A}{k_{NA}+N_A} \tag{2.13}$$

Taking into account this new formalism leads to the following equations:

$$\frac{dG}{dt} = G\frac{\alpha_G G+1}{\gamma_G G+1}\frac{u_G\beta_G N_A}{k_{NA}+N_A} + G\frac{\alpha_G G+1}{\gamma_G G+1}\frac{u_G(1-\beta_G)N_N}{k_{NN}+N_N} - (d_G+l_G)G \tag{2.14}$$

$$\frac{dT}{dt} = T\frac{\alpha_T T+1}{\gamma_T T+1}\frac{u_T\beta_T N_A}{k_{NA}+N_A} + T\frac{\alpha_T T+1}{\gamma_T T+1}\frac{u_T(1-\beta_T)N_N}{k_{NN}+N_N} - (d_T+l_T)T \tag{2.15}$$

$$\frac{dO}{dt} = R_O + d_G G + d_T T - (m+l_O)O \tag{2.16}$$

$$\frac{dN_A}{dt} = R_{NA} + mO - G\frac{\alpha_G G+1}{\gamma_G G+1}\frac{u_G\beta_G N_A}{k_{NA}+N_A} - T\frac{\alpha_T T+1}{\gamma_T T+1}\frac{u_T\beta_T N_A}{k_{NA}+N_A} - (n+l_{NA})N_A \tag{2.17}$$

$$\frac{dN_N}{dt} = R_{NN} + mO - G\frac{\alpha_G G+1}{\gamma_G G+1}\frac{u_G(1-\beta_G)N_{NN}}{k_{NN}+N_N} - T\frac{\alpha_T T+1}{\gamma_T T+1}\frac{u_T(1-\beta_T)N_N}{k_{NN}+N_N} - l_{NN}N_N \tag{2.18}$$

Rastetter et al. (2002) also showed that $\alpha < \gamma$ is a necessary condition to allow the coexistence of more than one species on a single resource. Because existing data on the Lamto savanna do not allow to easily parameterize the non linear uptake function (α_G, α_T, γ_G, γ_T, k_{NA} and k_{NN}), we considered $\alpha_G = \alpha_T$ and $k_{NA} = k_{NN}$ (k = 5) and chose values respecting the condition $\alpha < \gamma$ and allowing to obtain N stocks at equilibrium close to the values obtained with the linearly donor-recipient uptake functions (thus close to the real field values). Numerical simulations have been performed with two values of α (0.05 and 1.5) and one value for γ ($\gamma = 2$). We reproduced the same gradient in nitrification rate as in Fig. 2.4 of the main text.

When $\alpha = 0.05$, the region of coexistence is quite different and larger than in the initial model (Fig. 2.11-a). For a low nitrification ($n = 2.7\ yr^{-1}$), coexistence is possible for all combinations of β_G

and β_T. When nitrification rate increases, a zone where grasses exclude trees appear while the zone of coexistence decreases and coexistence is now possible for all values of β_G and when trees prefer NO_3^-. The region of coexistence becomes much smaller for high nitrification rates but the general coexistence pattern remains unchanged. When $\alpha = 1.5$, two zones appear as in the initial model (see main text Fig. 2.4a). For low nitrification, there is a zone of coexistence when grasses prefer NO_3^- and trees prefer NH_4^+ and a zone where grasses invade and exclude trees (Fig. 2.11-b). With increasing nitrification rate ($n = 5\ yr^{-1}$), the size of the zone of coexistence decreases. When nitrification rate increases further ($n = 6\ yr^{-1}$), the zone of coexistence virtually disappears. When nitrification rate is very high ($n = 10\ yr^{-1}$), coexistence reappears and becomes possible when grasses prefer NH_4^+ and trees prefer NO_3^-.

The study of Rastetter et al. (2002) suggests to explore more complex uptake functions allowing coexistence on a single resource. Our results confirm that the functions used for N uptake influences the conditions of coexistence. In particular, in some cases this lead to coexistence whatever tree and grass preferences for NH_4^+ and NO_3^- (cf Fig. 2.11-a). Nevertheless, the nonlinear uptake function does not fully change our results. For example, the general pattern of coexistence is conserved in the case of Fig. 2.11-b. Taken together, this suggests that it could be interesting in future models to consider other N uptake functions but this would require field work to be able to parameterize these functions. This has never been achieved in the Lamto savanna.

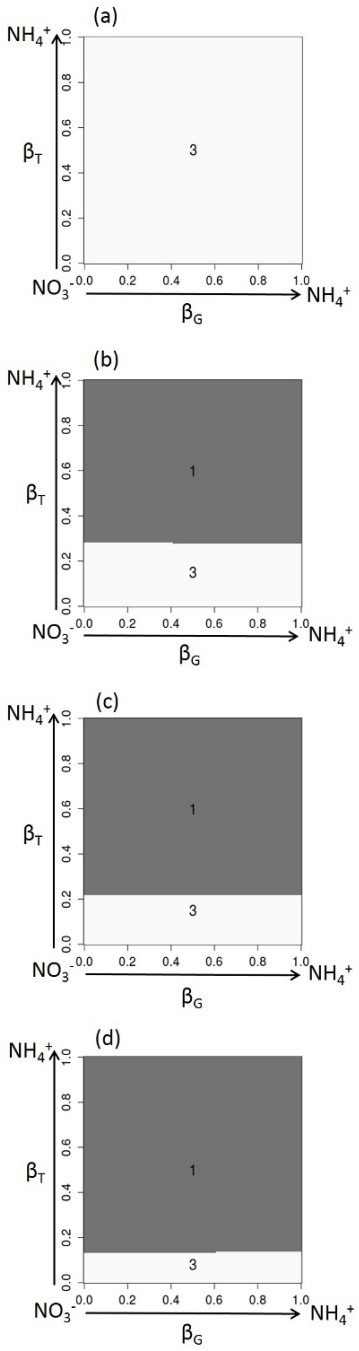

Figure 2.10 – Diagrams of mutual invasion between trees and grasses according to different nitrification rates. Simulations have been performed with the formula proposed by Rastetter et al. (2002) with α = 0.5. Nitrification rate increases from the top to the bottom (a): $n = 2.7\ yr^{-1}$, (b): $n = 5\ yr^{-1}$, (c): $n = 6\ yr^{-1}$, (d): $n = 10\ yr^{-1}$. Invasion zones: 1, grasses invade and exclude trees; 3, trees and grasses coexist.

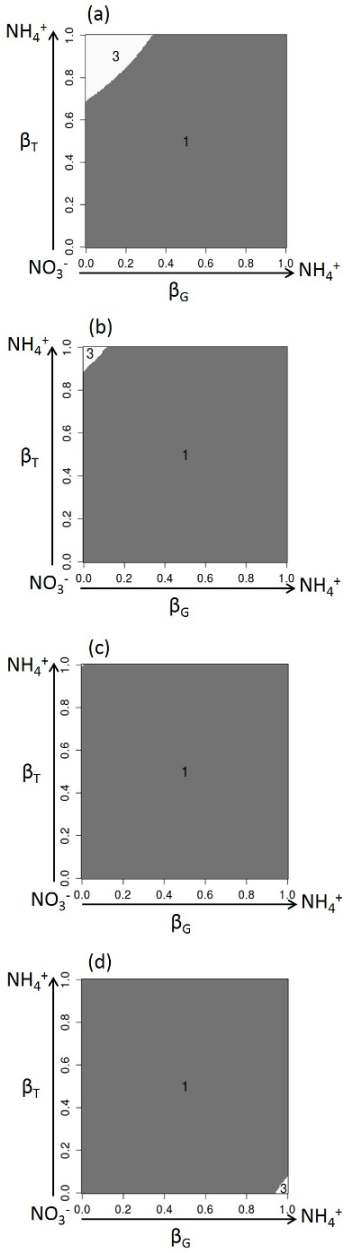

Figure 2.11 – Diagrams of mutual invasion between trees and grasses according to different nitrification rates. Simulations have been performed with the formula proposed by Rastetter et al. (2002) with α = 1.5. Nitrification rate increases from the top to the bottom (a): $n = 2.7\ yr^{-1}$, (b): $n = 5\ yr^{-1}$, (c): $n = 6\ yr^{-1}$, (d): $n = 10\ yr^{-1}$. Invasion zones: 1, grasses invade and exclude trees; 3, trees and grasses coexist.

3

Spatial heterogeneity in nitrification fluxes and horizontal soil exploration favour source-sink dynamics in a humid savanna

Spatial heterogeneity in nitrification and horizontal soil exploration favour source-sink dynamics in a humid savanna

S Konaré [1] *, S Boudsocq [2], J Gignoux [1], J-C Lata [1,3], X Raynaud [1] and S Barot [1]

[1] Sorbonne Université, IRD, CNRS, INRA, UPEC, Univ Paris Diderot, Institute of Ecology and Environmental Sciences, iEES Paris, 75005 Paris, France; [2] Eco&Sols, INRA, CIRAD, IRD, Montpellier SupaAgro, Univ Montpellier, Montpellier, France; [3] Department of Geoecology and Geochemistry, Institute of Natural Resources, Tomsk Polytechnic University, 30, Lenin Street, Tomsk 634050, Russia

Abstract

Savannas are structured ecosystems characterized by a grass layer interspersed with tree clumps. Trees strongly modify their local environment and favor 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. 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 analyzed the impact of spatial heterogeneity in nitrification and soil horizontal exploration on N budget and plant biomass. Our results show that horizontal soil exploration by roots allows trees to access more nutrients and leads to an asymmetric N flux from the open patch to tree clumps, which contributes to nutrient enrichment under tree clumps and increases tree growth. Even though trees are able to accumulate nutrients under their canopy through nutrient redistribution, increasing the surface occupied by tree clumps increases N losses due to the increased nitrification under trees and thus decreases the quantity of N available under tree canopy. The heterogeneity in N cycling created by savanna trees and grasses, the proportion of tree cover and the horizontal extension of tree roots strongly alter N budget and plant biomass 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. These factors should be determinant in West African humid savannas but should be further tested using empirical approaches.

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

3.1 Introduction

Savannas are spatially structured ecosystems dominated by C_4 grasses and trees that are more or less clumped (Scholes and Archer, 1997). Savanna functioning is determined by the interactions between plants, disturbances and resource availability (Hoffmann et al., 2012; Sankaran et al., 2005; Scholes and 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 and 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...) than in the open (Belsky et al., 1989; Mordelet et al., 1993). The increase of 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, 2001). 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 aboveground 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 and 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*, *Andropogon gayanus* and sorghum (Rossiter-Rachor et al., 2009; Subbarao et al., 2013). Suppressing nitrification allows keeping 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 canopy 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, 1996). This resultingly 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 center 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.

The aim of this study is to analyze how spatial heterogeneity due to nitrification control by plants and horizontal N fluxes between the open and tree clump patches through soil exploration by trees influence 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: (**i**) increasing horizontal soil exploration leads to an increasing asymmetric net N flux from the open to tree clumps, which increases tree biomass and contributes to the fertility of tree clump soil, (**ii**) 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 and (**iii**) 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", i.e. 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 *versus* low nitrification patches) and the intensity of fluxes between patches (N fluxes).

3.2 Two patch model

3.2.1 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. 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 (Fig. 3.1). Model compartments are N stocks expressed in kilograms of N per hectare of patch (kg N ha^{-1}) and exchange rates between compartments and patches are N fluxes, expressed in kilograms of N per hectare of patch per year

(kg N $ha^{-1}yr^{-1}$). Note that the term "plant biomass" only refers to the size of N pools in plants (trees or grasses). All parameters but 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.

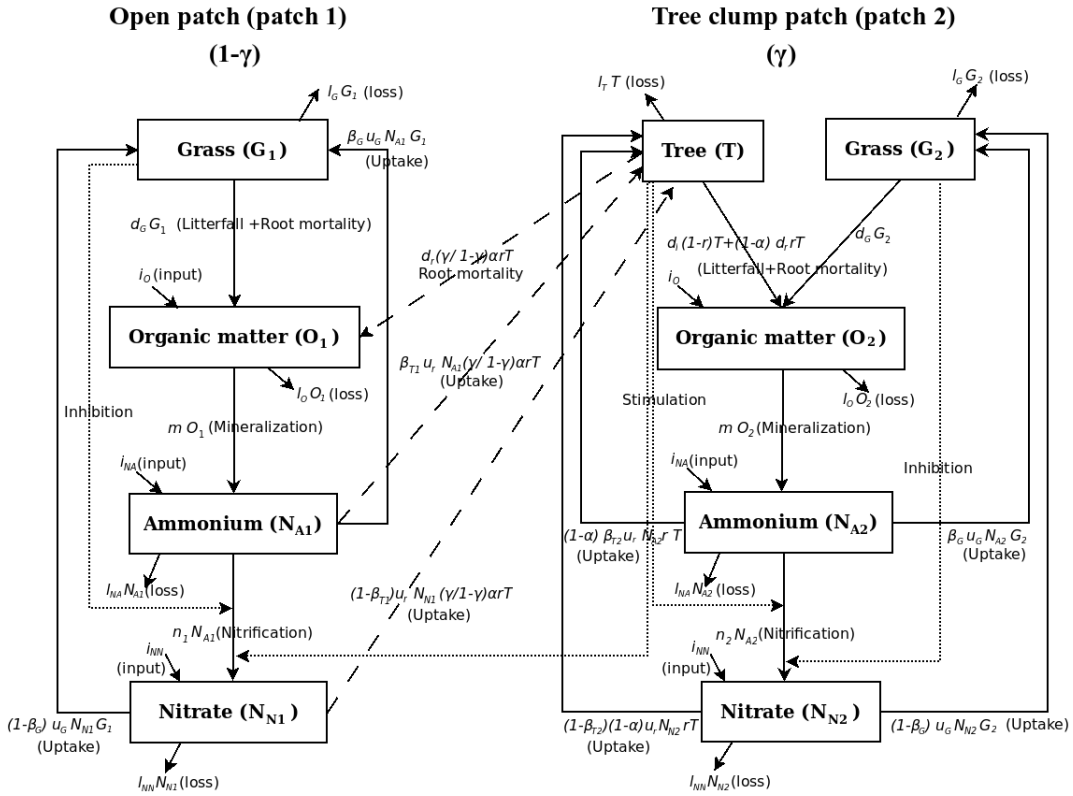

Figure 3.1 – Two patch model representing N dynamics between an open patch and a patch of tree clump in savanna ecosystem. Dashed lines correspond to horizontal exploration of tree roots under grasses and dotted lines correspond to the influence of plants on nitrification.

Following Boudsocq et al. (2012), grasses and trees can use N under 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), 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 α *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 modeled using donor-recipient functions, i.e., 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 $(1\text{-}\beta_{T1})\ u_r$ and $(1\text{-}\beta_{T2})\ u_r$ 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-γ). We thus considered the tree root biomass in the open (α r T) and we divided γ by (1-γ) to express N uptake by trees in kg N per hectare of the open. This leads to the following expressions:

$$\beta_{T1}\left(\frac{\gamma}{1-\gamma}\right) u_r N_{A1}\, \alpha r T$$

for NH_4^+ uptake and

$$(1-\beta_{T1})\left(\frac{\gamma}{1-\gamma}\right) u_r N_{N1}\, \alpha r T$$

for NO_3^- uptake.

It must be noted than in the field, the observed α depends on (1) the proportion of roots outside the canopy projection of each individual tree, (2) the proportion of tree cover (γ) and (3) the spatial distribution of individual trees. Nevertheless, in order to analyze the respective influence of α and γ, 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. 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 (rain and dust) bring N in organic or mineral forms (Abbadie, 2006) and are represented by fixed inputs, independent of model compartments, i_O, i_{NA}, 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-γ) and γ in the open and tree clump patches respectively (Appendix 1). Overall, the two patch model is represented by the following system of equation :

Open patch (patch 1):

$$\frac{dG_1}{dt} = \beta_G u_G N_{A1} G_1 + (1-\beta_G) u_G N_{N1} G_1 - (d_G + l_G)\, G_1 \tag{3.1}$$

$$\frac{dO_1}{dt} = i_O + d_G G_1 + d_r\left(\frac{\gamma}{1-\gamma}\right) \alpha r T - (m + l_O)\, O_1 \tag{3.2}$$

$$\frac{dN_{A1}}{dt} = i_{NA} + m\, O_1 - \left(\beta_G u_G\, G_1 + n_1 + l_{NA} + \beta_{T1} u_r\left(\frac{\gamma}{1-\gamma}\right) \alpha r T\right) N_{A1} \tag{3.3}$$

$$\frac{dN_{N1}}{dt} = i_{NN} + n_1\, N_{A1} - \left((1-\beta_G) u_G\, G_1 + l_{NN} + (1-\beta_{T1})\left(\frac{\gamma}{1-\gamma}\right) u_r \alpha r T\right) N_{N1} \tag{3.4}$$

Tree clump patch (patch 2):

$$\frac{dG_2}{dt} = \beta_G u_G N_{A2} G_2 + (1-\beta_G) u_G N_{N2} G_2 - (d_G + l_G)\, G_2 \tag{3.5}$$

$$\begin{aligned}\frac{dT}{dt} = {} & (1-\alpha)(\beta_{T2} u_r N_{A2} rT + (1-\beta_{T2}) u_r N_{N2} rT) + \alpha(\beta_{T1} u_r N_{A1} rT + \\ & (1-\beta_{T1}) u_r N_{N1} rT - (d_l(1-r) + d_r \alpha r + (1-\alpha) d_r r + l_T)\, T\end{aligned} \tag{3.6}$$

$$\frac{dO_2}{dt} = i_O + d_G G_2 + (1-\alpha) d_r rT + d_l(1-r)T - (m + l_O)\, O_2 \tag{3.7}$$

$$\frac{dN_{A2}}{dt} = i_{NA} + m\, O_2 - (\beta_G u_G G_2 + (1-\alpha)\, \beta_{T2} u_r rT + n_2 + l_{NA})\, N_{A2} \tag{3.8}$$

$$\frac{dN_{N2}}{dt} = i_{NN} + n_2\, N_{A2} - ((1-\beta_G) u_G\, G_2 + l_{NN} + (1-\beta_{T2})(1-\alpha) u_r rT)\, N_{N2} \tag{3.9}$$

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

3.2.2 Model analysis and parameterization

Because the model could not be analytically solved, we analyzed it through numerical simulations. The model has been implemented in R (R Core Team, 2019) and the resolution of the differential equations was performed using the deSolve package (Soetaert et al., 2010). All displayed results correspond to compartment size after 3000 years of simulation, which was a time sufficient to reach steady states of all compartments.

Parameter values used are summarized in Table 4.1 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 1200 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 used parameters from Konaré et al. (2019). The ratio of roots in the tree biomass (r) was estimated from (Menaut and Cesar, 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} ; Menaut and Cesar (1979)). Regarding the mortality rate of tree leaves (dl), we divided the annual leaf fall by total tree biomass (Menaut and Cesar, 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%) (Gautier, 1990; Menaut and Cesar, 1979). 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). γ = 0.15 and γ = 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 and 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}) with an increment of 0.01.

Table 3.1 – Parameters of the two-patch model

Parameters	Definition	Unit	Values
Grass parameters			
d_G	Turnover rate of grass	yr^{-1}	0.6
l_G	Rate of N losses from grass compartment	yr^{-1}	0.4
u_G	N uptake rate	ha kg^{-1} N yr^{-1}	0.14186
β_G	Preference for NH_4^+	No unit	-
Tree parameters			
d_r	Turnover rate of tree roots	yr^{-1}	0.08
d_l	Turnover rate of tree leaves	yr^{-1}	0.073
l_T	Rate of N losses from tree compartment	yr^{-1}	0.11
u_r	N uptake rate by tree roots	ha kg^{-1} N yr^{-1}	0.08
β_{T1}	Preference for NH_4^+ in the open patch	No unit	-
β_{T2}	Preference for NH_4^+ in the tree clump patch	No unit	0.25
α	Fraction of roots in the open	No unit	-
γ	Tree clumps proportion	No unit	-
r	Root shoot ratio	No unit	0.5
Soil parameters			
i_O	N organic input to the savanna	kg N ha^{-1} yr^{-1}	16.5
m	N mineralization rate	yr^{-1}	0.025
l_O	N loss from the N organic compartment in surface soil layer	yr^{-1}	0.0027
i_{NA}	NH_4^+ inputs to the savanna	kg N ha^{-1} yr^{-1}	23
n_1	Nitrification rate in the open patch	yr^{-1}	0.09
n_2	Nitrification rate in the tree clump patch	yr^{-1}	4.16
l_{NA}	NH_4^+ loss rate	yr^{-1}	0.0133
i_{NN}	NO_3^- inputs to the savanna	kg N ha^{-1} yr^{-1}	4.1
l_{NN}	NO_3^- loss rate	yr^{-1}	2.7

3.3 Results

3.3.1 Soil N pools in the open and tree clump patch

Plant type (grass or tree) significantly affected soil N pools at the patch scale (Fig. 3.2). For a proportion of tree roots outside tree canopy (α) of 25% and a surface of 15% occupied by tree clumps (γ), two main trends appear (Fig. 3.2a): when tree preference for NH_4^+ in the open patch is lower than grass preference for NH_4^+, the clump/open ratio of organic N (i.e., the ratio between soil organic N beneath the tree clump patch and the open patch) is lower than 1. Conversely, the clump/open organic N ratio is higher than 1 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 8 times higher than in the open patch. The NH_4^+ stock is always higher in the open patch than under tree clump (Fig. 3.2b). When tree preference for NH_4^+ in the open patch is lower than grass preference for NH_4^+, the clump/open NO_3^- ratio (i.e., the ratio between NO_3^- pool beneath the tree clump patch and the open patch) is higher than 1 and 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 clump/open NO_3^- ratio is low and below 1 (Fig. 3.2c).

3.3.2 α and γ have contrasted 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 (Fig. 3.3). At low values of α and γ (α = 0.25 and γ = 0.15) (Fig. 3.3c), the net horizontal N flux 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} yr^{-1} to zero depending on tree preference for NH_4^+ in the open patch. With increasing α (α = 0.5 and γ = 0.15) (Fig. 3.3a), 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} yr^{-1} (Fig. 3.3c). But when γ increases (α = 0.25 and γ = 0.3, Fig. 3.3d), the net horizontal N flux does not exceed 27 kg N ha^{-1} yr^{-1} in this zone. When grass preference for NH_4^+ increases, the net horizontal N flux decreases from 27 kg N ha^{-1} yr^{-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 (Fig. 3.4). Horizontal N fluxes to the tree clump patch feedback to tree biomass 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^+ (Fig. 3.4c). Tree biomass increases with α (Figs 3.4a and 3.4c) but decreases with γ (Figs 3.4b and 3.4d). 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 kgN ha^{-1} (Figs 3.4a and 3.4b) or 200 kgN ha^{-1} (Figs 3.4b and 3.4d). Appendix S2 also shows that the effects of α and γ

impact the grass and total biomass. The decrease of tree biomass favors the growth of grasses beneath tree clump and in the open.

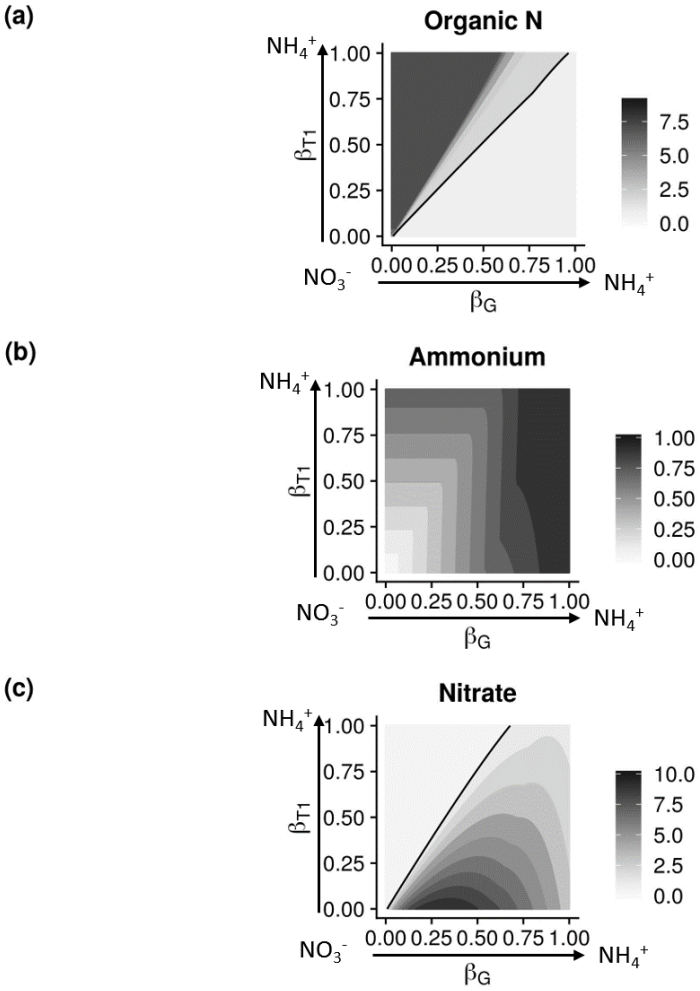

Figure 3.2 – Ratio of the soil N pools in the tree clump patch over the N pools in the open patch as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+ in the open patch: (a) organic N pool, (b) NH_4^+ pool, (c) NO_3^- pool. The solid line represents the 1:1 ratio, i.e. where the N pools are equal in both patches. These figures correspond to simulations with $\alpha = 0.25$ and $\gamma = 0.15$.

3.3.3 N budget in the Lamto savanna

Figure 3.5 displays 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^{-1}) than in the tree clump patch (8.50 kg N ha^{-1}) while the NO_3^- stock is about 3 times higher in the tree clump (2.51 kg N ha^{-1}) than in the open patch (0.88 kg N ha^{-1}). 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} yr^{-1}) than in the open patch (0.70 kg N kg N ha^{-1} yr^{-1}) but total N losses are more important in the open (7.21 kg N ha^{-1} yr^{-1}) than in the tree clump patch (1.84 kg N ha^{-1} yr^{-1}).

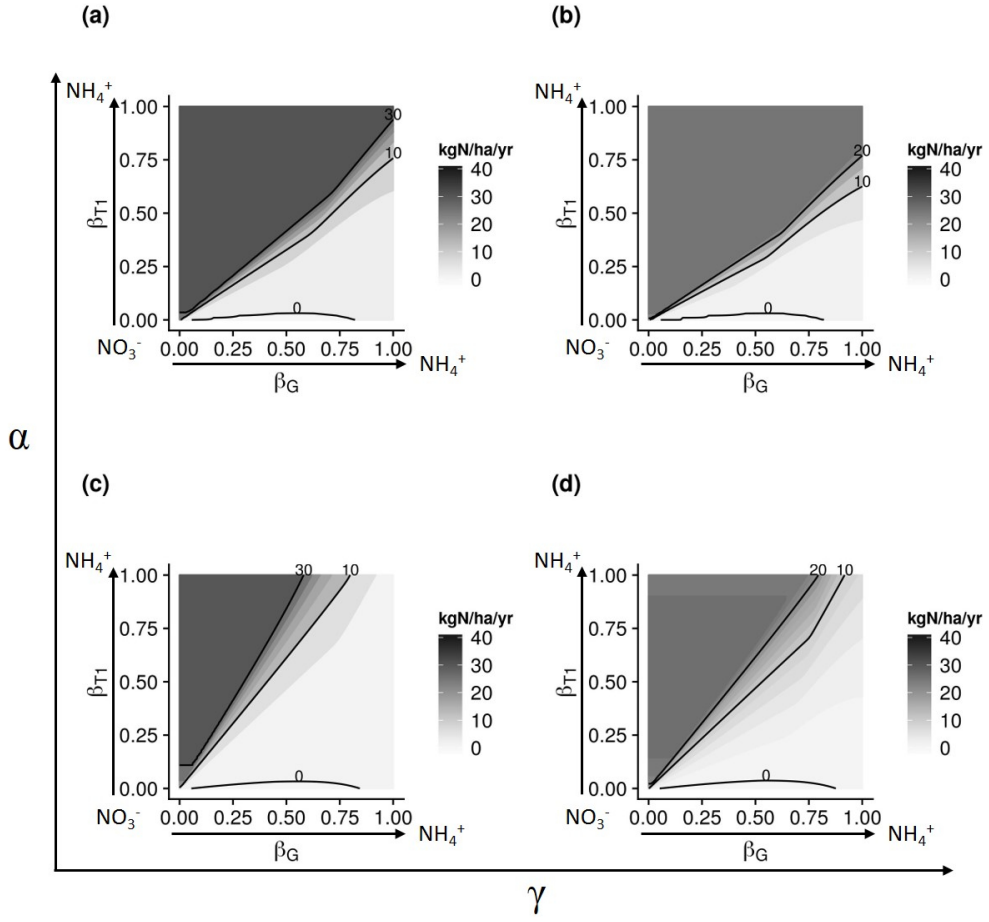

Figure 3.3 – Net horizontal N flux from the open to the tree clump patch as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+ in the open patch according to different values of α and γ at the savanna scale. The proportion of roots outside tree canopy (α) increases from the bottom to the top, and the surface occupied by tree clumps (γ) increases from the left to the right (a: α = 0.5 and γ = 0.15, b: α = 0.5 and γ = 0.3, c: α = 0.25 and γ = 0.15, d: α = 0.25 and γ = 0.3). Solid lines show N flux contours for remarkable values.

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 ($n_1 = n_2 = 4.16\ yr^{-1}$), nitrification flux in the open patch increases (23.97 kg N $ha^{-1}\ yr^{-1}$) and is about 5 times higher than in the tree clump patch (5.30 kg N $ha^{-1}\ yr^{-1}$). 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 $ha^{-1}\ yr^{-1}$) than in the tree clump patch (1.83 kg N $ha^{-1}\ yr^{-1}$). 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. 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. 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 $ha^{-1}\ yr^{-1}$) than in the case of spatial heterogeneity in nitrification fluxes (4.89 kg N $ha^{-1}\ yr^{-1}$). Horizontal N fluxes respectively represent 35.58% and 38.08% of total N uptake by trees in the spatial heterogeneity and homogeneity cases.

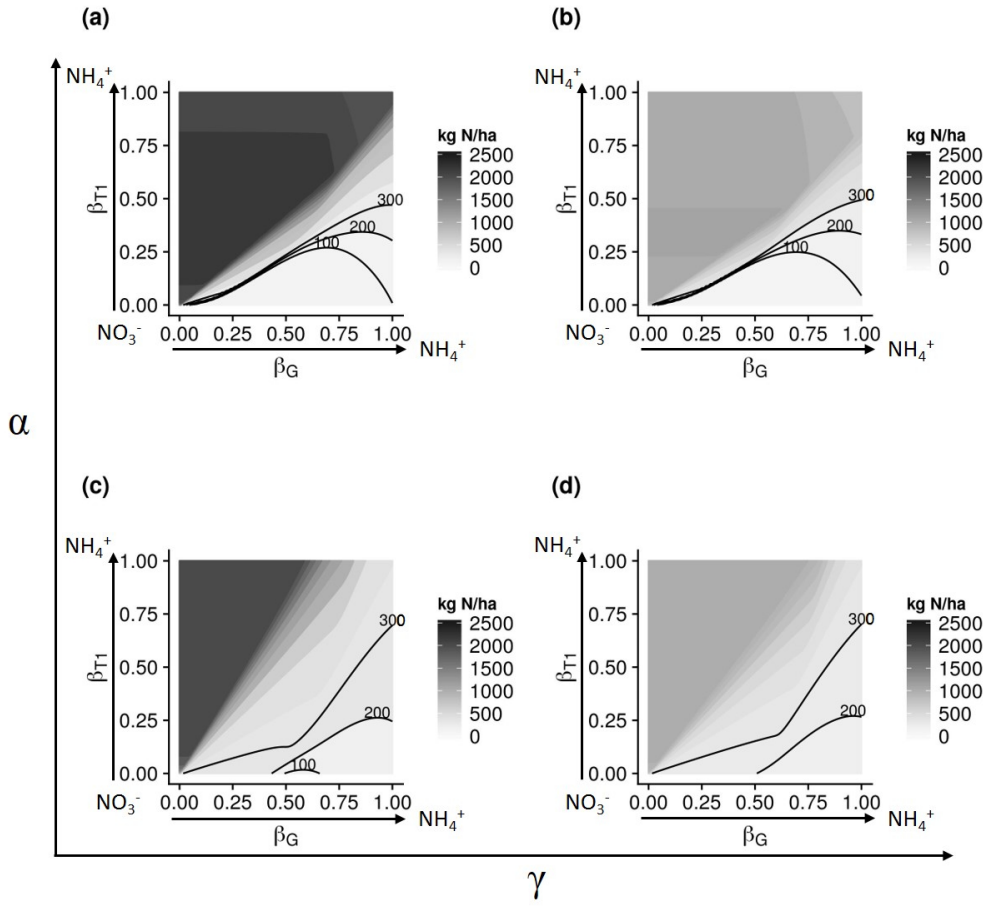

Figure 3.4 – Tree biomass as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+ in the open patch, according to different values of α and γ at savanna scale. The proportion of roots outside tree canopy (α) increases from the bottom to the top, and the surface occupied by tree clumps (γ) increases from the left to the right (a: α = 0.5 and γ = 0.15, b: α = 0.5 and γ = 0.3, c: α = 0.25 and γ = 0.15, d: α = 0.25 and γ = 0.3). Solid lines show N flux contours for remarkable values.

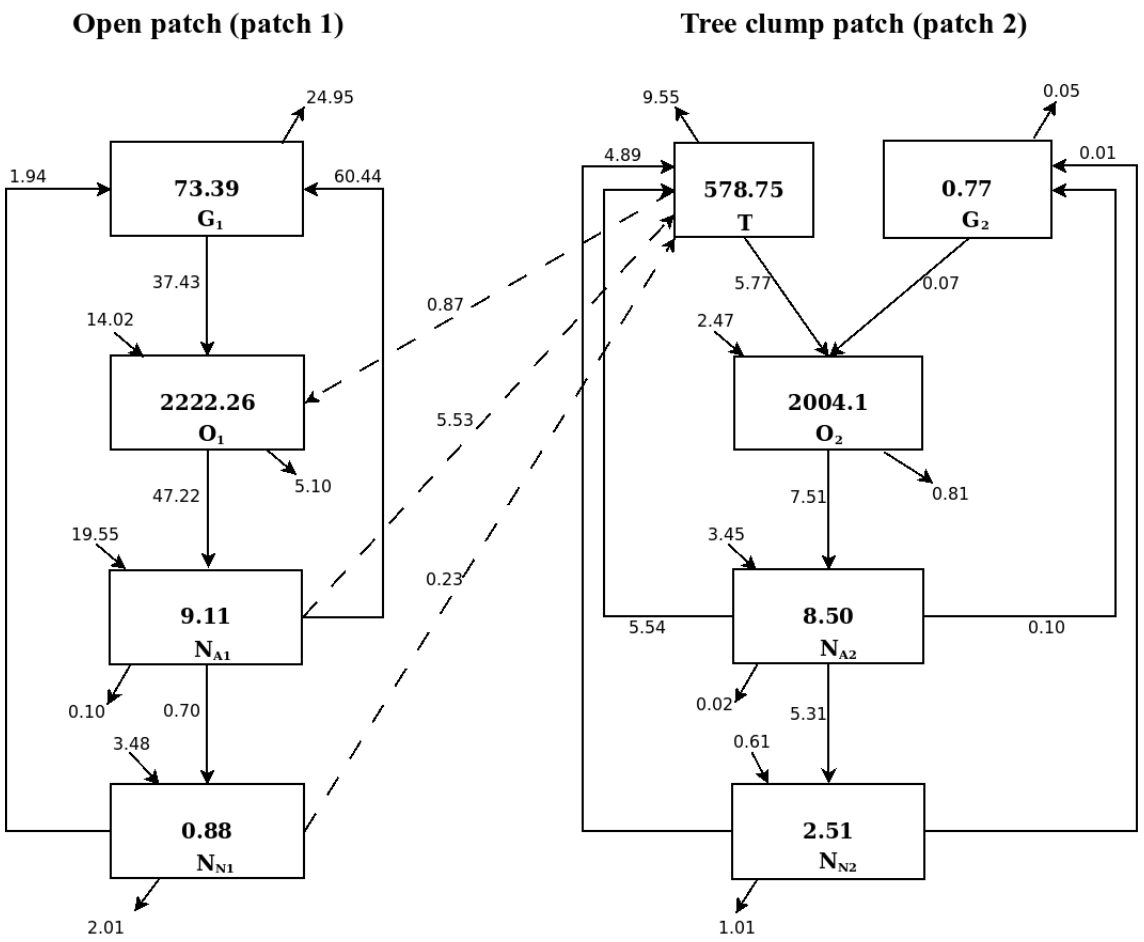

Figure 3.5 – Estimate of the N stocks (kg N ha^{-1}) and N fluxes (kg N ha^{-1} yr^{-1}) at model equilibrium. We fixed β_G =0.75 and β_{T1} = 0.7.

3.4 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 allows confirming our hypotheses that: (i) 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; (ii) although soil exploration by trees increases N acquisition and favors 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; (iii) 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.

3.4.1 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) 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 a N sink. These N exchanges between the open and tree clumps 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 (Figs 3.3 and 3.4). 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. Interestingly, 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 and 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 (Barot personal communication). 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 (Fig. 3.2). Even if this high N enrichment below tree clumps leads to values of tree biomass too high for the Lamto savanna (Fig. 3.4), this suggests a preferential NH_4^+ uptake of trees in the open and a particular root foraging strategy aiming at exploiting the high NH_4^+ availability outside tree clumps.

Consequently, our model also suggests that different parts of the tree root systems have contrasted 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 and 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 the preference for NH_4^+ *versus* NO_3^-, confirming that this preference has important consequences at the ecosystem scale (Boudsocq et al., 2012).

3.4.2 Impact of the surface occupied by tree clumps on plant biomass

Tree biomass tends to decrease with tree cover. 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 by denitrification, which accordingly decreases the quantity of N available for trees (Appendix S4) and tree biomass. Numerous studies demonstrated that changes from grass and tree dominance to tree dominance lead to an increase of 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 larger 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) results 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.

Besides, 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 (Fig. 3.4b). Increasing tree dominance indeed reduces the surface occupied by the open area and therefore the tree access to this NH_4^+ rich area. 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 modeling. 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.

3.4.3 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 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 high than 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 an 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, is likely to lead 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 *versus* 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.

3.5 Conclusion

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), our study shows that, at a larger scale, extending soil exploration in the open is beneficial for trees

because it improves their N uptake.

Little is known about the occurrence of nitrification-inhibiting grasses and nitrification-stimulating trees outside the Lamto savanna. However, we hypothesize that our findings would at least hold for all humid West African savannas where vegetation is similar to the Lamto savanna and that share many grass and tree species with this savanna. Our model can readily be used to assess the generality of our results to other savannas where grasses and trees might have different influences on N cycling. 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 included in our model. 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 and Levin, 2017). Finally, our work will be relevant to analyze the influence of agroforestery practices in savannas on N cycling (Isaac and Borden, 2019).

Bibliography

Abbadie, L. (2006). Nitrogen inputs to and outputs from the soil-plant system. In *Lamto: structure, functioning, and dynamics of a savanna ecosystem*, pages 255–275. New York: Springer.

Abbadie, L., Gignoux, J., Le Roux, X., and Lepage, M. (2006). *Lamto: structure, functioning, and dynamics of a savanna ecosystem*. New York: Springer.

Abbadie, L., Mariotti, A., and Menaut, J.-C. (1992). Independence of savanna grasses from soil organic matter for their nitrogen supply. *Ecology*, 73(2):608–613.

Belsky, A., Amundson, R., Duxbury, J., Riha, S., Ali, A., and Mwonga, S. (1989). The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in kenya. *Journal of applied ecology*, 26(3):1005–1024.

Belsky, A. J. (1994). Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology*, 75(4):922–932.

Bernhard-Reversat, F. (1982). Biogeochemical cycle of nitrogen in a semi-arid savanna. *Oikos*, 38(3):321–332.

Blaser, W. J., Shanungu, G. K., Edwards, P. J., and Olde Venterink, H. (2014). Woody encroachment reduces nutrient limitation and promotes soil carbon sequestration. *Ecology and evolution*, 4(8):1423–1438.

Boudsocq, S., Lata, J.-C., Mathieu, J., Abbadie, L., and Barot, S. (2009). Modelling approach to analyse the effects of nitrification inhibition on primary production. *Functional Ecology*, 23(1):220–230.

Boudsocq, S., Niboyet, A., Lata, J. C., Raynaud, X., Loeuille, N., Mathieu, J., Blouin, M., Abbadie, L., and Barot, S. (2012). Plant preference for ammonium versus nitrate: a neglected determinant of ecosystem functioning? *The American Naturalist*, 180(1):60–69.

Britto, D. T. and Kronzucker, H. J. (2013). Ecological significance and complexity of N-source preference in plants. *Annals of botany*, 112(6):957–963.

de Parseval, H., Abbadie, L., Barot, S., Gignoux, J., Lata, J.-C., and Raynaud, X. (2016). Explore less to control more: why and when should plants limit the horizontal exploration of soil by their roots? *Oikos*, 125(8):1110–1120.

Devine, A. P., McDonald, R. A., Quaife, T., and Maclean, I. M. (2017). Determinants of woody encroachment and cover in african savannas. *Oecologia*, 183(4):939–951.

Gautier, L. (1990). Contact forêt-savane en côte-d'ivoire centrale: évolution du recouvrement ligneux des savanes de la réserve de lamto (sud du v-baoulé). *Candollea*, 45(2):627–641.

Gounand, I., Harvey, E., Little, C. J., and Altermatt, F. (2018). Meta-ecosystems 2.0: rooting the theory into the field. *Trends in ecology & evolution*, 33(1):36–46.

Hobbie, S. E. (1992). Effects of plant species on nutrient cycling. *Trends in ecology & evolution*, 7(10):336–339.

Hobbie, S. E. (2015). Plant species effects on nutrient cycling: revisiting litter feedbacks. *Trends in ecology & evolution*, 30(6):357–363.

Hochberg, M. E., Menaut, J. C., and Gignoux, J. (1994). The influences of tree biology and fire in the spatial structure of the west african savannah. *Journal of Ecology*, 82:217–226.

Hoffmann, W. A., Geiger, E. L., Gotsch, S. G., Rossatto, D. R., Silva, L. C., Lau, O. L., Haridasan, M., and Franco, A. C. (2012). Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecology letters*, 15(7):759–768.

Holdo, R. M. (2013). Revisiting the two-layer hypothesis: coexistence of alternative functional rooting strategies in savannas. *PLoS One*, 8(8).

Isaac, M. E. and Borden, K. A. (2019). Nutrient acquisition strategies in agroforestry systems. *Plant and Soil*, 444(1-2):1–19.

Isichei, A. O. and Muoghalu, J. I. (1992). The effects of tree canopy cover on soil fertility in a nigerian savanna. *Journal of Tropical Ecology*, 8(3):329–338.

Kambatuku, J. R., Cramer, M. D., and Ward, D. (2013). Nitrogen fertilisation reduces grass-induced N_2 fixation of tree seedlings from semi-arid savannas. *Plant and soil*, 365:307–320.

Kellman, M. (1979). Soil enrichment by neotropical savanna trees. *Journal of Ecology*, 67(2):565–577.

Konaré, S., Boudsocq, S., Gignoux, J., Lata, J.-C., Raynaud, X., and Barot, S. (2019). Effects of mineral nitrogen partitioning on tree–grass coexistence in west african savannas. *Ecosystems*, 22(7):1676–1690.

Konaté, S., Le Roux, X., Tessier, D., and Lepage, M. (1999). Influence of large termitaria on soil characteristics, soil water regime, and tree leaf shedding pattern in a west african savanna. *Plant and Soil*, 206(1):47–60.

Lata, J.-C., Degrange, V., Raynaud, X., Maron, P.-A., Lensi, R., and Abbadie, L. (2004). Grass populations control nitrification in savanna soils. *Functional Ecology*, 18(4):605–611.

Le Roux, X., Abbadie, L., Fritz, H., and Leriche, H. (2006). Modifications of the savanna functioning by herbivores. In *Lamto: structure, functioning, and dynamics of a savanna ecosystem*, pages 185–198. New York: Springer.

Lieth, H. and Whittaker, R. H. (1975). *Primary productivity of the biosphere*. Berlin:Springer Verlag Ecological studies 14.

Loreau, M., Mouquet, N., and Holt, R. D. (2003). Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters*, 6(8):673–679.

Ludwig, F., De Kroon, H., Berendse, F., and Prins, H. H. (2004). The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology*, 170(1):93–105.

Ludwig, F., de Kroon, H., Prins, H. H., and Berendse, F. (2001). Effects of nutrients and shade on tree-grass interactions in an east african savanna. *Journal of Vegetation Science*, 12(4):579–588.

Menaut, J. and Cesar, J. (1979). Structure and primary productivty of lamto savannas, ivory coast. *Ecology*, 60(6):1197–1210.

Menge, D. N. and Levin, S. A. (2017). Spatial heterogeneity can resolve the nitrogen paradox of tropical forests. *Ecology*, 98(4):1049–1061.

Mordelet, P. (1993). *Influence des arbres sur la strate herbacée d'une savane humide (Lamto, Côte d'Ivoire)*. PhD thesis, Paris 6.

Mordelet, P., Abbadie, L., and Menaut, J.-C. (1993). Effects of tree clumps on soil characteristics in a humid savanna of west africa (lamto, côte d'ivoire). *Plant and Soil*, 153(1):103–111.

Mordelet, P., Barot, S., and Abbadie, L. (1996). Root foraging strategies and soil patchiness in a humid savanna. *Plant and Soil*, 182(1):171–176.

Mordelet, P., Menaut, J.-C., and Mariotti, A. (1997). Tree and grass rooting patterns in an african humid savanna. *Journal of Vegetation Science*, 8(1):65–70.

Pellegrini, A. F. (2016). Nutrient limitation in tropical savannas across multiple scales and mechanisms. *Ecology*, 97(2):313–324.

R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rhoades, C. (1996). Single-tree influences on soil properties in agroforestry: lessons from natural forest and savanna ecosystems. *Agroforestry systems*, 35(1):71–94.

Rossiter-Rachor, N., Setterfield, S., Douglas, M., Hutley, L. B., Cook, G., and Schmidt, S. (2009). Invasive *Andropogon gayanus* (gamba grass) is an ecosystem transformer of nitrogen relations in australian savanna. *Ecological Applications*, 19(6):1546–1560.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., Gignoux, J., Higgins, S. I., Le Roux, X., Ludwig, F., et al. (2005). Determinants of woody cover in african savannas. *Nature*, 438(7069):846–849.

Schenk, H. J. and Jackson, R. B. (2002). Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, 90(3):480–494.

Scholes, R. (1990). The influence of soil fertility on the ecology of southern african dry savannas. *Journal of Biogeography*, 17:415–419.

Scholes, R. and Archer, S. (1997). Tree-grass interactions in savannas. *Annual review of Ecology and Systematics*, 28(1):517–544.

Soetaert, K. E., Petzoldt, T., and Setzer, R. W. (2010). Solving differential equations in R: package desolve. *Journal of Statistical Software*, 33.

Srikanthasamy, T., Leloup, J., N'Dri, A. B., Barot, S., Gervaix, J., Koné, A. W., Koffi, K. F., Le Roux, X., Raynaud, X., and Lata, J.-C. (2018). Contrasting effects of grasses and trees on microbial n-cycling in an african humid savanna. *Soil Biology and Biochemistry*, 117:153–163.

Sternberg, L. S. L., Bucci, S., Franco, A., Goldstein, G., Hoffman, W. A., Meinzer, F. C., Moreira, M. Z., and Scholz, F. (2004). Long range lateral root activity by neo-tropical savanna trees. *Plant and Soil*, 270(1):169–178.

Subbarao, G., Sahrawat, K. L., Nakahara, K., Rao, I. M., Ishitani, M., Hash, C., Kishii, M., Bonnett, D., Berry, W., and Lata, J.-C. (2013). A paradigm shift towards low-nitrifying production systems: the role of biological nitrification inhibition (BNI). *Annals of botany*, 112(2):297–316.

Walter, H. (1971). *Ecology of tropical and subtropical vegetation*. Edinburgh: Oliver Boyd.

Wang, L. and Macko, S. A. (2011). Constrained preferences in nitrogen uptake across plant species and environments. *Plant, cell & environment*, 34(3):525–534.

Ward, D., Trinogga, J., Wiegand, K., du Toit, J., Okubamichael, D., Reinsch, S., and Schleicher, J. (2018). Large shrubs increase soil nutrients in a semi-arid savanna. *Geoderma*, 310:153–162.

Zhou, Y., Boutton, T. W., and Wu, X. B. (2018). Soil phosphorus does not keep pace with soil carbon and nitrogen accumulation following woody encroachment. *Global change biology*, 24(5):1992–2007.

3.6 Appendix

3.6.1 Appendix S1: Equations at the savanna scale

The two patch model at the savanna scale is represented by the following system of equation :
Open patch (patch 1)

$$\frac{d\mathrm{G}_1}{dt} = (1-\gamma)(\beta_\mathrm{G} u_\mathrm{G} \mathrm{N}_{\mathrm{A}1} \mathrm{G}_1 + (1-\beta_\mathrm{G}) u_\mathrm{G} \mathrm{N}_{\mathrm{N}1} \mathrm{G}_1 - (d_\mathrm{G} + l_\mathrm{G})\ \mathrm{G}_1) \tag{3.10}$$

$$\frac{d\mathrm{O}_1}{dt} = (1-\gamma)(i_\mathrm{O} + d_\mathrm{G} \mathrm{G}_1 + d_r (\frac{\gamma}{1-\gamma}) \alpha r \mathrm{T} - (m + l_\mathrm{O})\ \mathrm{O}_1) \tag{3.11}$$

$$\frac{d\mathrm{N}_{\mathrm{A}1}}{dt} = (1-\gamma)(i_\mathrm{NA} + m\ \mathrm{O}_1 - (\beta_\mathrm{G} u_\mathrm{G} \mathrm{G}_1 + n_1 + l_\mathrm{NA} + \beta_{\mathrm{T}1} u_r (\frac{\gamma}{1-\gamma}) \alpha r \mathrm{T})\ \mathrm{N}_{\mathrm{A}1}) \tag{3.12}$$

$$\frac{d\mathrm{N}_{\mathrm{N}1}}{dt} = (1-\gamma)(i_\mathrm{NN} + n_1 \mathrm{N}_{\mathrm{A}1} - ((1-\beta_\mathrm{G}) u_\mathrm{G} \mathrm{G}_1 + l_\mathrm{NN} + (1-\beta_{\mathrm{T}1}) (\frac{\gamma}{1-\gamma}) u_r \alpha r \mathrm{T})\ \mathrm{N}_{\mathrm{N}1}) \tag{3.13}$$

Tree clump patch (patch 2):

$$\frac{d\mathrm{G}_2}{dt} = \gamma(\beta_\mathrm{G} u_\mathrm{G} \mathrm{N}_{\mathrm{A}2} \mathrm{G}_2 + (1-\beta_\mathrm{G}) u_\mathrm{G} \mathrm{N}_{\mathrm{N}2} \mathrm{G}_2 - (d_\mathrm{G} + l_\mathrm{G})\ \mathrm{G}_2) \tag{3.14}$$

$$\begin{aligned}\frac{d\mathrm{T}}{dt} = \gamma((1-\alpha)(\beta_{\mathrm{T}2} u_r \mathrm{N}_{\mathrm{A}2} r \mathrm{T} + (1-\beta_{\mathrm{T}2}) u_r \mathrm{N}_{\mathrm{N}2} r \mathrm{T}) + \alpha(\beta_{\mathrm{T}1} u_r \mathrm{N}_{\mathrm{A}1} r \mathrm{T} + \\ (1-\beta_{\mathrm{T}1}) u_r \mathrm{N}_{\mathrm{N}1} r \mathrm{T} - (d_1 (1-r) + d_r \alpha r + (1-\alpha) d_r r + l_\mathrm{T})\ \mathrm{T})\end{aligned} \tag{3.15}$$

$$\frac{d\mathrm{O}_2}{dt} = \gamma(i_\mathrm{O} + d_\mathrm{G} \mathrm{G}_2 + (1-\alpha) d_r r \mathrm{T} + d_l (1-r) \mathrm{T} - (m + l_\mathrm{O})\ \mathrm{O}_2) \tag{3.16}$$

$$\frac{d\mathrm{N}_{\mathrm{A}2}}{dt} = \gamma(i_\mathrm{NA} + m\ \mathrm{O}_2 - (\beta_\mathrm{G} u_\mathrm{G} \mathrm{G}_2 + (1-\alpha)\ \beta_{\mathrm{T}2} u_r r \mathrm{T} + n_2 + l_\mathrm{NA})\ \mathrm{N}_{\mathrm{A}2}) \tag{3.17}$$

$$\frac{d\mathrm{N}_{\mathrm{N}2}}{dt} = \gamma(i_\mathrm{NN} + n_2 \mathrm{N}_{\mathrm{A}2} - ((1-\beta_\mathrm{G}) u_\mathrm{G} \mathrm{G}_2 + l_\mathrm{NN} + (1-\beta_{\mathrm{T}2})(1-\alpha) u_r r \mathrm{T})\ \mathrm{N}_{\mathrm{N}2}) \tag{3.18}$$

3.6.2 Plant biomass at the savanna scale

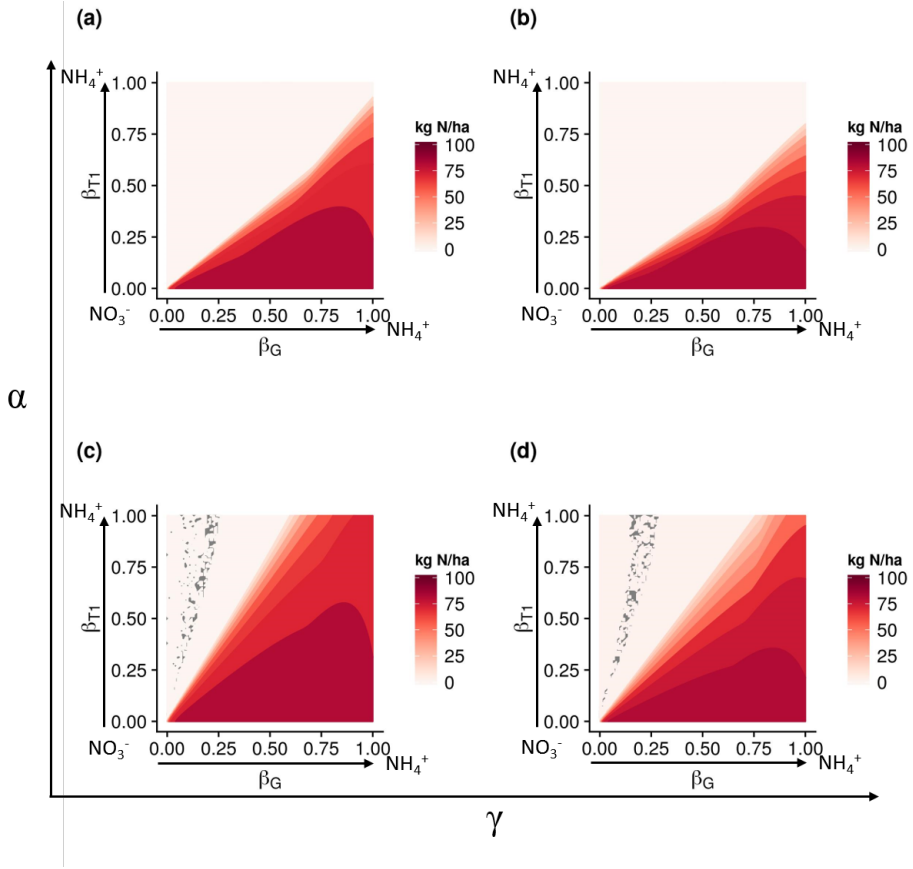

Figure 3.6 – Grass biomass in the open patch as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+, according to different values of α and γ at the savanna scale. The proportion of roots outside tree canopy (α) increases from the bottom to the top, and the surface occupied by tree clumps (γ) increases from the left to the right (a: α = 0.5 and γ = 0.15, b: α = 0.5 and γ = 0.3, c: α = 0.25 and γ = 0.15, d: α = 0.25 and γ = 0.3). Solid lines show N flux contours for remarkable values.

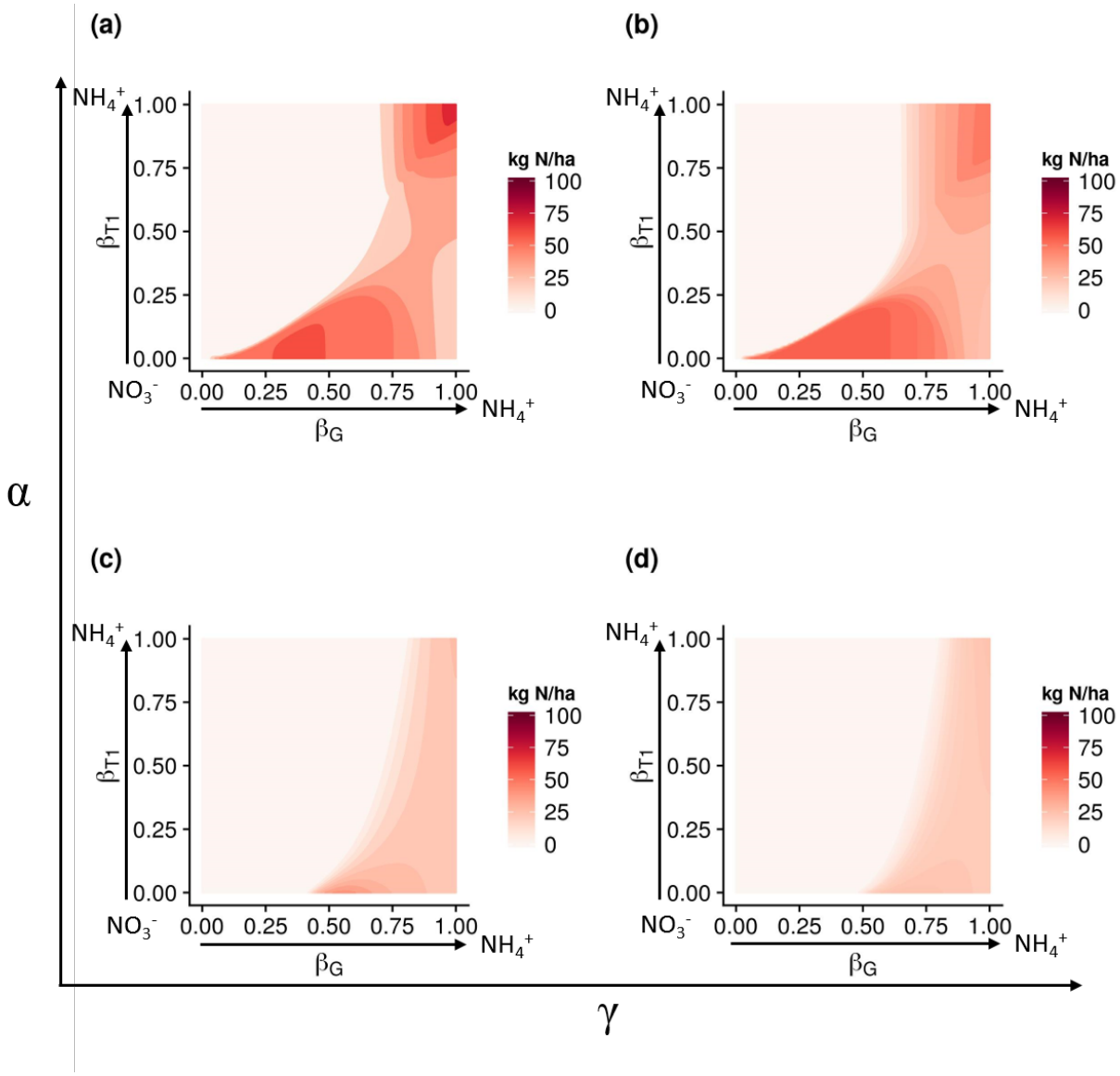

Figure 3.7 – Grass biomass in the tree clump patch as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+, according to different values of α and γ at the savanna scale. The proportion of roots outside tree canopy (α) increases from the bottom to the top, and the surface occupied by tree clumps (γ) increases from the left to the right (a: α = 0.5 and γ = 0.15, b: α = 0.5 and γ = 0.3, c: α = 0.25 and γ = 0.15, d: α = 0.25 and γ = 0.3). Solid lines show N flux contours for remarkable values.

3.6.3 Appendix S3: Nitrification flux and N losses at patch scale

We determine here the nitrification flux and total N losses (organic and mineral) at the patch scale for a proportion of tree roots outside tree canopy (α) of 25% and a surface of 15% occupied by tree clumps (γ). We observe that nitrification flux is higher under tree clumps than in the open patch, which significantly impact N losses. N losses are higher in the tree clump patch than in the open patch. The high nitrification flux under tree clumps increases N losses as NO_3^- is easily lost by leaching and by denitrification. In the case where tree roots in the open patch and grasses have a high preference for NO_3^-, nitrification flux and N losses in the open patch are very high.

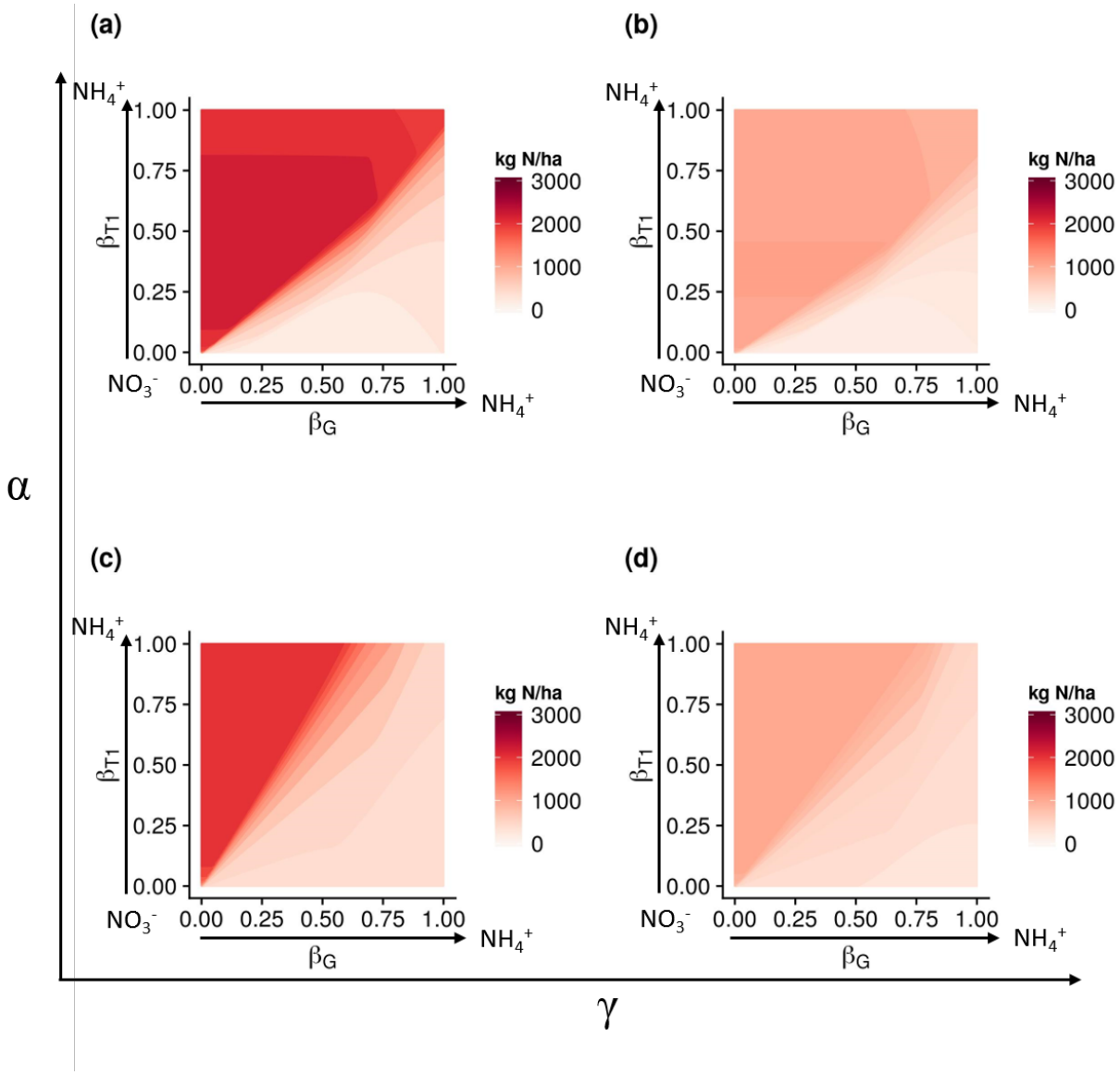

Figure 3.8 – Total biomass (tree and grass biomass) as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+, according to different values of α and γ at the savanna scale. The proportion of roots outside tree canopy (α) increases from the bottom to the top, and the surface occupied by tree clumps (γ) increases from the left to the right (a: α = 0.5 and γ = 0.15, b: α = 0.5 and γ = 0.3, c: α = 0.25 and γ = 0.15, d: α = 0.25 and γ = 0.3). Solid lines show N flux contours for remarkable values.

3.6.4 Appendix S4: N losses at the savanna scale

In this appendix, we focus on the total N losses (organic and mineral) at the savanna scale depending on α and γ. Figure 3.10 shows that at low values of α and γ (α = 0.25 and γ = 0.15), N losses in the open patch are lower than 5 kg N/ha/yr when grasses have a preference for NO_3^- and $0.32 < \beta_{T1} < 0.65$. N losses are higher than 8 $kgN\ ha^{-1}\ yr^{-1}$ when $\beta_G > 0.84$ and for all values of β_{T1}, and when trees in the open patch and grasses have a strong preference for NO_3^-. N losses are between 5 $kgN\ ha^{-1}\ yr^{-1}$ and 8 $kgN\ ha^{-1}\ yr^{-1}$ for other combinations of β_G and β_{T1}. When α increases (α = 0.5 and γ = 0.15), the size of the zone where N losses are lower than 5 $kgN\ ha^{-1}\ yr^{-1}$ increases. When γ increases, the size of this zone also increases, and the size of the zone where N losses are higher than 8 $kgN\ ha^{-1}\ yr^{-1}$ decreases.

Regarding N losses in the tree clump patch (Fig. 3.11), N losses are below 5 $kgN\ ha^{-1}\ yr^{-1}$

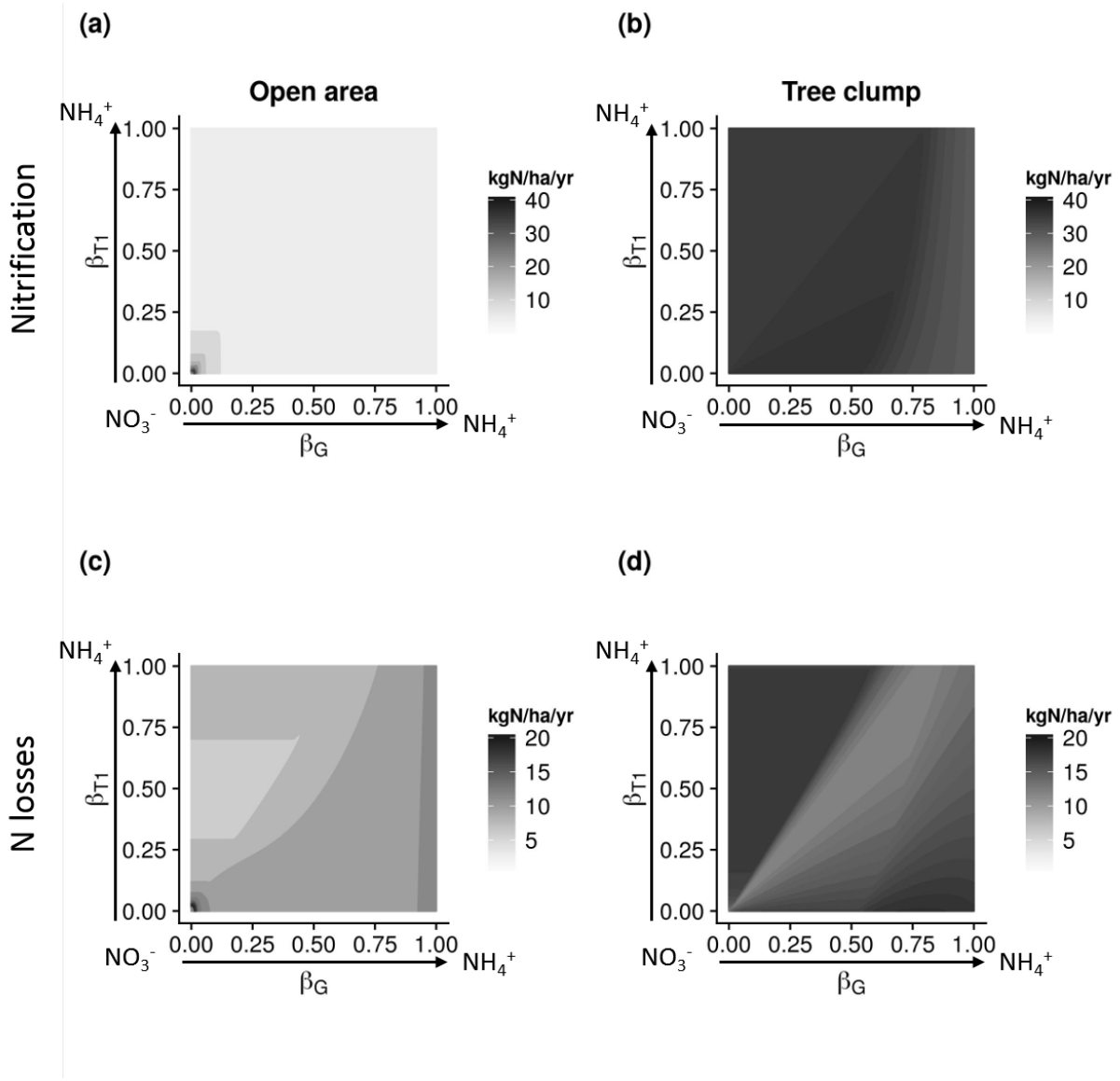

Figure 3.9 – Nitrification flux and N losses at the patch scale as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+. These figures correspond to simulations with $\alpha = 0.25$ and $\gamma = 0.15$.

regardless tree and grass preference for the two values of α (0.25 and 0.5). When γ increases, N losses are higher than 5 kgN ha^{-1} yr^{-1} when tree preference for NH_4^+ in the open patch is lower than grass preference for NH_4^+. They are lower than 5 kgN ha^{-1} yr^{-1} for other combinations of β_G and β_{T1}. There is a small zone where N losses are higher than 8 kgN ha^{-1} yr^{-1} when $0.8 < \beta_G < 0.93$ and $0 < \beta_{T1} < 0.05$. Taken together, total N losses decrease in the open while they increase in the tree clump patch with increasing γ.

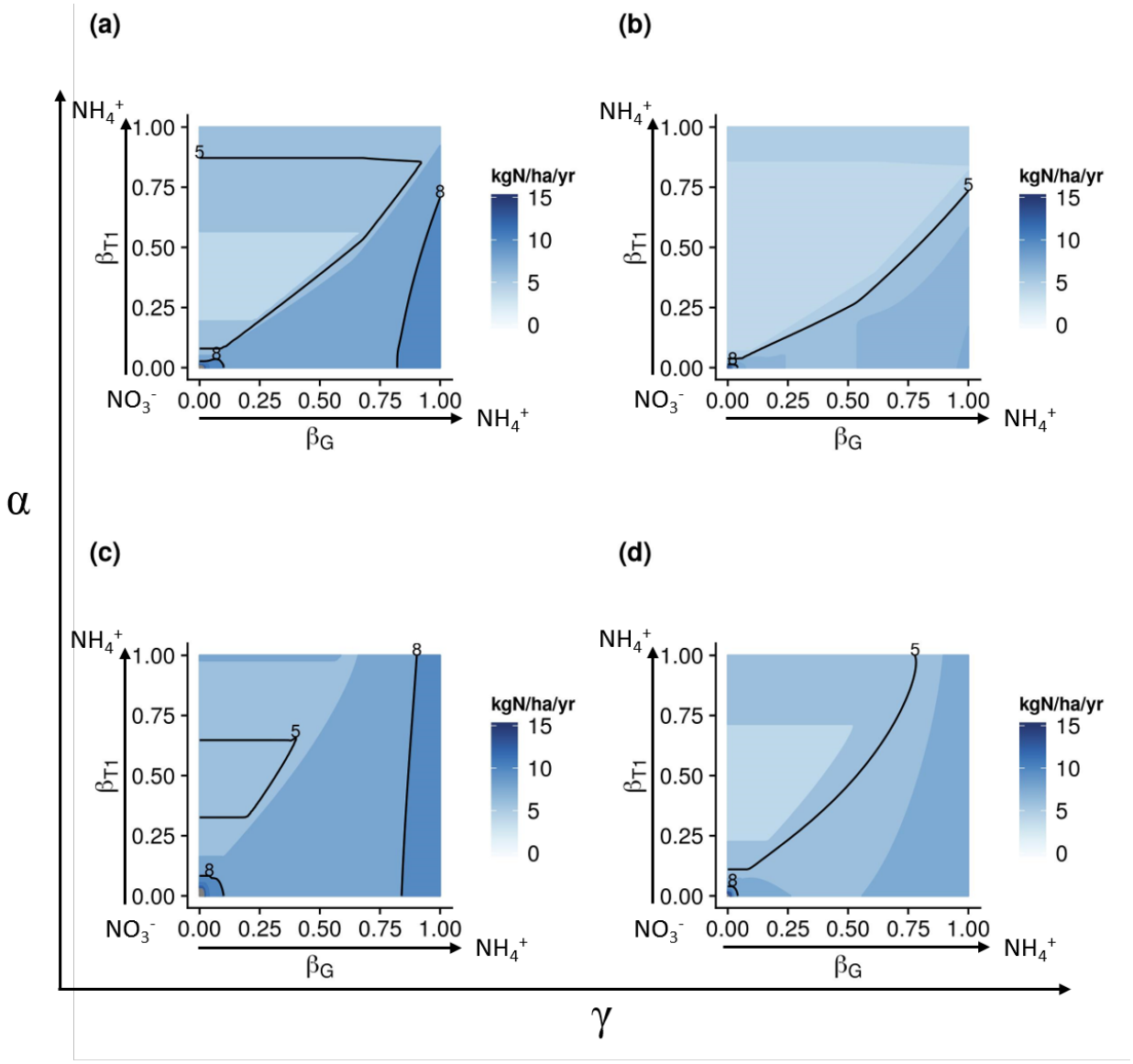

Figure 3.10 – N losses in the open patch as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+ according to different values of α and γ at the savanna scale. The proportion of roots outside tree canopy (α) increases from the bottom to the top, and the surface occupied by tree clumps (γ) increases from the left to the right (a: α = 0.5 and γ = 0.15, b: α = 0.5 and γ = 0.3, c: α = 0.25 and γ = 0.15, d: α = 0.25 and γ = 0.3). Solid lines show N flux contours for remarkable values.

3.6.5 Appendix S5: Scenario of non plasticity of tree roots

We performed simulations in the case where tree roots exhibit the same preference for NH_4^+ *versus* NO_3^- in the open and in the tree clumps patch by scanning different combinations of β_G and β_T with an increment of 0.01. We found the same trends observed on N pools when tree roots have different preference for NH_4^+ *versus* NO_3^- (Fig. 3.12). The clump/open ratio of organic N is lower than 1 when tree preference for NH_4^+ is lower than grass preference for NH_4^+. However, when tree preference for NH_4^+ is higher than grass preference for NH_4^+, the clump/open organic N ratio is higher than 1. This ratio increases and leads to a zone where soil organic matter in the tree clump patch is about 9 times higher than in the open patch. The NH_4^+ stock is always higher in the open patch than under tree clump. Concerning the NO_3^- stock, the clump/open NO_3^- ratio is higher than 1 when tree preference for NH_4^+ is lower than grass preference for NH_4^+ and the reverse when tree preference for NH_4^+ is higher

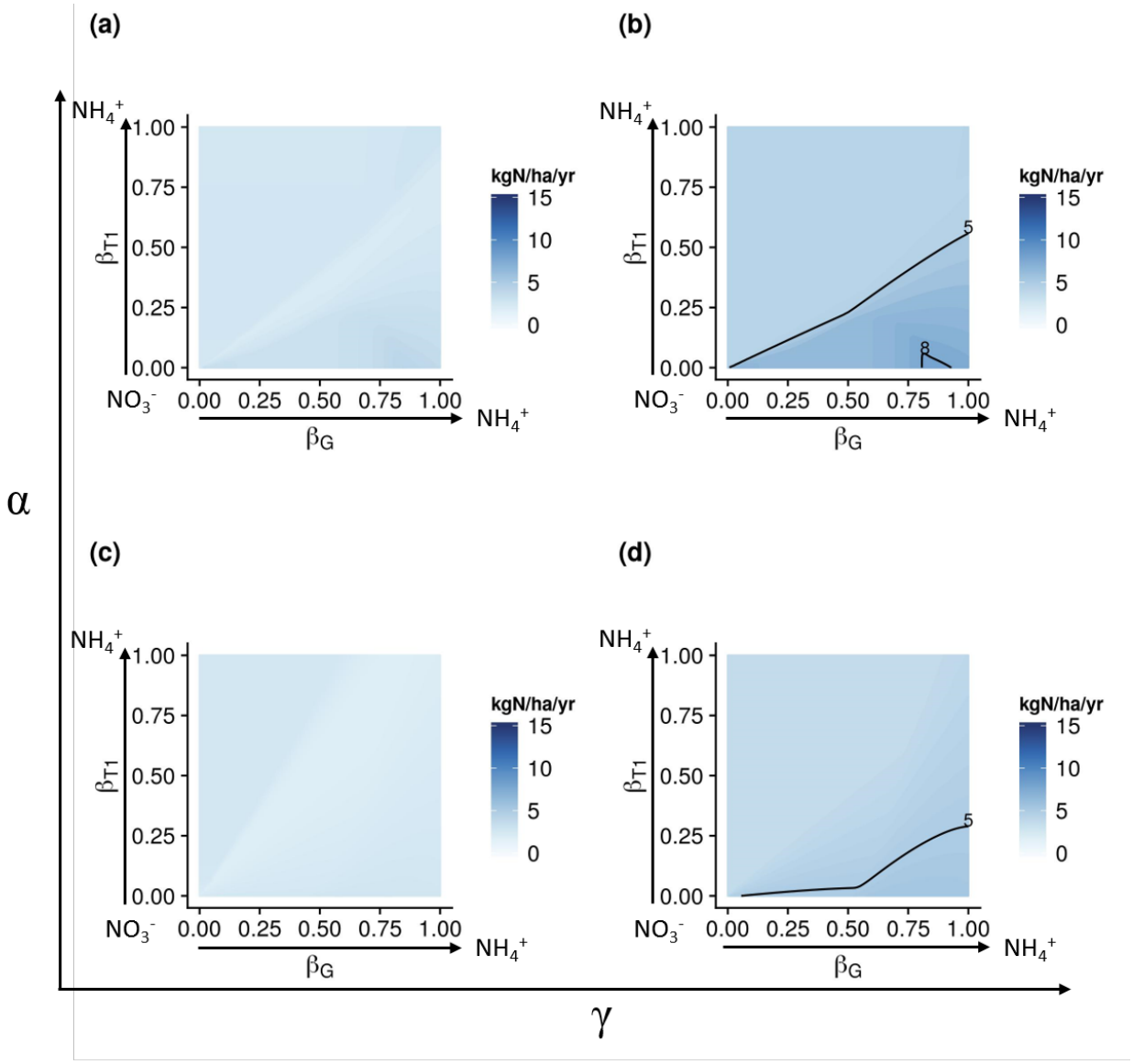

Figure 3.11 – N losses in the tree clump patch as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+ according to different values of α and γ at the savanna scale. The proportion of roots outside tree canopy (α) increases from the bottom to the top, and the surface occupied by tree clumps (γ) increases from the left to the right (a: α = 0.5 and γ = 0.15, b: α = 0.5 and γ = 0.3, c: α = 0.25 and γ = 0.15, d: α = 0.25 and γ = 0.3). Solid lines show N flux contours for remarkable values.

than grass preference for NH_4^+. Fig. 3.13 shows that at low values of α and (α = 0.25 and γ = 0.15), tree biomass is very high when tree preference for NH_4^+ is higher than grass preference for NH_4^+ ($0 < \beta_G < 0.6$). The size of this zone increases with α while it decreases with γ. When grass preference for NH_4^+ is higher than tree preference for NH_4^+, tree biomass decreases to values lower than 100 $kgN\ ha^{-1}$. This appendix shows that N enrichment under tree clumps occurs when trees have a preference for NH_4^+ in the open and under tree clumps. Our results also suggest that trees preferentially absorb NH_4^+ in the open. As explained in the main text, this could be realistic because of the high NH_4^+ availability in the open but a preference of trees for NH_4^+ beneath tree clumps is not expected as trees stimulate nitrification.

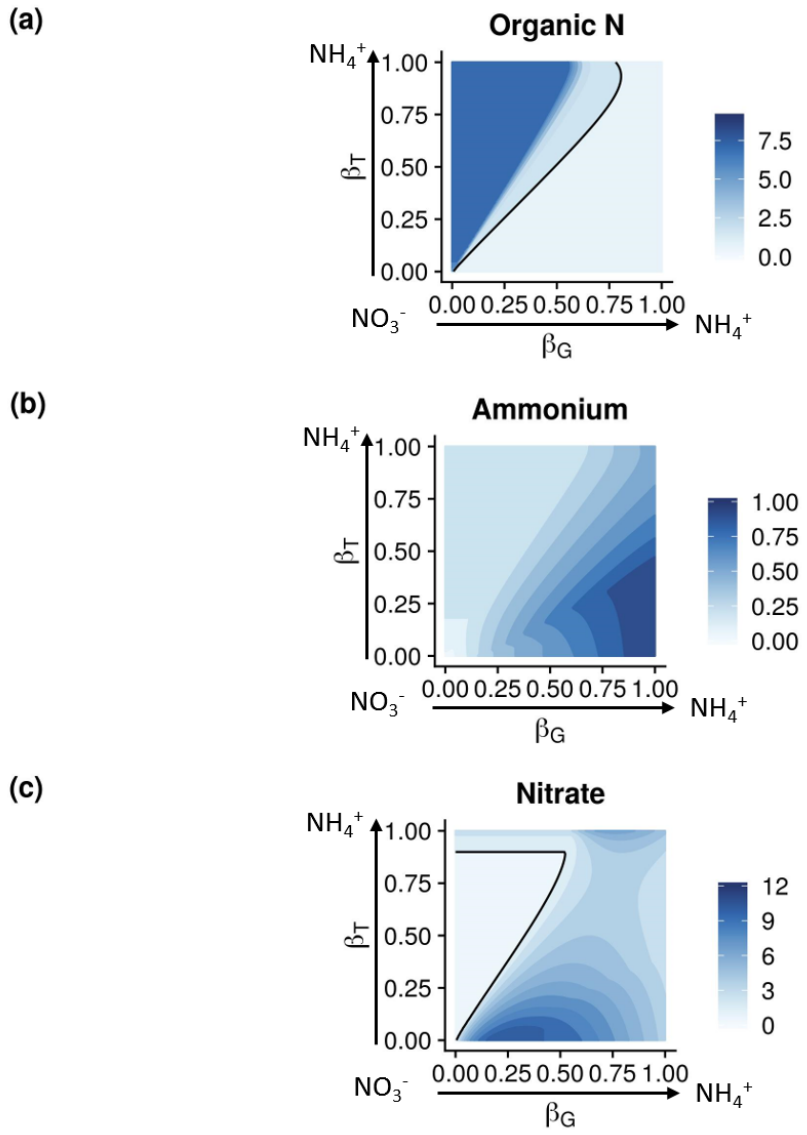

Figure 3.12 – Ratio of the soil N pools in the tree clump patch over the N pools in the open patch as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+: (a) organic N pool, (b) NH_4^+ pool, (c) NO_3^- pool. The solid line represents the 1:1 ratio, i.e. where the N pools are equal in both patches. These figures correspond to simulations of the scenario of non plasticity of trees ($\alpha = 0.25$ and $\gamma = 0.15$).

3.6.6 Appendix S6: Homogeneity of nitrification fluxes

In the Lamto savanna, nitrification control by plants create a spatial heterogeneity in nitrification fluxes. We study here a case where grasses do not inhibit nitrification to assess the possible influence of this homogeneity in nitrification rates on N dynamics and tree biomass. To do so, we performed simulations with the same nitrification rate in the open and tree clump patches ($n_1 = n_2 = 4.16\ yr^{-1}$). We found that the clump/open ratio of organic N is still higher than 1 regardless tree preference for NH_4^+ in the open patch and grass preference for NH_4^+ (Fig.3.14). The clump/open ratio of NH_4^+ stock is lower than 1 for $0 < \beta_G < 0.5$ and higher than 1 for $\beta_G > 0.5$. Concerning the NO_3^- stock, the clump/open NO3- ratio is still lower than 1 regardless tree preference for NH_4^+ and grass preference for NH_4^+. These results suggest that organic N content is always higher under tree clumps while NO_3^- content is always higher in the open because the increase of nitrification flux. Regarding tree biomass (Fig. 3.15), it increases with increasing α when $\gamma = 0.15$ but no difference is observed when $\gamma = 0.3$. In the same way,

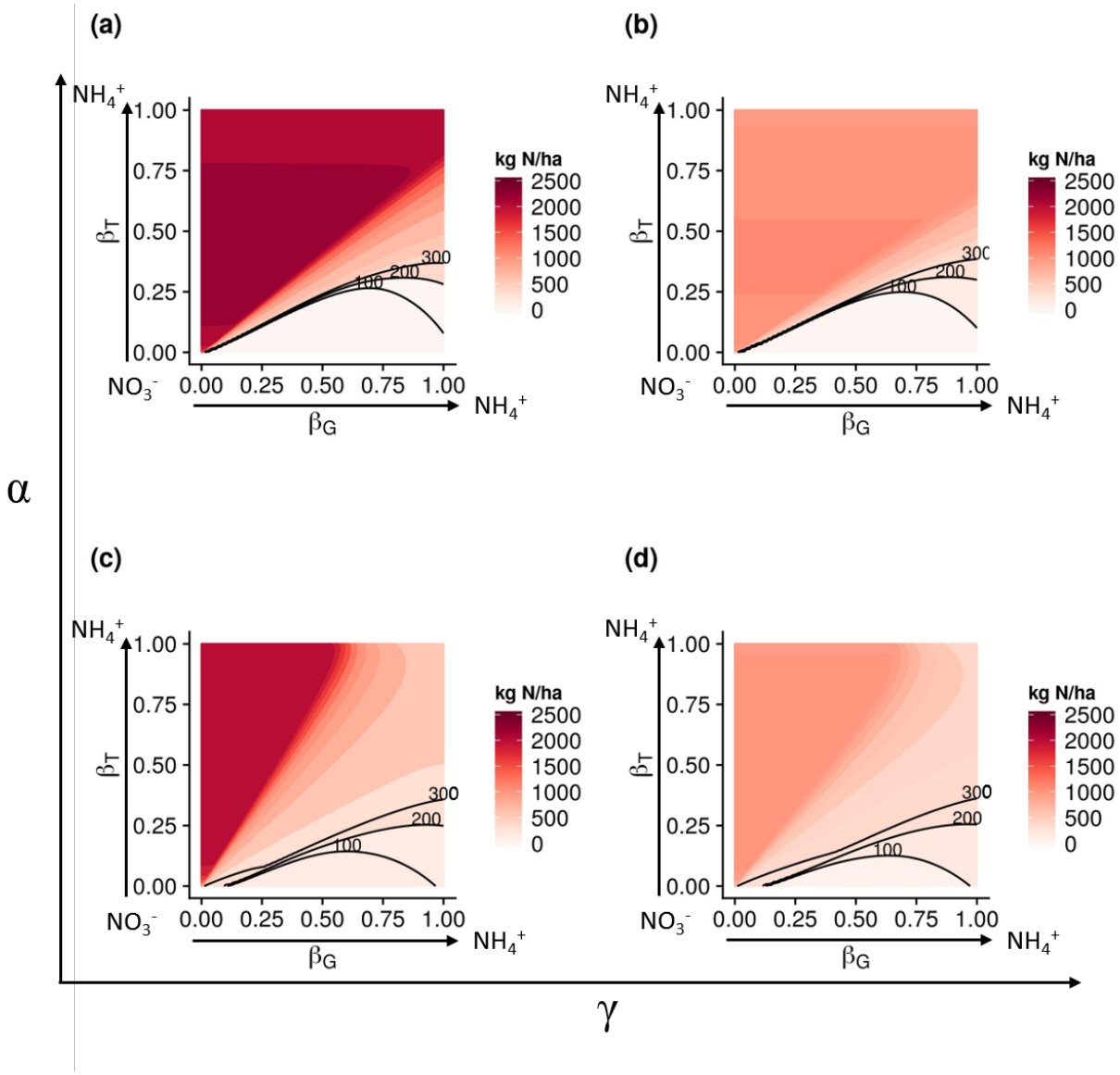

Figure 3.13 – Tree biomass as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+ according to different values of α and γ at the savanna scale. The proportion of roots outside tree canopy (α) increases from the bottom to the top, and the surface occupied by tree clumps (γ) increases from the left to the right (a: α = 0.5 and γ = 0.15, b: α = 0.5 and γ = 0.3, c: α = 0.25 and γ = 0.15, d: α = 0.25 and γ = 0.3). Solid lines show N flux contours for remarkable values.

tree biomass decreases with increasing γ only when α = 0.5.

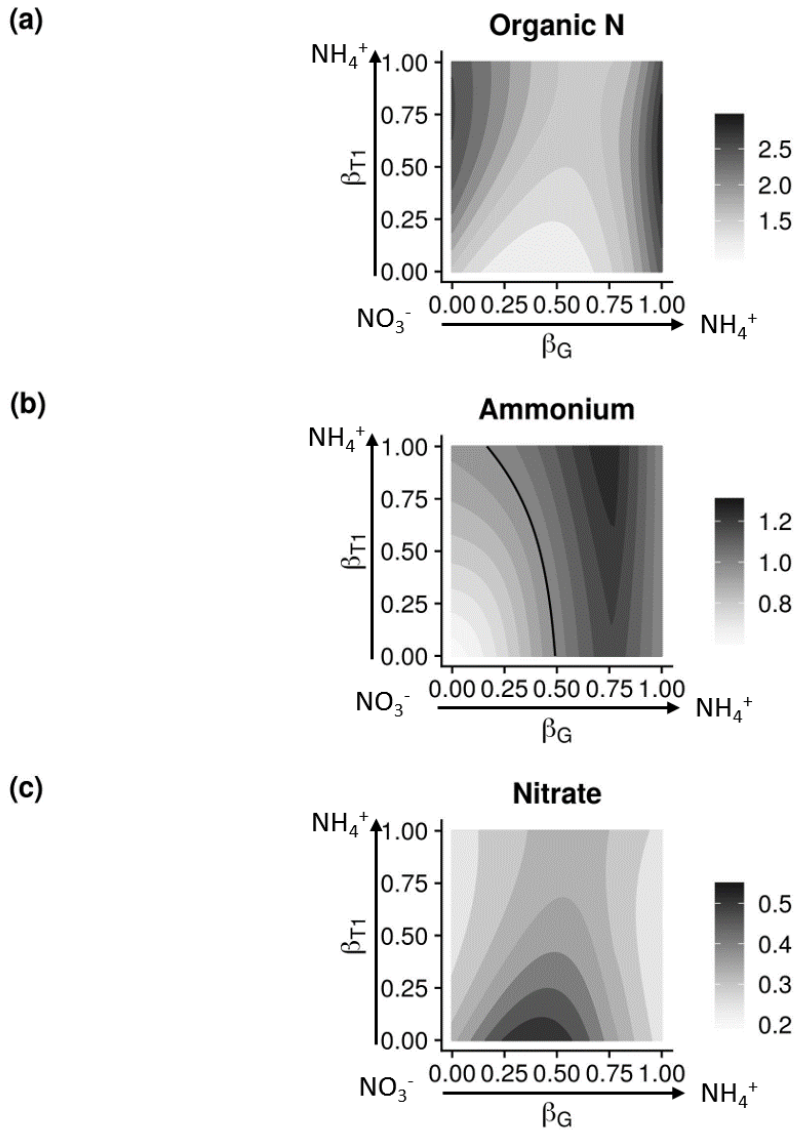

Figure 3.14 – Ratio of the soil N pools in the tree clump patch over the N pools in the open patch as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+: (a) organic N pool, (b) NH_4^+ pool, (c) NO_3^- pool. The solid line represents the 1:1 ratio, i.e. where the N pools are equal in both patches. These figures correspond to simulations of spatial homogeneity in N cycling ($\alpha = 0.25$ and $\gamma = 0.15$).

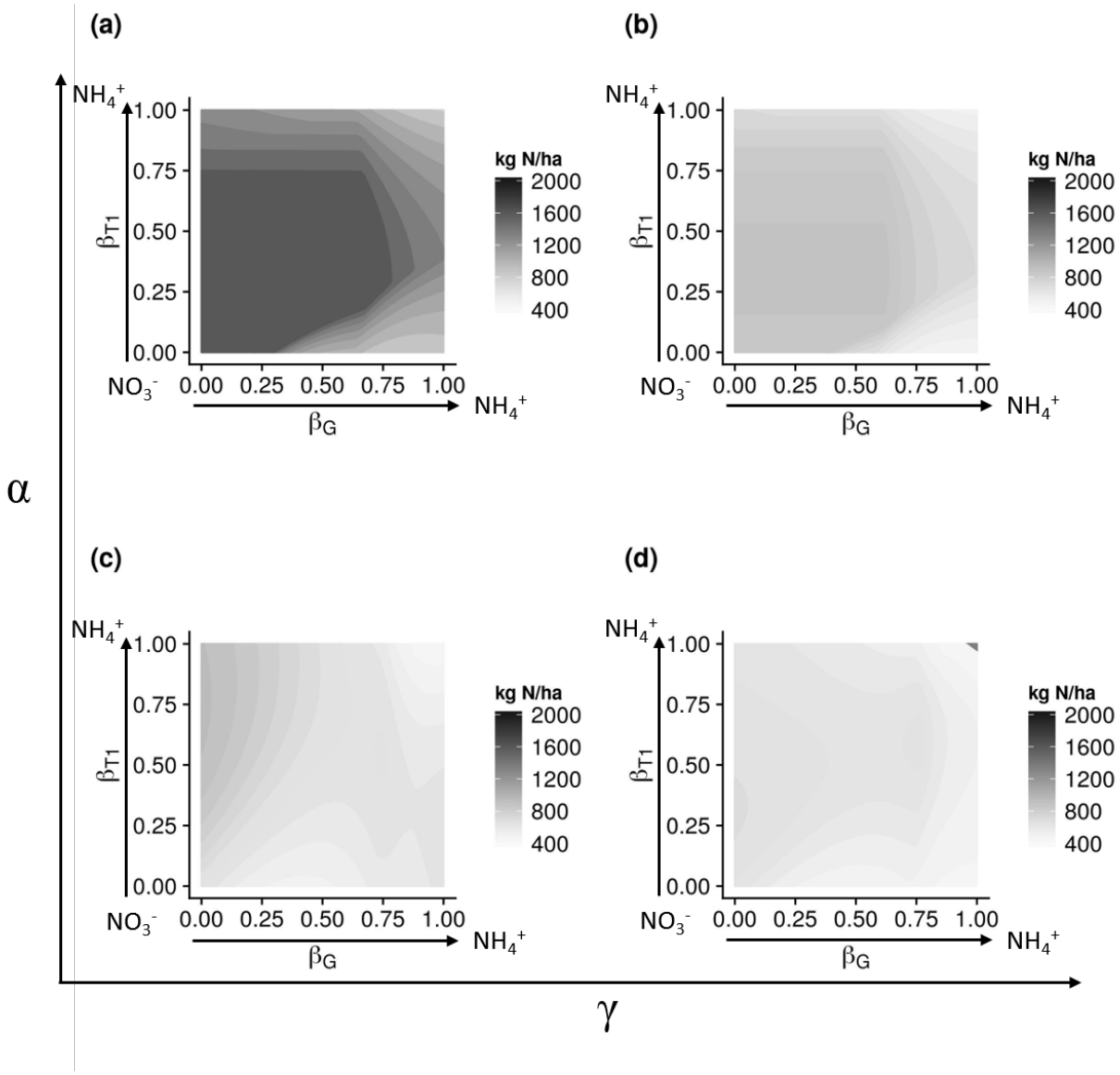

Figure 3.15 – Tree biomass as a function of grass (abscissa) and tree (ordinate) preference for NH_4^+ according to different values of α and γ at the savanna scale. The proportion of roots outside tree canopy (α) increases from the bottom to the top, and the surface occupied by tree clumps (γ) increases from the left to the right (a: α = 0.5 and γ = 0.15, b: α = 0.5 and γ = 0.3, c: α = 0.25 and γ = 0.15, d: α = 0.25 and γ = 0.3). Solid lines show N flux contours for remarkable values.

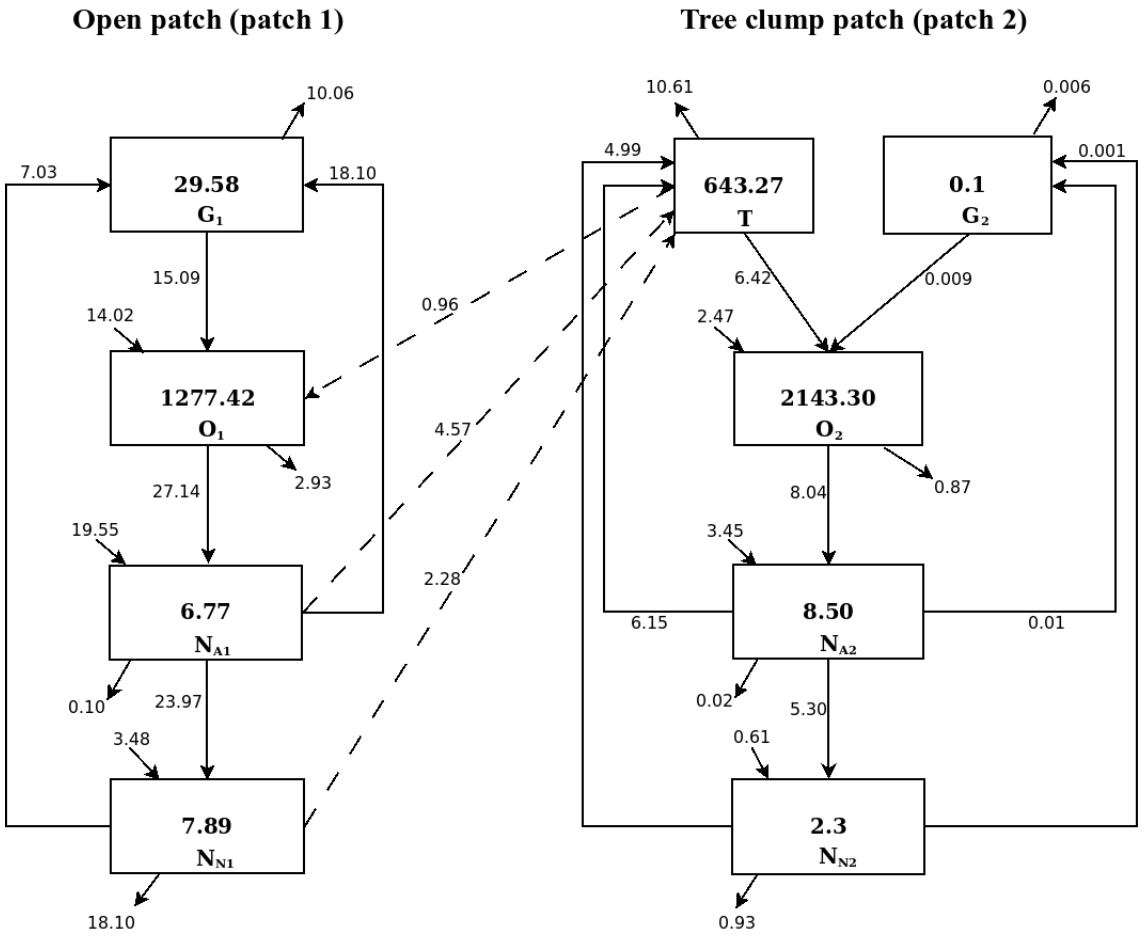

Figure 3.16 – Estimate of the N stocks (kg N ha^{-1}) and N fluxes (kg N ha^{-1} yr^{-1}) at model equilibrium. We fixed β_G =0.75 and β_{T1} = 0.7.

4

Spatial heterogeneity of nitrification contributes to tree-grass coexistence in West African savannas

Spatial heterogeneity of nitrification contributes to tree-grass coexistence in West African savannas

S Konaré [1] *, S Boudsocq [2], J Gignoux [1], J-C Lata [1,3], X Raynaud [1] and S Barot [1]

[1] Sorbonne Université, IRD, CNRS, INRA, UPEC, Univ Paris Diderot, Institute of Ecology and Environmental Sciences, iEES Paris, 75005 Paris, France; [2] Eco&Sols, INRA, CIRAD, IRD, Montpellier SupaAgro, Univ Montpellier, Montpellier, France; [3] Department of Geoecology and Geochemistry, Institute of Natural Resources, Tomsk Polytechnic University, 30, Lenin Street, Tomsk 634050, Russia

Abstract

1. In savanna ecosystems, the coexistence between trees and grasses is determined by complex mechanisms based on resource partitioning and disturbances. In the Lamto savanna (Côte d'Ivoire), nitrification inhibition by grasses and nitrification stimulation by trees create spatial heterogeneity of nitrification fluxes. Besides, savanna trees can also extend a part of their roots in the surrounding open area to take up N.

2. To investigate the role of spatial heterogeneity on tree-grass coexistence, we used a two-patch model simulating N dynamics between an open patch (without trees) and a tree clump patch (trees with grasses under their canopy). The open patch was characterized by a low nitrification rate while the tree clump patch was characterized by a high nitrification rate. Both patches were connected through horizontal fluxes due to the horizontal soil exploration by tree roots. We also tested predictions of coexistence for different spatial tree distributions as they strongly influence savanna dynamics.

3. Our results show that spatial heterogeneity of nitrification induces a spatial partitioning between NH_4^+ and NO_3^- that promotes the coexistence between trees and grasses. As nitrification inhibition by grasses leads to high NH_4^+ availability in the open, tree-grass coexistence is observed when grasses prefer NH_4^+ and trees prefer NH_4^+ in the open and NO_3^- under their canopy.

4. In contrast to random tree distribution, clustered tree distribution enhances coexistence. Intraspecific aggregation enhances the effect of spatial heterogeneity, which decreases interspecific competition and favors tree-grass coexistence. By contrast, increasing the surface explored by tree roots in the open tends to increase the competition between trees and grasses. This enhances the competitive ability of trees for N acquisition and consequently favors invasion by trees.

5. Compared to the mean-field model without spatial heterogeneity, this two-patch model predicts different possible cases of coexistence leading to different landscape structures. This study shows that this new mechanism based on mineral N partitioning into NH_4^+ and NO_3^- can be determinant in the functioning of the Lamto savanna and should at least hold for all West African humid savannas where plants influence N cycling.

Keywords: ammonium, N partitioning, NH_4^+ *versus* NO_3^- preference, nitrate, savanna, spatial heterogeneity, tree-grass coexistence

4.1 Introduction

Savanna vegetation is characterized by a continuous layer of grasses intermixed with a discontinuous stratum of trees. The coexistence of these two contrasting plant types has long been debated and has been attributed to two main theories, resource partitioning and disturbances (Sankaran et al., 2004). In dry savannas, the scarcity of resources, and especially water, lead to niche partitioning as grasses are more competitive than trees in the top layers of the soil while trees are able to explore the soil vertically and take up water at greater depth (Schenk and Jackson, 2002). This niche differentiation through different rooting depths can favor coexistence between trees and grasses (Walker and Noy-Meir, 1982; Walter, 1971). In contrast to dry savannas, wet savannas are not limited by water and could turn into forests, but the presence of disturbances such as fire or herbivory reduces the density of trees (Sankaran et al., 2005; Staver et al., 2011). Fire is the main disturbance limiting woody cover by affecting the survival of tree seedlings and saplings (Gignoux et al., 2009). In the same way, herbivores such as grazers and browsers can have negative effects on grass and tree growth and contribute to regulate the tree-grass ratio (Sankaran et al., 2008; Van Langevelde et al., 2003). While some studies tend to show that tree-grass coexistence can be explained by either resource partitioning (Walker and Noy-Meir, 1982; Walter, 1971) or disturbances (Higgins et al., 2000; Jeltsch et al., 2000), other studies suggest that both mechanisms are involved in tree-grass coexistence (Sankaran et al., 2004).

In the Lamto savanna in Côte d'Ivoire, the dominant grass species inhibit nitrification (Lata et al., 2004; Srikanthasamy et al., 2018). This biological nitrification inhibition (BNI) occurs through the release of grass root exudates impeding the activity of nitrifying microorganisms (Lata et al., 2004; Srikanthasamy et al., 2018). Because ammonium (NH_4^+) is less prone to leaching than nitrate (NO_3^-), keeping nitrogen (N) in the NH_4^+ form decreases N losses by NO_3^- leaching and therefore maintains a high productivity (Boudsocq et al., 2009). BNI capacity has been identified in other African grass species *Brachiaria spp.*, *Sorghum bicolor* (Lata et al., 2004; Subbarao et al., 2009). By contrast, the dominant Lamto savanna tree species have been found to stimulate nitrification (Srikanthasamy et al., 2018). The mechanism explaining this stimulation is not known but one hypothesis would be that as for grasses, specific molecules from the tree root system directly impact microbial communities. Another hypothesis is that the observed increase of soil organic matter and soil humidity below tree canopy could also increase soil microorganisms activity and therefore mineralization and nitrification processes (Mordelet et al., 1993).

Plant-soil feedbacks are important drivers for ecosystem functioning as they strongly influence plant communities dynamics and ecosystem processes such as nutrient cycling (Bonanomi et al., 2008; Van Der Heijden et al., 2008). In nutrient-limited ecosystems such as savannas, plant-soil feedbacks on N cycling can locally impact N availability (Knops et al., 2002) by creating a spatial heterogeneity in soil resources, and thereby influencing primary productivity. Lamto savanna grasses and trees respond differently to the N limitation by favoring their preferred N form through nitrification inhibition and stimulation (Lata et al., 2004; Srikanthasamy et al., 2018). These strategies could induce a resource partitioning, if grasses preferentially absorb NH_4^+ and trees NO_3^- promoting tree-grass coexistence in the Lamto savanna ((Boudsocq et al., 2012; Konaré et al., 2019). Indeed, such heterogeneity can reduce niche overlap as plants differ in their resource use, which likely decreases interspecific interactions and

promotes coexistence of different species even on a single limiting resource (Adler et al., 2013; Barot and Gignoux, 2004; Brandt et al., 2013; Chesson, 2000; Huston and DeAngelis, 1994). Although the two resources we consider are not independent as in some models (Chesson, 2000; Huston and DeAngelis, 1994), they are linked as one is produced from the other by microorganisms, with a possible control by plants. Furthermore, Lamto savanna plants seem to prefer one or the other of these resources depending on the control they have on them. This yields a much more complex picture, which requires a spatially structured model to understand the consequences of plant-soil feedbacks on coexistence.

Although plant preferences strongly vary depending on physiological and environmental conditions (Britto and Kronzucker, 2013), some studies showed that plants can differ in their preference for chemical N forms use (organic and mineral N), which can subsequently facilitate their coexistence (Ashton et al., 2010; McKane et al., 2002). Moreover, the plasticity in resource use can induce different preferences within a species depending on the N form available.

Many studies highlighted the relevance of spatial patterns in ecological dynamics (Dieckmann et al., 2000; Tilman and Kareiva, 1997). For example, intraspecific aggregation alters the strength of intra and inter specific competition so that individuals are likely to interact more with conspecifics (Pacala, 1997; Stoll and Prati, 2001)). This can reduce the intensity of interspecific competition and consequently slow down competitive exclusion (Armstrong and McGehee, 1980). Spatial tree distribution is known to play an important role in savanna dynamics and is strongly affected by disturbances (Menaut et al., 1990). In addition, tree clumps are generally considered as nutrient-rich patches and this higher soil fertility under tree canopy is partly due to the horizontal soil exploration by tree roots in the open (Belsky, 1994) as it improves nutrient transfers between the open and tree clumps (Chapter 3). However, these horizontal fluxes can reduce the heterogeneity in nitrification and lead to a homogenization of NH_4^+ and NO_3^- availability between these two patches (Barot et al., 2015, 2014). While spatial heterogeneity tends to foster niche partitioning (Amarasekare, 2003), horizontal fluxes can minimize the impact of this heterogeneity (Barot et al., 2015, 2014) and could thus be influential for predictions of tree-grass coexistence.

Compared to Chapter 3 where the study was focused on the effects of spatial heterogeneity on N fluxes and N budget, here the goal is to understand the role of spatial heterogeneity on tree-grass coexistence. To study the importance of spatial heterogeneity, we used a modified version of the two-patch model (Chapter 4) considering a patch of open area characterized by a low nitrification rate and a tree clump patch characterized by a high nitrification rate. These two patches are linked through horizontal fluxes due to horizontal soil exploration by tree roots. This model is a spatially explicit extension of a previously published mean-field model (Konaré et al., 2019). Using this model, we tested the following hypotheses: (**i**) Compared to the mean-field model (Konaré et al., 2019), taking into account the existence of distinct N pools below tree clumps and outside tree clumps fosters coexistence. (**ii**) Spatial heterogeneity increases the likelihood of tree-grass coexistence with grasses preferring NH_4^+ and trees preferring NO_3^- under tree canopy and NH_4^+ in the open. Indeed, this spatial heterogeneity leads to a spatial niche partitioning that reduces exclusion and favors coexistence. (**iii**) Because the horizontal soil exploration of tree roots in the open should allow trees to benefit from the high NH_4^+ availability under grasses while trees prefer NO_3^- under their canopy, coexistence is more expected

when trees have different preference under their canopy and in the open. (**iv**) Tree-grass coexistence depends on spatial tree distributions and is facilitated when trees are clumped. More specifically, tree clumping reduces soil exploration by tree roots in the open and thus reduces competition between trees and grasses in the open. (**v**) Increasing the surface explored by tree roots in the open increases horizontal fluxes between the open and the tree clump patches, which increases the competition between trees and grasses for N and consequently reduces the chances of tree-grass coexistence.

4.2 Two patch model

4.2.1 Model description

The two patch model is derived from a published mean-field model (Konaré et al., 2019) and builds on our previous work (Chapter 3). The open patch is occupied by grasses and some tree roots, while the tree clump patch is occupied by grasses and trees. This leads to a grass compartment (G_1) in the open and a grass (G_2) and a tree (T) compartments in the tree clump patch. The model also tracks soil organic matter (O) and mineral N (N_A and N_N) compartments in both patches (see Fig. 3.1, Chapter 3). Both patches are interconnected through horizontal fluxes due to the horizontal soil exploration by tree roots in the open patch. All compartments are N stocks expressed as a quantity of N by surface unit of patch, i.e, kilograms of N per hectare of the open patch and kilograms of N per hectare of the tree clump patch ($kgN\ ha^{-1}$). All parameters but nitrification rates are equal between the two patches to keep the model relatively simple and focus on the effects of nitrification heterogeneity through nitrification inhibition by grasses causing a low nitrification in the open and nitrification stimulation by trees leading to a high nitrification under tree clumps.

In the model, N is supposed to be the limiting factor of primary production and grass and tree growth depend on the acquisition of mineral N forms, that can be acquired under two forms (NH_4^+ and NO_3^-) with a certain preference (β) for NH_4^+ *versus* NO_3^-. This preference ranges between 0 and 1 with high values of β corresponding to a high preference for NH_4^+. N uptake by plants is considered as donor (mineral N)-recipient (plants) functions: it increases with both nutrient availability and plant biomass. N is absorbed by plants through N uptake rates β u for NH_4^+ uptake and (1-β) u for NO_3^- uptake. Plants release N into organic N pool at constant mortality rates d_G, d_l and d_r respectively for grasses, tree leaves and tree roots. Organic N is mineralized into NH_4^+ at rate (m) and NH_4^+ can be transformed into NO_3^- at rate (n).

In our model, savanna tree roots tend to proliferate horizontally outside their canopy projection (α) favoring horizontal fluxes between the open and the tree clump patch. These horizontal fluxes constitute an important part of the total N uptake by trees (Chapter 3). The N uptake also depends on the proportion of the surface occupied by tree clumps (γ) and by the open (1-γ). Each patch receives fixed N inputs through dry and wet depositions that provide N under organic and mineral forms into the O, N_A and N_N compartments at rates i_O, i_{NA}, i_{NN}. Non-symbiotic fixation contributes to the input of NH_4^+ and is included in i_{NA} (Abbadie, 2006). N losses from savannas result from the burning of the plant compartments (l_G and l_T), and leaching for other compartments (l_O, l_{NA} and l_{NN}). NO_3^- losses by denitrification are included in l_{NN}. In order to obtain N dynamics at the savanna scale, all

equations are multiplied by (1-γ) in the open and γ in the tree clump patch (see Chapter 4). This leads to this system of differential equations:

Open patch (patch 1)

$$\frac{dG_1}{dt} = (1-\gamma)(\beta_G u_G N_{A1} G_1 + (1-\beta_G) u_G N_{N1} G_1 - (d_G + l_G)\, G_1) \tag{4.1}$$

$$\frac{dO_1}{dt} = (1-\gamma)(i_O + d_G G_1 + d_r(\frac{\gamma}{1-\gamma})\alpha r T - (m + l_O)\, O_1) \tag{4.2}$$

$$\frac{dN_{A1}}{dt} = (1-\gamma)(i_{NA} + m\, O_1 - (\beta_G u_G G_1 + n_1 + l_{NA} + \beta_{T1} u_r(\frac{\gamma}{1-\gamma})\alpha r T)\, N_{A1}) \tag{4.3}$$

$$\frac{dN_{N1}}{dt} = (1-\gamma)(i_{NN} + n_1 N_{A1} - ((1-\beta_G) u_G G_1 + l_{NN} + (1-\beta_{T1})(\frac{\gamma}{1-\gamma}) u_r \alpha r T)\, N_{N1}) \tag{4.4}$$

Tree clump patch (patch 2):

$$\frac{dG_2}{dt} = \gamma(\beta_G u_G N_{A2} G_2 + (1-\beta_G) u_G\, N_{N2} G_2 - (d_G + l_G)\, G_2) \tag{4.5}$$

$$\begin{aligned}\frac{dT}{dt} = \gamma((1-\alpha)(\beta_{T2} u_r N_{A2} r\, T + (1-\beta_{T2}) u_r N_{N2} r\, T) + \alpha(\beta_{T1} u_r N_{A1} r T + \\ (1-\beta_{T1}) u_r N_{N1} r\, T - (d_l(1-r) + d_r \alpha r + (1-\alpha) d_r r + l_T)\, T)\end{aligned} \tag{4.6}$$

$$\frac{dO_2}{dt} = \gamma(i_O + d_G G_2 + (1-\alpha) d_r r T + d_l(1-r) T - (m + l_O)\, O_2) \tag{4.7}$$

$$\frac{dN_{A2}}{dt} = \gamma(i_{NA} + m\, O_2 - (\beta_G u_G G_2 + (1-\alpha)\, \beta_{T2} u_r r T + n_2 + l_{NA})\, N_{A2}) \tag{4.8}$$

$$\frac{dN_{N2}}{dt} = \gamma(i_{NN} + n_2 N_{A2} - ((1-\beta_G) u_G G_2 + l_{NN} + (1-\beta_{T2})(1-\alpha) u_r r\, T)\, N_{N2}) \tag{4.9}$$

4.2.2 Links between α, γ and T

To describe the spatial setting of our model, we considered the proportion α of tree roots in the open and γ as the proportion of the savanna surface covered by tree clumps. Compared to Chapter 3 where α and γ had fixed values, in this version of the model, α is a function of γ and γ is a function of tree biomass (T). We assume that α depends on the proportion of tree cover and the spatial patterns of trees: for a given canopy and root system radius, α should decrease with γ. However, this relation should also depend on the tree distribution with lower values of α when trees are clumped and high values of α when they are randomly or regularly distributed. Although tree distribution can vary in different savanna ecosystems, it is often clustered (Barot et al., 1999; Gignoux et al., 2006). Similarly, there should be a positive relationship between γ and tree biomass (T). The way these relations are

parameterized is described below in the parameterization section.

The shape of the relation between α and γ, and between γ and T was studied by simulations. To do so, we simulated different distributions of trees, assuming that trees are represented as superimposed discs describing the canopy and the root system. Tree roots can extend more than 20 m away from tree clump center (Abbadie et al., 2006). In our simulations, canopy radius was set to 2 m and root system radius to 6 m. The relation between α and γ was obtained by calculating the proportion of root system that did not fall under the canopy of other trees, for a random, clustered and regular tree distribution. A Poisson process varying from 1 to 100 by step of 10 and from 100 to 2000 trees ha^{-1} by step of 100 was used to simulate random patterns. In contrast to simulate clumped patterns, we used a Matérn cluster process (Matérn, 1960) with a density of tree clumps that varied from 1 to 100 by step of 10 and from 100 to 1000 trees ha^{-1} by step of 100 with a mean clump radius of 2 m and a mean number of trees per clump of 10. Finally, regular patterns were modeled using a Matérn hard-core process (Matérn, 1960, 1986) with an inhibition distance of 2 m and the same densities as for random patterns. To determine the relation between α and γ, and γ between and T, we calculated the quantity of tree roots outside tree canopy at the individual scale and the mean of all individual values to obtain α for a given tree density. We then calculated γ for each tree density by determining the total space occupied by trees. Linear regression models were then used to determine the relation between α and γ and between γ and tree biomass (T). Model equations and parameters were included in the two-patch model to link α, γ and T. We also tested the sensibility of results to the root radius by increasing this radius from 6 to 12 m to assess the relationship between α and γ.

4.2.3 Model analysis and parameterization

The model relied on numerical simulations as it could not be analytically solved. All simulations were coded in R (R Core Team, 2019) using deSolve package for the resolution of differential equations (Soetaert et al., 2010). All simulations were run for 3000 years, which was sufficient to reach steady states for all compartments.

We used the same parameter sets as in Chapter 3 but run a completely different simulation experiment. These parameters are based on data from the Lamto savanna in Côte d'Ivoire (06°13'N, 05°02'W) (Abbadie et al., 2006) (Appendix 1). Lamto savanna vegetation is composed of perennial grasses, small tree clumps and tall palm trees. Trees are generally aggregated (Gignoux et al., 2006).

Tree-grass coexistence was determined using the mutual invasibility criterion (Chesson and Ellner, 1989). This criterion considers a pair of invader and resident species (for example grasses as the invading species with a negligible biomass of 0.01 kg N ha^{-1} compared to trees as the resident species with a high biomass of 10 kg N ha^{-1}, and then the reverse situation with grasses at high biomass and trees at negligible biomass). When the two species are able to invade each other, they are assumed to mutually coexist over the long term (Chesson and Ellner, 1989). We first simulated mutual invasion between trees and grasses for different combinations of tree and grass preference (preference for NH_4^+ *versus* NO_3^- by trees was the same in the open and under tree canopy) *versus* different combinations of grass and tree preferences in the open. Moreover, the proportion of tree roots in the open does not

depend only on tree density or biomass, but also on the spatial distribution of individual trees. We thus tested the effects of tree distributions in space on tree-grass coexistence by comparing simulations for a random *versus* clustered tree distribution. Spatial heterogeneity was included in the model by considering a low nitrification rate in the open patch (n_1) and a high nitrification rate under trees (n_2). Those rates were calculated by dividing nitrification fluxes under grasses and under trees by their respective ammonium stocks (Srikanthasamy et al., 2018). We then increased the nitrification rate in the open to compare a spatial homogeneity to a spatial heterogeneous nitrification rate to test the importance of heterogeneity in nitrification flux on tree-grass coexistence. Although existing data do not allow to estimate 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^+ because NH_4^+ should the dominant N form in the open. 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}) with an increment of 0.005.

4.3 Results

4.3.1 Links between soil exploration by tree roots and tree cover and between tree biomass and tree cover

A negative linear relation is observed between α and γ regardless tree distributions (p-value < 0.0001 and $R^2 = 0.998$ for random; p-value < 0.0001 and $R^2 = 0.997$ for cluster; p-value < 0.0001 and $R^2 = 0.999$ for regular tree pattern) (Fig. 4.1A). As expected in the case of clustered trees, the relation yields lower α values compared to random. This leads to the following regression lines: $\alpha = -0.897\gamma + 0.889$, $\alpha = -0.882\gamma + 0.892$ and $\alpha = -0.692\gamma + 0.686$ respectively for random, regular and clustered tree patterns. We observe a significant difference between cluster and random or regular patterns but the difference between random and regular patterns was not significant. Fig. 4.1B shows that α significantly increases with tree biomass (p-value < 0.005, $R^2 = 0.962$), which leads to this equation $T = 530.56\gamma - 2.81$. Despite the potential non linearity between γ and T, we chose to use a linear relationship in our model for simplicity.

4.3.2 Tree-grass coexistence is affected by the difference between tree preference for NH_4^+ in the open and under tree canopy

Model simulation leads to three cases of coexistence: (1) a coexistence where trees and grasses are spatially separated (no grasses under trees, only in the open hereafter called tree-grass mosaic), (2) a coexistence where grasses can only grow in tree clumps (no open area) hereafter called savanna woodland, and (3) a coexistence where grasses grow both under tree canopy and in the open (hereafter savanna). When tree preference is the same in the open and under tree canopy (Fig. 4.2), grasses successfully invade and exclude trees if grasses prefer NH_4^+ and trees prefer NO_3^-. Tree-grass mosaic occurs when grasses have a higher preference for NH_4^+ than trees. By contrast, when tree preference

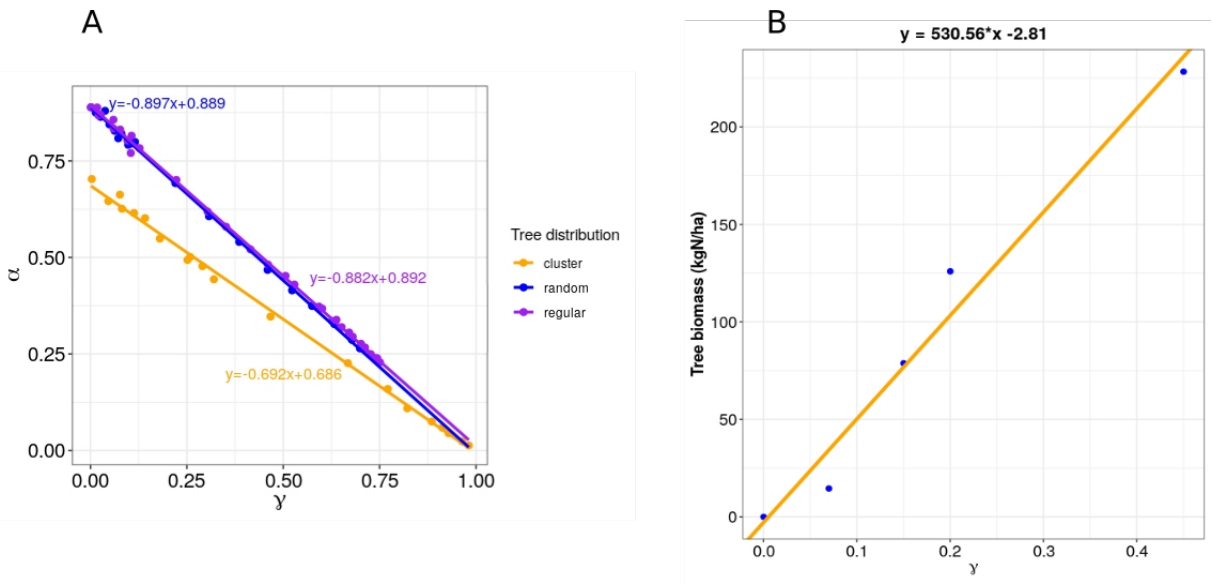

Figure 4.1 – (A) Proportion of tree roots in the open (α) as a function of tree cover (γ) according to cluster, random and regular tree distribution, (B) Tree biomass as a function of tree cover (γ) for a root radius equals to 6 m.

for NH_4^+ is higher than grasses, trees completely invade and exclude grasses. We also observe a small portion of the parameter space where tree clumps establish when grasses prefer NO_3^- and trees strongly prefer NH_4^+ ($\beta_{T1} > 0.98$). Savanna tree-grass coexistence is possible when grasses have a high preference for NH_4^+ and trees prefer NO_3^-. When tree preference is the same in the open and under tree canopy, this reduces possibilities of complete coexistence between trees and grasses but favors tree-grass mosaic.

If trees have different preferences in the open *versus* under tree canopy, the sizes of the zone of savanna woodland and savanna strongly increases while the zone of tree-grass mosaic decreases. Savanna is favored for a large range of tree preference in the open (β_{T1}) and a grass preference for NH_4^+. Tree clumps establishment becomes possible when grasses and trees in the open prefer NH_4^+. Taken together, different tree preference in the open and under tree canopy increase possibilities of coexistence between trees and grasses.

4.3.3 Tree-grass coexistence depends on tree spatial distributions

Tree distribution strongly influences the conditions of coexistence between trees and grasses (Fig. 4.3). For random tree distributions, grasses invade and exclude trees when grasses have a higher preference for NH_4^+ than trees in the open. However, when tree roots in the open have a higher preference for NH_4^+ than grasses, trees successfully invade and exclude grasses. The model also predicts a zone in which savanna establishes when $\beta_G > 0.7$ and $0.4 < \beta_{T1} < 0.73$, a zone where tree clumps invade when grasses and trees in the open prefer NH_4^+ and a small zone of tree-grass mosaic.

Compared to a random distribution of trees, clustered pattern strongly increases the size of the zones of savanna and tree-grass mosaic. Tree-grass mosaic is enhanced when the grass preference for NH_4^+ is higher than the tree preference for NH_4^+ in the open (β_{T1}). Savanna zone extends to large range of β_{T1} values and a preference of grasses for NH_4^+. Switching from random to clustered tree

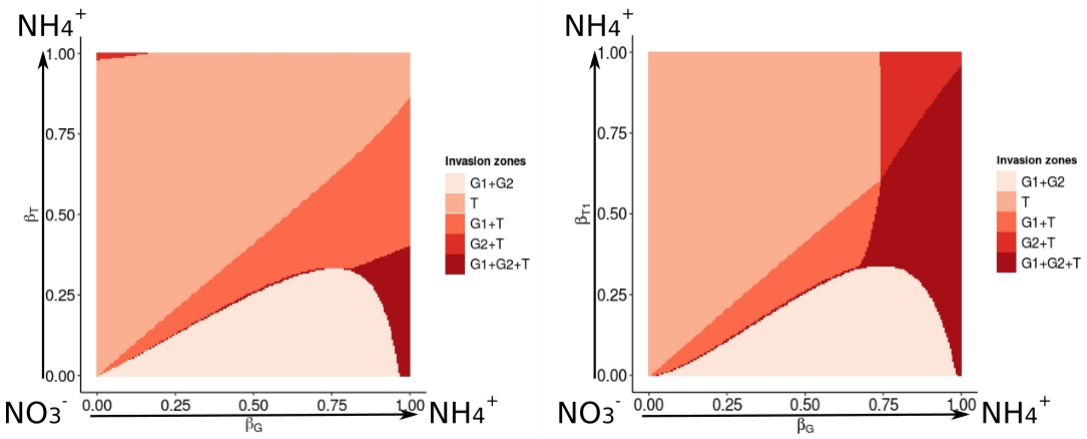

Figure 4.2 – Mutual invasibility plots between trees and grasses according to grass (β_G) and tree (β_T) preference for NH_4^+ (left), and grass (β_G) and tree (β_{T1}) preference for NH_4^+ in the open patch (right) at the savanna scale. Simulations correspond to clustered tree distributions. Invasion zones: G1+G2: grasses invade and exclude trees, T: Trees invade and exclude grasses, G1+T: tree-grass mosaic (coexistence between trees and grasses in the open), G2+T: savanna woodland (coexistence between trees and grasses under their canopy), G1+G2+T: savanna (coexistence between trees and grasses under their canopy and in the open).

distribution also reduces the size of the zone of invasion by grasses or by trees or by savanna woodland.

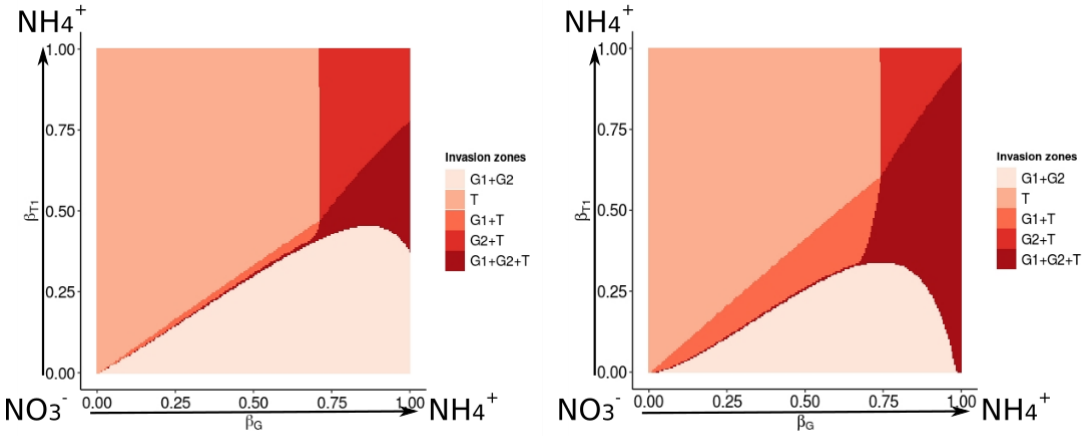

Figure 4.3 – Mutual invasibility plots between trees and grasses according to random (left) and clustered (right) tree distributions at the savanna scale. Invasion zones: G1+G2: grasses invade and exclude trees, T: Trees invade and exclude grasses, G1+T: tree-grass mosaic (coexistence between trees and grasses in the open), G2+T: savanna woodland (coexistence between trees and grasses under their canopy), G1+G2+T: savanna (coexistence between trees and grasses under their canopy and in the open).

4.3.4 Impact of spatial heterogeneity in nitrification on tree-grass coexistence

Spatial heterogeneity of nitrification due to its control by plants alters conditions of coexistence between trees and grasses. We compared a case of spatial homogeneity where grasses do not inhibit

nitrification (Fig. 4.4) to a case of spatial heterogeneity (Fig. 4.3). For a random tree distribution, increasing nitrification rate in the open promotes invasion by trees with grasses under their canopy ($\beta_G > 0.7$ and $\beta_{T1} > 0.35$) or by trees only ($\beta_G < 0.7$ and for all combinations of β_{T1}). Compared to cases of spatial heterogeneity (Fig. 4.4), we observed a reduced zone of tree-grass mosaic for $0.4 < \beta_G < 0.62$ and $\beta_{T1} < 0.13$ and a reduced zone of savanna when grasses prefer NH_4^+ ($\beta_G > 0.62$) and trees prefer NO_3^- in the open ($\beta_{T1} > 0.28$). For a clustered tree distribution, the overall pattern is virtually the same but a second zone of tree-grass mosaic appears when grasses and trees in the open strongly prefer respectively NO_3^- ($\beta_G < 0.2$) and NH_4^+ ($\beta_{T1} > 0.95$). Increasing nitrification rate reduces total coexistence between trees and grasses and facilitates zones with only trees or trees with grasses under their canopy. This shows that different nitrification rates in the open and in the tree clump patch improve chances of tree-grass coexistence.

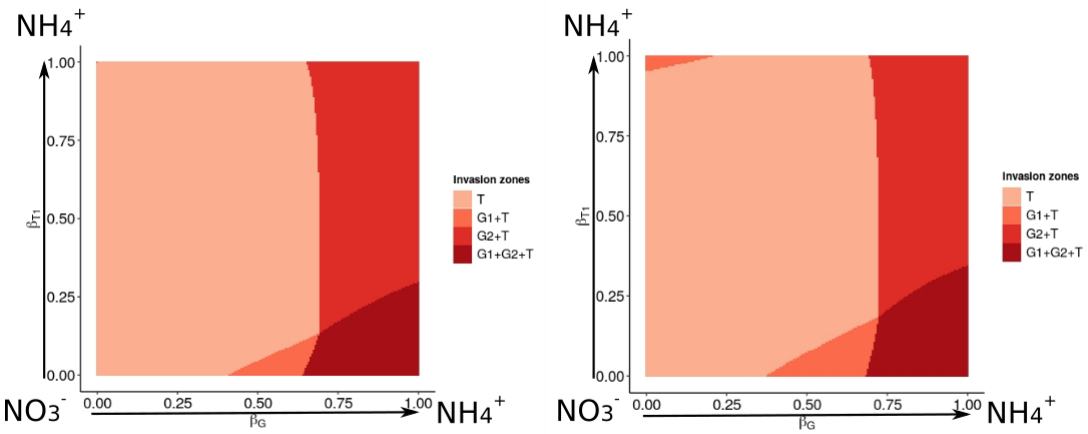

Figure 4.4 – Mutual invasibility plots between trees and grasses according to random (left) and clustered (right) tree distributions at the savanna scale. These figures correspond to cases where grasses do not inhibit nitrification (spatial homogeneity: $n_1 = n_2 = 4.16\ yr^{-1}$). Invasion zones: G1+G2: grasses invade and exclude trees, T: Trees invade and exclude grasses, G1+T: tree-grass mosaic (coexistence between trees and grasses in the open), G2+T: savanna woodland (coexistence between trees and grasses under their canopy), G1+G2+T: savanna (coexistence between trees and grasses under their canopy and in the open).

4.3.5 Soil exploration by tree roots affects tree-grass coexistence

Figure 4.5 displays the outcome of mutual invasion between trees and grasses when the tree root system radius is increased from 6 m to 12 m. As described above, savanna in random distribution cases is possible for $\beta_G > 0.7$ and $0.4 < \beta_{T1} < 0.73$ and the size of this zone increases and extends to more combinations of β_{T1} when we switch from a random to a clustered tree distribution (root radius = 6 m, Fig. 4.5). We observe the same tendencies when the root radius is increased to 12 m (Appendix 3). Overall, clustered distributions tend to increase the size of the savanna zone. However, increasing the surface explored by tree roots reduces the sizes of the zone of tree-grass coexistence in cases of both random and clustered distributions. This is more perceptible for clustered patterns for which the size of the savanna and tree-grass mosaic zones largely decreases while the zone of invasion by grasses increases.

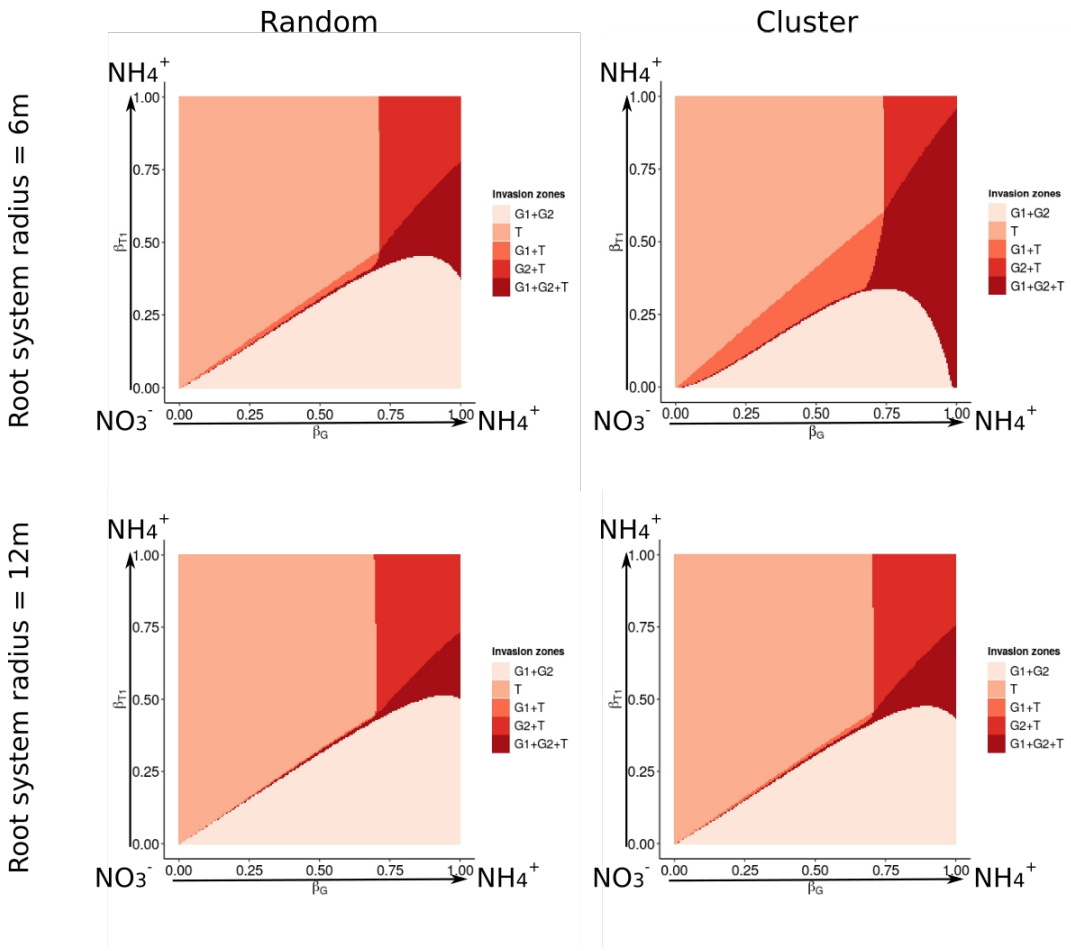

Figure 4.5 – Mutual invasibility plots between trees and grasses according to random (left) and clustered (right) tree distributions at the savanna scale. The first (second) row of graphs corresponds to simulations of tree distributions with a root system radius of 6 (12) m when determining the relation between and . Invasion zones: G1+G2: grasses invade and exclude trees, T: Trees invade and exclude grasses, G1+T: tree-grass mosaic (coexistence between trees and grasses in the open), G2+T: savanna woodland (coexistence between trees and grasses under their canopy), G1+G2+T: savanna (coexistence between trees and grasses under their canopy and in the open).

4.4 Discussion

In our model, tree-grass coexistence occurs when plants have contrasted preferences for NH_4^+ *versus* NO_3^-. This is in agreement with theories showing that the coexistence of different species is possible when they differ in their use of resources (Armstrong and McGehee, 1980). This is also in agreement with published work on competition for NH_4^+ and NO_3^- (Boudsocq et al., 2012; Konaré et al., 2019). These results are also supported by empirical studies on N partitioning indicating that plant having different preferences for different chemical N forms can coexist (Ashton et al., 2010; McKane et al., 2002; Miller and Bowman, 2002). In our case, NH_4^+ and NO_3^- initially represent a single resource that is N, and the two resources are linked by nitrifcation, i.e., one of the resources is produced from the other, something yet unexplored. Despite this dependency, mineral N partitioning into two forms can contribute to the coexistence of two species. NH_4^+ and NO_3^- partitioning reduces niche overlap and hence reduces interspecific competition and competitive exclusion(Barot and Gignoux, 2004; Chesson, 2000; Hardin, 1960) : mineral N partitioning appears as a stabilizing mechanism (Barot and Gignoux, 2004; Chesson, 2000) fostering coexistence between trees and grasses.

4.4.1 Comparison between the one-patch and the two-patch model

Compared to the mean-field model (Konaré et al., 2019), the two-patch model allows simulating distinct pools of mineral N available below tree clumps and in the open. Although the sizes of the zone of savanna in the two-patch model (cluster distribution, Fig. 4.3) and in the mean-field model (Fig. 2A, Konaré et al. (2019)) are not significantly different, the two-patch model predicts different possible cases of coexistence possibly describing different landscape structures. Indeed, the mean-field model only allows one possible case of tree-grass coexistence while the two-patch model favors savanna woodland (trees and grasses under their canopy), tree-grass mosaic (trees and grasses in the open) and savanna (trees and grasses of the open and under tree canopy) zones. These results are in accordance with theories showing that coexistence in a spatially heterogeneous environment is facilitated (Amarasekare, 2003; Chesson, 2000) even with a single resource. Such heterogeneity spatially separates the mineral N resource so that this resource is no longer fully shared between the competitors. This increases the number of degrees of freedom of the system and explains that the two-patch model leads to more diverse scenarios of coexistence than the one-patch model.

4.4.2 Heterogeneity in nitrification influences tree-grass coexistence in the Lamto savanna

Studies on resource-based mechanisms of tree-grass coexistence in savannas have focused on water competition (Walker and Noy-Meir, 1982; Walter, 1971). But little is known about other resources that are essential for plant growth, such as N (Donzelli et al., 2013). In the Lamto savanna, plants have developed strategies to inhibit (grasses) or stimulate (trees) nitrification, which locally creates NH_4^+ rich patches in the open and NO_3^- rich patches under trees suggesting a grass preference for NH_4^+ and tree preference for NO_3^- (Lata et al., 2004; Srikanthasamy et al., 2018). In our model, when trees have the same preference in the open and under tree canopy, savannas occur when grasses have a high preference for NH_4^+ and trees a high preference for NO_3^-. This confirms that tree-grass coexistence is possible when grasses prefer NH_4^+ and trees prefer NO_3^- at least under tree canopy. Wang and Macko (2011) studied the preference of grasses depending on climatic conditions and found that grasses tend to prefer NH_4^+ in humid areas. Moreover, ongoing studies on *Hyparrhenia diplandra* in the Lamto savanna (Barot, personal communication) as well as a study on *Andropogon gayanus* (Rossiter-Rachor et al., 2009) suggest that these two species that inhibit nitrification, have a preference for NH_4^+. The spatial heterogeneity in nitrification favors the availability of two forms of mineral N exploitable by plants, NH_4^+ and NO_3^- in two different patches: NH_4^+ availability is higher in the open while NO_3^- availability is higher under tree clumps. Unlike the mean-field model where trees and grasses coexist when grasses prefer NO_3^- and trees prefer NH_4^+ (Konaré et al., 2019), in the two-patch model tree-grass coexistence becomes possible when grasses prefer NH_4^+ and trees prefer NO_3^-. This is more in accordance with the Lamto savanna case as grasses are know to inhibit nitrification while trees stimulate it (Lata et al., 2004; Srikanthasamy et al., 2018). The N limitation in the Lamto savanna (Abbadie et al., 2006) have induced the evolution of different strategies: a conservative strategy for grasses through BNI capacity and an acquisitive strategy for trees through nitrification stimulation (Barot et al., 2014). However, the high availability of NH_4^+ under grasses in the open suggests a preferential uptake of NH_4^+ for tree roots growing outside tree canopy. This horizontal soil exploration by tree roots can be viewed as a strategy developed in response to the

high NH_4^+ availability (Maire et al., 2009). Results of Chapter 3 have shown that a high NH_4^+ uptake by tree roots outside tree canopy (35.58% of total N uptake by trees) increased tree biomass. Our results confirm this scenario because when trees have different preference in the open and under tree canopy, the zone of savanna is much larger and coexistence becomes possible if trees prefer NH_4^+ in the open and NO_3^- under their canopy. Besides, simulations testing different values of tree preference for NH_4^+ *versus* NO_3^- under their canopy (β_{T2}) showed that increasing this tree preference for NH_4^+ reduces the establishment of savanna zones but promotes tree-grass mosaic (Appendix 4). These results suggest that plasticity of tree root systems in their preferences for NH_4^+ *versus* NO_3^- should occur depending on the spatial distribution of NH_4^+ and NO_3^- (Britto and Kronzucker, 2013). In both cases (same *versus* different tree preferences), our results show that local interactions between species and their environment can locally induce a spatial heterogeneity leading to niche partitioning and thus promote their coexistence (Amarasekare, 2003; Huston and DeAngelis, 1994). These different impacts of trees and grasses on nitrification create small-scale heterogeneities by increasing the availability of their preferred N form, which induces niche complementarity for N acquisition. In comparison, increasing nitrification rate in the open reduces coexistence and favors the establishment of zones with only trees and savanna woodland. Indeed, increasing this rate reduces heterogeneity in nitrification which increases niche overlap (Amarasekare, 2003; Chesson, 2000) and increases the competitive ability of trees for N. Taken together, these feedbacks based on N recycling tend to stabilize the open and tree clump patches and to favor tree-grass coexistence at a larger scale. Besides, the preference for NH_4^+ *versus* NO_3^- qualitatively influences the Lamto savanna dynamics, suggesting that this preference can have important consequences at the ecosystem scale (Boudsocq et al., 2012) and quantitatively on plant biomass (Appendix 2).

4.4.3 Tree spatial distribution impacts coexistence

Many modeling studies demonstrated that species coexistence can be facilitated by intraspecific clustered distributions (Hartley and Shorrocks, 2002; Inouye, 1999). Our results confirm that coexistence is easier when trees are clumped than when they are randomly distributed. In a random tree distribution, grass and tree roots growing outside tree canopy easily overlap in the open. This increases competitive interactions between trees and grasses for N acquisition in the open through lateral N exchanges following the horizontal soil exploration by tree roots. The strong competition between trees and grasses in the open prevents the establishment of tree-grass mosaic and savanna zones whereas it facilitates invasions by grasses or by trees depending on their preferences for NH_4^+ *versus* NO_3^-. By contrast, tree clumping limits the proportion of tree roots in the open as they are surrounded by more conspecifics (tree roots tend to be more under the canopy of neighbouring trees). This decreases transfers of N between the open and the tree clump patch through horizontal fluxes and highlights the impact of spatialization: intraspecific aggregation tends to foster intraspecific competition over interspecific competition. Some studies found that intraspecific aggregation is influential for species coexistence as it impacts the performance of weaker competitors (Monzeglio and Stoll, 2005; Stoll and Prati, 2001). Taken together, tree spatial patterns influence the outcomes of competition by impacting the strength of intra relative to interspecific competition (Stoll and Prati, 2001). Besides, in some savannas (Couteron and Kokou, 1997; Skarpe, 1991) and particularly in the Lamto savanna (Barot et al., 1999; Gignoux et al., 2006), trees often show an aggregated spatial distribution. They form clumps

leaving an important proportion of the surface covered by grasses. Tree clumps are maintained by fires: reduced grass biomass under tree shading decreases fire intensity and hence increases tree sapling survival (Gignoux et al., 2006; Hochberg et al., 1994). This mechanism somehow increases the likelihood of tree-grass coexistence by impeding fires (promoted by grass biomass) to kill all tree saplings. Our results suggest that the fact that trees are clumped may favor tree-grass coexistence and savanna maintenance through an original mechanism: a decrease in the competition for mineral N.

4.4.4 The impact of horizontal soil exploration on coexistence

Horizontal soil exploration contributes to nutrient enrichment under tree canopy but little is known about their possible effects on coexistence. Our results show that regardless tree distribution, savanna and tree-grass mosaic zones are reduced by the increase of the surface explored by tree roots. Indeed, horizontal soil exploration by tree roots leads to spatial transfers of N between the open and the tree clump patches. Increasing the proportion of tree roots in the open increases the competitive ability of trees to take up N and thus the competition between trees and grasses for N in the open. Although, cluster distribution allows a spatial partitioning by increasing intraspecific competition, this proliferation of tree roots in the open increases the strength of interspecific competition relative to intraspecific competition (Stoll and Prati, 2001) and consequently prevent grass establishment. These lateral fluxes between these two patches lowers the spatial heterogeneity by homogenizing the N availability between these two patches (Barot et al., 2015, 2014), which tends to reduce complete coexistence and favors the zones of exclusion by trees and by grasses. Moreover, when the size of the tree root system relative to the canopy increases, the relation between the proportion of tree roots in the open and tree cover is virtually the same (Appendix 3). As a result, increasing the surface explored by tree roots decreases the differences between random and clustered tree distribution.

4.5 Conclusion

Spatial heterogeneity in nitrification leads to NH_4^+ and NO_3^- partitioning, which promotes the coexistence between trees and grasses. Our model shows that mineral N partitioning can play an important role by influencing competitive interactions between savanna trees and grasses and therefore by impacting their dynamics. Although the capacity to inhibit nitrification seems to be common in African perennial grasses (Lata et al., 2004; Rossiter-Rachor et al., 2009; Subbarao et al., 2009), little is known about environmental conditions that have selected for this behavior. Even if this inhibition has not been assessed in other savanna types, mineral N partitioning could be involved in the tree-grass coexistence of all West African humid savannas that have virtually the same grass and tree species. The high performance of African grasses and their effects on N cycling in northern Australian and South American savannas (D'Antonio and Vitousek, 1992; Rossiter-Rachor et al., 2017) seem to be linked to their BNI capacity and tend to show that this capacity is restricted to African perennial grasses. But the frequency of this capacity in other African grasses is not known and needs to be studied at a large geographical scale to assess whether our mechanism applies to other savanna types. Besides, N fixing trees and large herbivores absent from the Lamto savanna are known to be influential in the functioning of other savannas such as East African savannas (Sankaran et al., 2008). These mechanisms provide important N inputs through symbiotic fixation and animal dungs and hence differently impact

N cycling and should be included in new models to assess the robustness of our results.

Clearly, the mechanism we are highlighting with our model is interacting with formerly identified mechanisms based on the impact of disturbances on tree demography (Higgins et al., 2000). Thus, new individual-based models should be built to take into account mechanisms based on both resource competition and demography, e.g., the effects of fire on plant demography (Higgins et al., 2000). Such models should allow assessing the relative influence of both types of coexistence and analyze how they react. Our new mechanism of coexistence based on the partition of the mineral N resource, should interact with these disturbance-based mechanisms to explain tree-grass coexistence. Although fire is determinant for the maintenance of the Lamto savanna by reducing woody cover (Gignoux et al., 2006), mineral N partitioning likely acts in interaction with fire as the intensity of fire partly depends on the biomass of flammable grasses and this grass biomass depends on their N acquisition, essential factor of their growth.

Moreover, mineral N partitioning could be affected by the current increasing woody cover observed in savannas worldwide (Blaser et al., 2014). Because of the capacity of trees to stimulate nitrification (Srikanthasamy et al., 2018), increasing woody cover can induce large N losses due to leaching switching Lamto savanna from more N conservative to less conservative system (Chapter 4). But the low intensity of fires resulting from woody encroachment and low grass biomass should decrease N losses through biomass burning. This suggests that there are complex feedbacks between savanna N budgets and tree-grass dynamics, at least in West African humid savannas.

Bibliography

Abbadie, L. (2006). Nitrogen inputs to and outputs from the soil-plant system. In *Lamto: structure, functioning, and dynamics of a savanna ecosystem*, pages 255–275. New York: Springer.

Abbadie, L., Gignoux, J., Le Roux, X., and Lepage, M. (2006). *Lamto: structure, functioning, and dynamics of a savanna ecosystem*. New York: Springer.

Adler, P. B., Fajardo, A., Kleinhesselink, A. R., and Kraft, N. J. (2013). Trait-based tests of coexistence mechanisms. *Ecology letters*, 16(10):1294–1306.

Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: a synthesis. *Ecology letters*, 6(12):1109–1122.

Armstrong, R. A. and McGehee, R. (1980). Competitive exclusion. *The American Naturalist*, 115(2):151–170.

Ashton, I. W., Miller, A. E., Bowman, W. D., and Suding, K. N. (2010). Niche complementarity due to plasticity in resource use: plant partitioning of chemical n forms. *Ecology*, 91(11):3252–3260.

Barot, S., Bornhofen, S., Boudsocq, S., Raynaud, X., and Loeuille, N. (2015). Evolution of nutrient acquisition: when space matters. *Functional ecology*, 30(2):283–294.

Barot, S., Bornhofen, S., Loeuille, N., Perveen, N., Shahzad, T., and Fontaine, S. (2014). Nutrient enrichment and local competition influence the evolution of plant mineralization strategy: a modelling approach. *Journal of Ecology*, 102(2):357–366.

Barot, S. and Gignoux, J. (2004). Mechanisms promoting plant coexistence: can all the proposed processes be reconciled? *Oikos*, 106(1):185–192.

Barot, S., Gignoux, J., and Menaut, J.-C. (1999). Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. *Ecology*, 80(6):1987–2005.

Belsky, A. J. (1994). Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology*, 75(4):922–932.

Blaser, W. J., Shanungu, G. K., Edwards, P. J., and Olde Venterink, H. (2014). Woody encroachment reduces nutrient limitation and promotes soil carbon sequestration. *Ecology and evolution*, 4(8):1423–1438.

Bonanomi, G., Rietkerk, M., Dekker, S. C., and Mazzoleni, S. (2008). Islands of fertility induce co-occurring negative and positive plant-soil feedbacks promoting coexistence. *Plant Ecology*, 197(2):207–218.

Boudsocq, S., Lata, J.-C., Mathieu, J., Abbadie, L., and Barot, S. (2009). Modelling approach to analyse the effects of nitrification inhibition on primary production. *Functional Ecology*, 23(1):220–230.

Boudsocq, S., Niboyet, A., Lata, J. C., Raynaud, X., Loeuille, N., Mathieu, J., Blouin, M., Abbadie, L., and Barot, S. (2012). Plant preference for ammonium versus nitrate: a neglected determinant of ecosystem functioning? *The American Naturalist*, 180(1):60–69.

Brandt, A. J., de Kroon, H., Reynolds, H. L., and Burns, J. H. (2013). Soil heterogeneity generated by plant–soil feedbacks has implications for species recruitment and coexistence. *Journal of Ecology*, 101(2):277–286.

Britto, D. T. and Kronzucker, H. J. (2013). Ecological significance and complexity of N-source preference in plants. *Annals of botany*, 112(6):957–963.

Chesson, P. (2000). General theory of competitive coexistence in spatially-varying environments. *Theoretical population biology*, 58(3):211–237.

Chesson, P. and Ellner, S. (1989). Invasibility and stochastic boundedness in monotonic competition models. *Journal of Mathematical Biology*, 27(2):117–138.

Couteron, P. and Kokou, K. (1997). Woody vegetation spatial patterns in a semi-arid savanna of burkina faso, west africa. *Plant Ecology*, 132(2):211–227.

D'Antonio, C. M. and Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual review of ecology and systematics*, 23(1):63–87.

Dieckmann, U., Law, R., and Metz, J. A. J. (2000). *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge University Press.

Donzelli, D., De Michele, C., and Scholes, R. (2013). Competition between trees and grasses for both soil water and mineral nitrogen in dry savannas. *Journal of theoretical biology*, 332:181–190.

Gignoux, J., Barot, S., Menaut, J.-C., and Vuattoux, R. (2006). Structure, long-term dynamics, and demography of the tree community. In *Lamto: structure, functioning, and dynamics of a savanna ecosystem*, pages 335–364. Springer.

Gignoux, J., Lahoreau, G., Julliard, R., and Barot, S. (2009). Establishment and early persistence of tree seedlings in an annually burned savanna. *Journal of Ecology*, 97(3):484–495.

Hardin, G. (1960). The competitive exclusion principle. *science*, 131(3409):1292–1297.

Hartley, S. and Shorrocks, B. (2002). A general framework for the aggregation model of coexistence. *Journal of Animal Ecology*, 71(4):651–662.

Higgins, S. I., Bond, W. J., and Trollope, W. S. (2000). Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology*, 88(2):213–229.

Hochberg, M. E., Menaut, J. C., and Gignoux, J. (1994). The influences of tree biology and fire in the spatial structure of the west african savannah. *Journal of Ecology*, 82:217–226.

Huston, M. A. and DeAngelis, D. L. (1994). Competition and coexistence: the effects of resource transport and supply rates. *The American Naturalist*, 144(6):954–977.

Inouye, B. D. (1999). Integrating nested spatial scales: implications for the coexistence of competitors on a patchy resource. *Journal of Animal Ecology*, 68(1):150–162.

Jeltsch, F., Weber, G. E., and Grimm, V. (2000). Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology*, 150(1-2):161–171.

Knops, J., Bradley, K., and Wedin, D. (2002). Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecology Letters*, 5(3):454–466.

Konaré, S., Boudsocq, S., Gignoux, J., Lata, J.-C., Raynaud, X., and Barot, S. (2019). Effects of mineral nitrogen partitioning on tree–grass coexistence in west african savannas. *Ecosystems*, 22(7):1676–1690.

Lata, J.-C., Degrange, V., Raynaud, X., Maron, P.-A., Lensi, R., and Abbadie, L. (2004). Grass populations control nitrification in savanna soils. *Functional Ecology*, 18(4):605–611.

Maire, V., Gross, N., da Silveira Pontes, L., Picon-Cochard, C., and Soussana, J.-F. (2009). Trade-off between root nitrogen acquisition and shoot nitrogen utilization across 13 co-occurring pasture grass species. *Functional Ecology*, 23(4):668–679.

Matérn, B. (1960). Spatial variation-stochastic models and their application to some problems in forest surveys and other sampling investigations. *Meddelanden fran statens skogsforskningsintitut*, 49(5):1–144.

Matérn, B. (1986). *Spatial variation, Lecture Notes in Statistics*. New York:Springer.

McKane, R. B., Johnson, L. C., Shaver, G. R., Nadelhoffer, K. J., Rastetter, E. B., Fry, B., Giblin, A. E., Kielland, K., Kwiatkowski, B. L., Laundre, J. A., et al. (2002). Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, 415(6867):68–71.

Menaut, J., Gignoux, J., Prado, C., and Clobert, J. (1990). Tree community dynamics in a humid savanna of the cote-d'ivoire: modelling the effects of fire and competition with grass and neighbours. *Journal of Biogeography*, pages 471–481.

Miller, A. E. and Bowman, W. D. (2002). Variation in nitrogen-15 natural abundance and nitrogen uptake traits among co-occurring alpine species: do species partition by nitrogen form? *Oecologia*, 130(4):609–616.

Monzeglio, U. and Stoll, P. (2005). Spatial patterns and species performances in experimental plant communities. *Oecologia*, 145(4):619–628.

Mordelet, P., Abbadie, L., and Menaut, J.-C. (1993). Effects of tree clumps on soil characteristics in a humid savanna of west africa (lamto, côte d'ivoire). *Plant and Soil*, 153(1):103–111.

Pacala, S. W. (1997). Dynamics of plant communities. In *M. J. Crawley, editor.Plant ecology*, pages 532–535. Blackwell Scientific, Oxford UK.

R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rossiter-Rachor, N., Setterfield, S., Douglas, M., Hutley, L. B., Cook, G., and Schmidt, S. (2009). Invasive *Andropogon gayanus* (gamba grass) is an ecosystem transformer of nitrogen relations in australian savanna. *Ecological Applications*, 19(6):1546–1560.

Rossiter-Rachor, N. A., Setterfield, S. A., Hutley, L., McMaster, D., Schmidt, S., and Douglas, M. M. (2017). Invasive *Andropogon gayanus* (gamba grass) alters decomposition and nitrogen fluxes in an australian tropical savanna. *Scientific reports*, 7:11705.

Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., Gignoux, J., Higgins, S. I., Le Roux, X., Ludwig, F., et al. (2005). Determinants of woody cover in african savannas. *Nature*, 438(7069):846–849.

Sankaran, M., Ratnam, J., and Hanan, N. (2008). Woody cover in african savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography*, 17(2):236–245.

Sankaran, M., Ratnam, J., and Hanan, N. P. (2004). Tree–grass coexistence in savannas revisited–insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology letters*, 7(6):480–490.

Schenk, H. J. and Jackson, R. B. (2002). Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, 90(3):480–494.

Skarpe, C. (1991). Spatial patterns and dynamics of woody vegetation in an arid savanna. *Journal of Vegetation Science*, 2(4):565–572.

Soetaert, K. E., Petzoldt, T., and Setzer, R. W. (2010). Solving differential equations in R: package desolve. *Journal of Statistical Software*, 33.

Srikanthasamy, T., Leloup, J., N'Dri, A. B., Barot, S., Gervaix, J., Koné, A. W., Koffi, K. F., Le Roux, X., Raynaud, X., and Lata, J.-C. (2018). Contrasting effects of grasses and trees on microbial n-cycling in an african humid savanna. *Soil Biology and Biochemistry*, 117:153–163.

Staver, A. C., Archibald, S., and Levin, S. (2011). Tree cover in sub-saharan africa: rainfall and fire constrain forest and savanna as alternative stable states. *Ecology*, 92(5):1063–1072.

Stoll, P. and Prati, D. (2001). Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology*, 82(2):319–327.

Subbarao, G., Nakahara, K., Hurtado, M. d. P., Ono, H., Moreta, D., Salcedo, A. F., Yoshihashi, A., Ishikawa, T., Ishitani, M., Ohnishi-Kameyama, M., et al. (2009). Evidence for biological nitrification inhibition in brachiaria pastures. *Proceedings of the National Academy of Sciences*, 106(41):17302–17307.

Tilman, D. and Kareiva, P. (1997). Spatial ecology princeton university press. *Princeton, NJ, US*.

Van Der Heijden, M. G., Bardgett, R. D., and Van Straalen, N. M. (2008). The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology letters*, 11(3):296–310.

Van Langevelde, F., Van De Vijver, C. A., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A. K., Hearne, J. W., Stroosnijder, L., Bond, W. J., et al. (2003). Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, 84(2):337–350.

Walker, B. H. and Noy-Meir, I. (1982). Aspects of the stability and resilience of savanna ecosystems. In *Ecology of tropical savannas*, pages 556–590. Springer.

Walter, H. (1971). *Ecology of tropical and subtropical vegetation.* Edinburgh: Oliver Boyd.

Wang, L. and Macko, S. A. (2011). Constrained preferences in nitrogen uptake across plant species and environments. *Plant, cell & environment*, 34(3):525–534.

4.6 Appendix

4.6.1 Appendix: Model parameters

Table 4.1 – Parameters of the two-patch model

Parameters	Definition	Unit	Values
Grass parameters			
d_G	Turnover rate of grass	yr^{-1}	0.6
l_G	Rate of N losses from grass compartment	yr^{-1}	0.4
u_G	N uptake rate	ha kg^{-1} N yr^{-1}	0.14186
β_G	Preference for NH_4^+	No unit	-
Tree parameters			
d_r	Turnover rate of tree roots	yr^{-1}	0.08
d_l	Turnover rate of tree leaves	yr^{-1}	0.073
l_T	Rate of N losses from tree compartment	yr^{-1}	0.11
u_r	N uptake rate by tree roots	ha kg^{-1} N yr^{-1}	0.08
β_{T1}	Preference for NH_4^+ in the open patch	No unit	-
β_{T2}	Preference for NH_4^+ in the tree clump patch	No unit	0.25
α	Fraction of roots in the open	No unit	-
γ	Tree clumps proportion	No unit	-
r	Root shoot ratio	No unit	0.5
Soil parameters			
i_O	N organic input to the savanna	kg N ha^{-1} yr^{-1}	16.5
m	N mineralization rate	yr^{-1}	0.025
l_O	N loss from the N organic compartment in surface soil layer	yr^{-1}	0.0027
i_{NA}	NH_4^+ inputs to the savanna	kg N ha^{-1} yr^{-1}	23
n_1	Nitrification rate in the open patch	yr^{-1}	0.09
n_2	Nitrification rate in the tree clump patch	yr^{-1}	4.16
l_{NA}	NH_4^+ loss rate	yr^{-1}	0.0133
i_{NN}	NO_3^- inputs to the savanna	kg N ha^{-1} yr^{-1}	4.1
l_{NN}	NO_3^- loss rate	yr^{-1}	2.7

4.6.2 Appendix 2: Influence of tree distributions on plant biomass

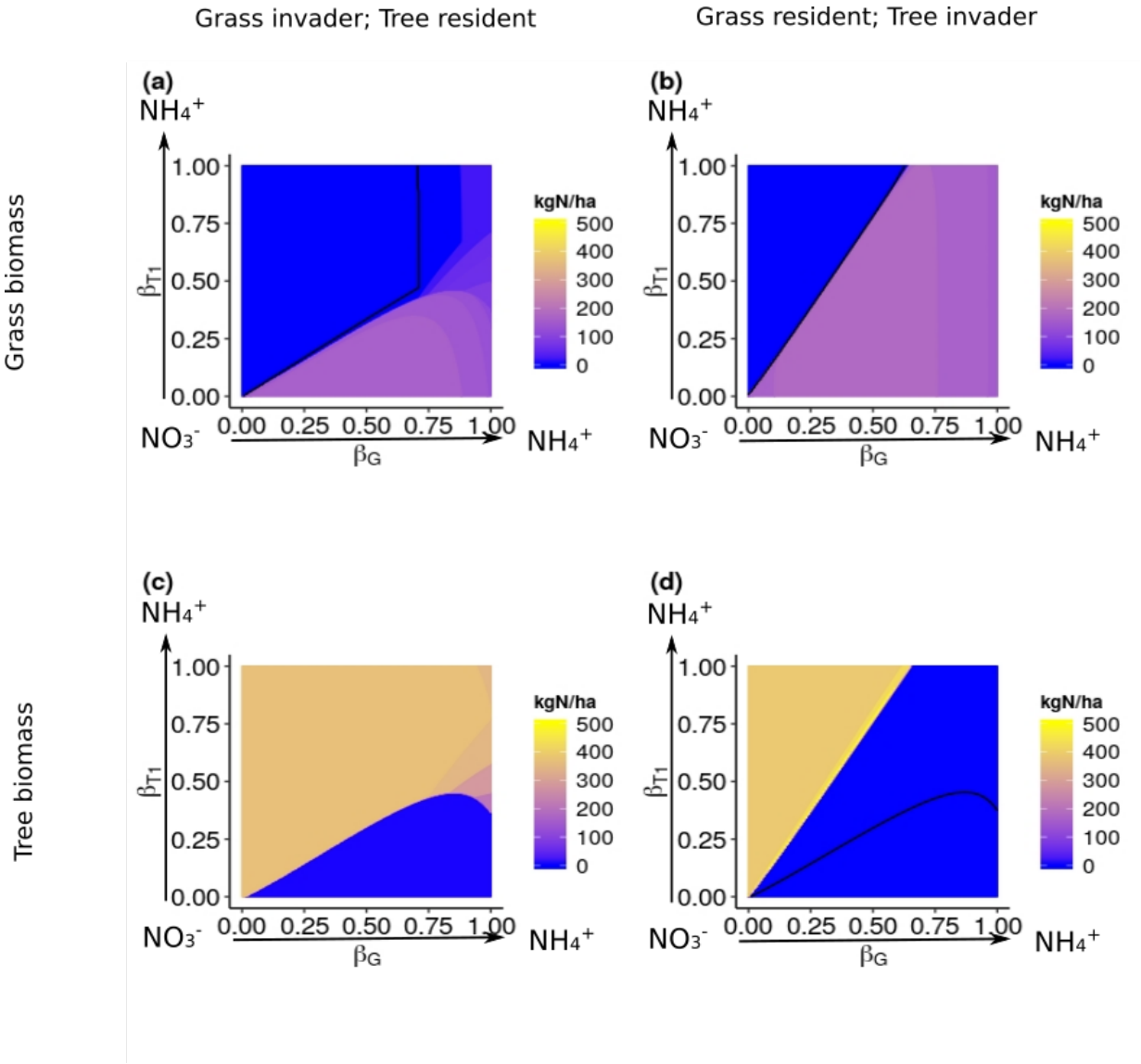

Figure 4.6 – Grass (patterns a and b) and tree (patterns c and d) biomass as a function of grass (β_G) and tree (β_{T1}) preference for NH_4^+ in the open according to random tree distributions at the savanna scale.

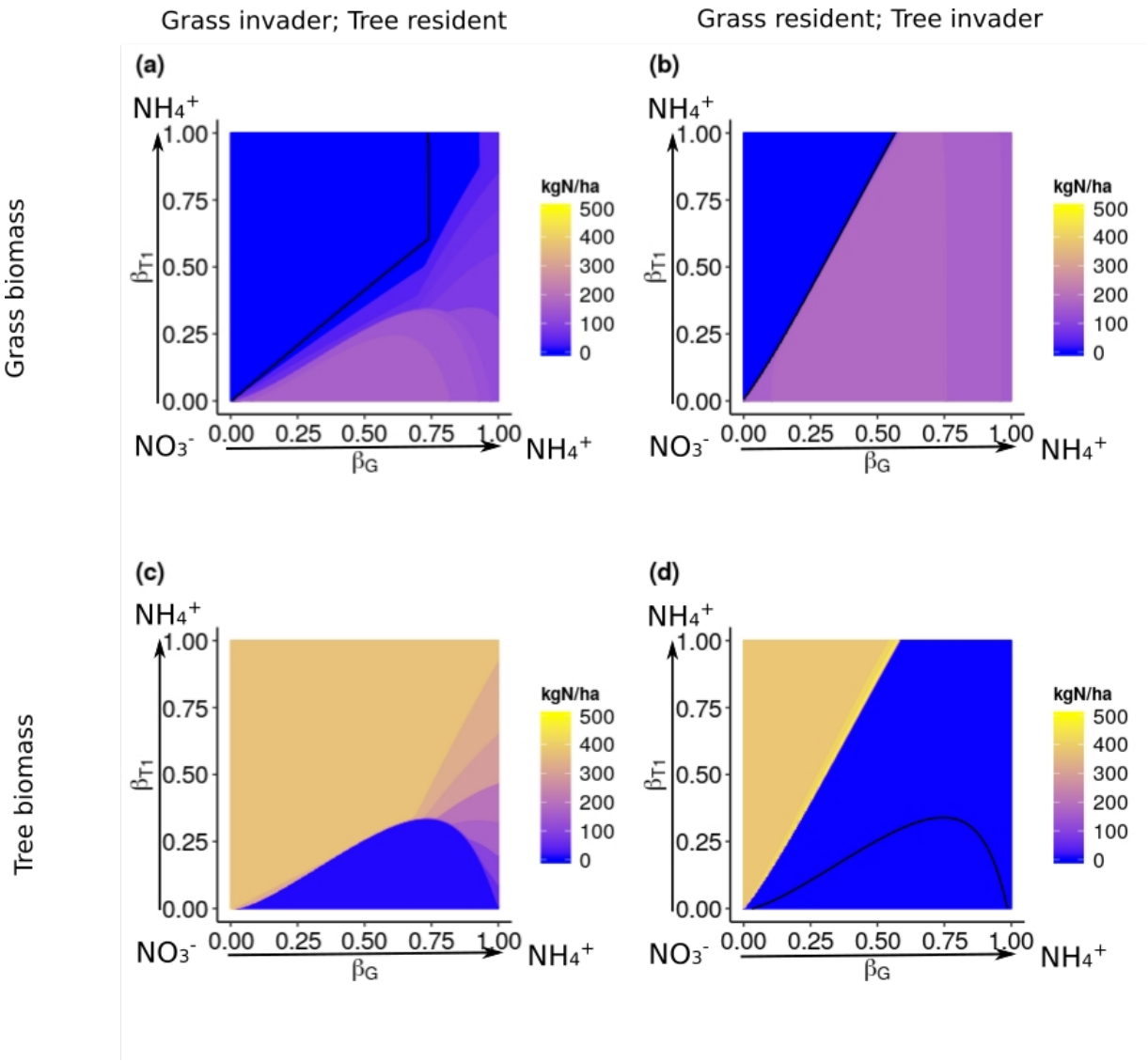

Figure 4.7 – Grass (patterns a and b) and tree (patterns c and d) as a function of grass (β_G) and tree (β_{T1}) preference for NH_4^+ in the open patch according to clustered tree distributions at the savanna scale.

4.6.3 Appendix 3: Effects of tree spatial distribution on tree root exploration

We performed simulations for different tree spatial distribution to determine the relation between tree cover (γ) and the proportion of tree roots in the open (α) and study spatial patterns effects on tree-grass coexistence (Fig. 4.8). This relation has been tested for random, cluster and regular tree distributions. We considered trees with 2 m crown radius and 12 m root radius for each distribution in 1ha plot.

α and γ are negatively correlated regardless tree distributions (p-value < 0.0001 and R^2=0.998 for random; p-value < 0.0001 and R^2=0.999 for cluster; p-value < 0.0001 and R^2=0.999 for regular tree pattern). α significantly decreases while γ increases regardless tree distributions. Clustered tree distributions have low values of α compared to regular and random tree distributions. This leads to these linear equations: α = -0.984γ +0.971, α= -0.977γ +0.973 and α = -0.932γ +0.924 respectively for random, regular and clustered tree distributions. There is no signifant difference between cluster and random or regular patterns.

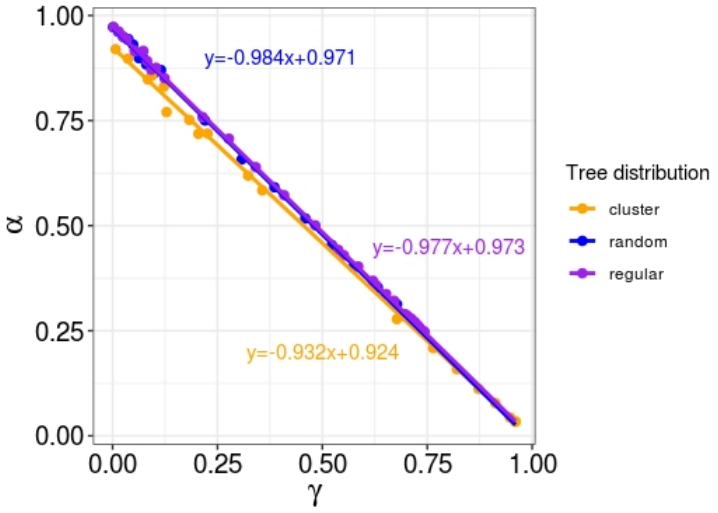

Figure 4.8 – (a) Proportion of tree roots in the open as a function of tree cover according to cluster, random and regular tree distribution, (b) Tree biomass as a function of tree cover for a root radius equals to 12 m.

4.6.4 Appendix 4: Effects of tree preference under their canopy depending on tree distributions

We did simulations for different combinations of grass and tree preference for NH_4^+ in the open. Here, we tested different tree preference for NH_4^+ under tree canopy by gradually increasing tree preference for NH_4^+ under their canopy ($\beta_{T2} = 0.35$; $\beta_{T2} = 0.5$) knowing that the value by default used in the main text is $\beta_{T2} = 0.25$ (Fig. 4.9). Increasing tree preference for NH_4^+ under tree canopy leads to an increase of a zone of coexistence between trees and grasses in the open but strongly reduces total coexistence in both cases random and cluster tree patterns. As described above, when $\beta_{T2} = 0.25$ total coexistence occurs if $\beta_G > 0.7$ and $0.4 < \beta_{T1} < 0.73$ for random tree pattern. When tree preference under tree canopy for NH_4^+ increases ($\beta_{T2} = 0.35$), trees tend to exclude grasses, which reduces the zone of total coexistence. This also increases conditions of coexistence between trees and grasses in the open. When tree preference under tree canopy for NH_4^+ increases further ($\beta_{T2} = 0.5$), trees completely exclude grasses under their canopy, which deletes the zone of total coexistence and increases conditions of coexistence between trees and grasses in the open. The overall pattern is similar for cluster pattern but the region of coexistence between trees and grasses in the open is larger than in the random tree pattern case.

Increasing tree preference for NH_4^+ under tree canopy tends to reduce total coexistence and the presence of grasses under tree canopy, which increases possibilities of coexistence between trees and grasses in the open.

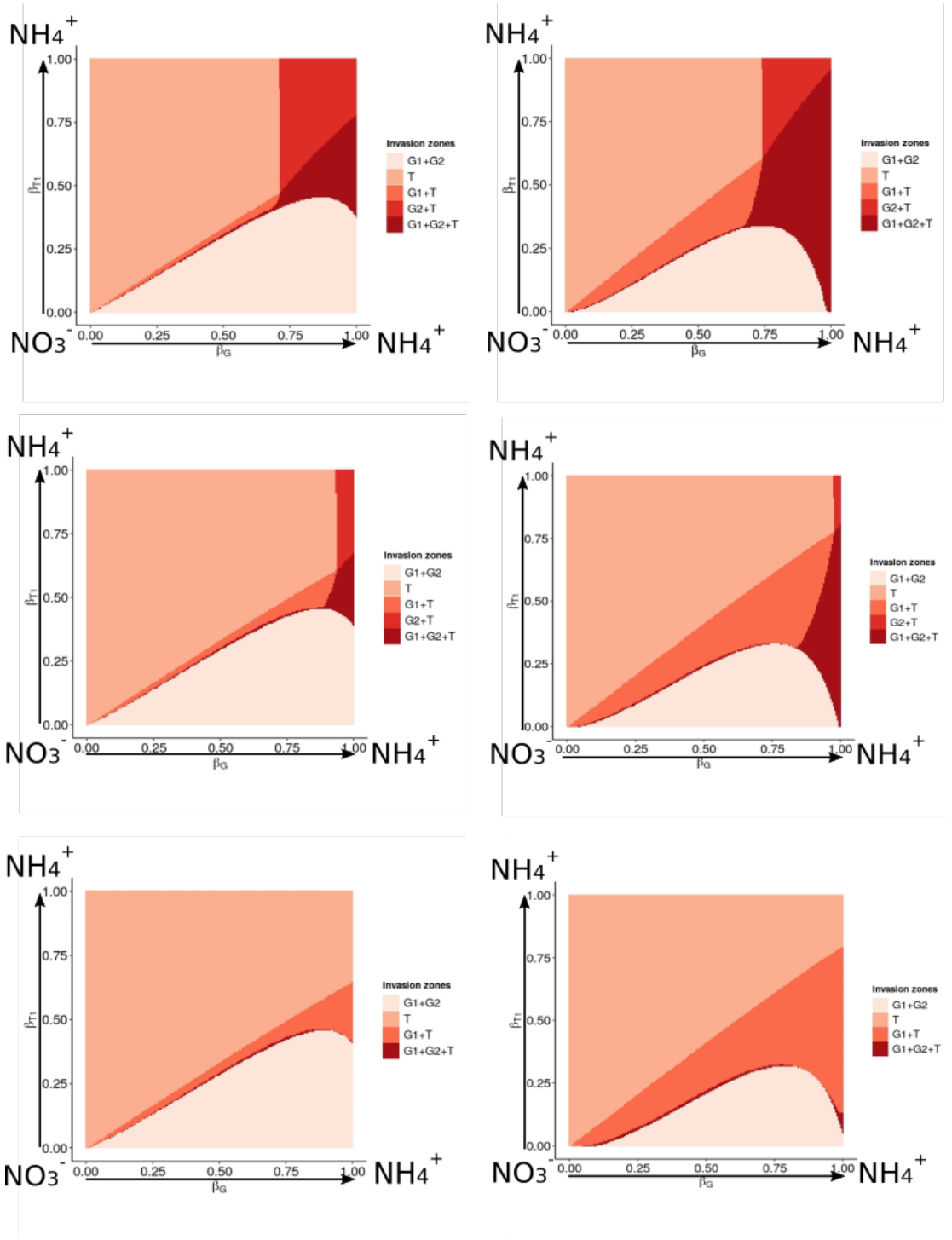

Figure 4.9 – Mutual invasibility plots between trees and grasses according to random (left) and clustered (right) tree distributions at the savanna scale. The preference of trees under tree canopy increases from the top to the bottom and correspond respectively to β_{T2} =0.25; β_{T2} = 0.35 and β_{T2} =0.5. Invasion zones: G1+G2: grasses invade and exclude trees, T: Trees invade and exclude grasses, G1+T: tree-grass mosaic (coexistence between trees and grasses in the open), G2+T:savanna woodland (coexistence between trees and grasses under their canopy), G1+G2+T: savanna (coexistence between trees and grasses under their canopy and in the open).

5 General discussion

5.1 Summary of the results

The coexistence between trees and grasses is a key feature of savannas. In the Lamto savanna, the impact of plants on nitrification through nitrification inhibition by grasses (Lata et al., 2004) and nitrification stimulation by trees (Srikanthasamy et al., 2018) suggest that the two plant types have different preferences for NH_4^+ and NO_3^-. **I show that this control of nitrification by plants can be involved in tree-grass coexistence through niche partitioning, which reduces interspecific competition.**

First, I have built a mean-field model of competitive interactions between trees and grasses, in which the whole NH_4^+ and NO_3^- compartments are fully available to both. I compared two formalisms for nitrification: a first one where nitrification only depends on NH_4^+ availability and a second one where nitrification also depends on plant biomass. A comparison between these two formalisms showed that biomass-dependent nitrification increased the domain of coexistence. At low nitrification rate, coexistence occurs when grasses prefer NO_3^- and trees prefer NH_4^+, which was not expected in the case of the Lamto savanna. But when the nitrification rate increases and reaches an intermediate value, coexistence becomes possible when grasses prefer NH_4^+ and trees prefer NO_3^-. **I have shown with this first model that mineral N partitioning in the forms of NH_4^+ and NO_3^- may promote coexistence between trees and grasses when they have contrasted preferences for NH_4^+ *versus* NO_3^-.**

Then, I have built a two-patch model in which NH_4^+ and NO_3^- are divided into two pools, one corresponding to tree clumps and, the other to savanna outside tree clumps, that are not fully accessible to all grasses and trees. This second model highlighted that the spatial heterogeneity in nitrification fluxes created by nitrification inhibition by grasses and nitrification stimulation by trees strongly impacts N fluxes. By extending their roots outside their canopy, trees increase their nutrient acquisition by taking up N in the open. **The horizontal fluxes between the open and tree clump patches create source-sink dynamics in the Lamto savanna.** Grasses appear as a N source for trees: they help to better conserve N through the inhibition of nitrification, which decreases N losses at the ecosystem level through leaching and denitrification. **This study also suggests that the horizontal soil exploration by trees in the open contributes to nutrient enrichment under tree canopy because nutrients absorbed by trees are eventually incorporated to the soil of tree clumps through the shedding of leaves and the decay of roots.** In contrast to the fact that the extension of tree roots in the open increases N uptake, **increasing tree cover tends to decrease tree biomass**, due to the increase of total N losses following the stimulation of nitrification by trees.

Besides effects on N fluxes, the heterogeneity in nitrification spatially separates the N resource that is already under two forms NH_4^+ and NO_3^-, thus promoting tree-grass coexistence. **I have shown that a different preference of trees in the open and under tree canopy increases the domain of coexistence, specifically when grasses prefer NH_4^+ and trees prefer NO_3^- under their canopy and NH_4^+ in the open.** This also confirms that mineral N partitioning can be considered as a stabilizing mechanism favoring coexistence even if NH_4^+ and NO_3^- are linked by nitrification, i.e., NO_3^- availability depends on NH_4^+ availability.

All in all, my thesis thus proposes a new mechanism based on N partition contributing to the coexistence between trees and grasses and therefore to the maintenance of savannas.

5.2 Nitrification control has a positive feedback in the functioning of the Lamto savanna

Dominant grass species of the Lamto savanna can inhibit nitrification (Lata et al., 2004, 2000; Srikanthasamy et al., 2018). As volatilization is not possible due to the acidic soil condition and as it is also less prone to leaching, impeding nitrification allows a greater conservation of N because only NO_3^- can be lost by denitrification and leaching. In a N-limited ecosystem such as the Lamto savanna, the capacity of grasses to inhibit nitrification increases the efficiency of N recycling especially when they have an affinity for NH_4^+ (Boudsocq et al., 2012), which in turn increases grass biomass.

Nitrification is higher under trees than under grasses. Experimental studies comparing nitrification potential between bare soil and soil under tree canopy showed that nitrification is higher under trees than under bare soil (Srikanthasamy et al., 2018). Two main hypotheses explaining this stimulation of nitrification can be proposed: (1) Trees stimulate nitrification by the release of specific molecules from their root system stimulating nitrifying communities. (2) The higher concentration of soil organic matter under tree clumps increases the activity of nitrifying communities (Srikanthasamy et al., 2018). Indeed, Mordelet et al. (1993) and Srikanthasamy et al. (2018) showed that the rate of N mineralization under tree clumps is higher than in the surrounding open area. The higher soil moisture and concentration of soil organic matter under tree clumps favors NH_4^+ availability via mineralization, and then NO_3^- availability by nitrification. In addition, tree clumps are often spatially associated to termite mounds (Mordelet and Le Roux, 2006). Most termite species prefer to forage on tree leaves rather than on grass leaves, which can explain the high activity of soil fauna under tree clumps and thus contributes to the macro-porosity under tree clumps (Mordelet and Le Roux, 2006). All these conditions create optimal conditions that can stimulate the activity of microbial communities. This is also in accordance with Abbadie (2006) that found that the nitrification rate under termite mounds is higher than far from termite mounds. So far, it remains difficult to fully determine what mechanism explains the stimulation of nitrification under tree canopy, which seems common to all the dominant species. Additional studies are needed to determine the mechanism promoting this stimulation.

Nitrification inhibition by grasses and nitrification stimulation by trees suggest that plants have developed different resource-use strategies (Grassein et al., 2015). BNI capacity can be viewed as an adaptation of some savanna grasses to conserve N and hence to use it efficiently, which is particularly relevant in natural N-limited ecosystems (Lata et al., 2004; Subbarao et al., 2006). This can contribute to the high primary productivity of the Lamto savanna. Similarly, the strategy of stimulation by trees appears as an acquisitive strategy (Barot et al., 2015). Even if this stimulation can increase N losses as NO_3^- is more prone to leaching, it could be a response of trees to acquire N as grasses would be more efficient to use NH_4^+ and trees have a deeper root system (Mordelet et al., 1997) that could be beneficial to take up N at greater depth. **Interestingly, plant influence on nitrification causes**

a positive feedback that allow plants to partition N resource and increase their own productivity. Such an effect is not only determinant for ecosystem properties but can also be influential in the dynamics and the diversity in plant communities (Bever et al., 1997).

5.3 Different plant preference for NH_4^+ and NO_3^- can facilitate coexistence

Field studies found some evidence of a preferential uptake of plants for different N forms such as organic N and mineral N, NH_4^+ and NO_3^- (Ashton et al., 2010). **The ability of grasses to inhibit nitrification logically suggests a preference of grasses for the expected more abundant form of mineral N in this case,** NH_4^+**.** Although this information is not yet completely confirmed by experimental studies in the Lamto savanna, some studies supported the preference of grasses for NH_4^+. Rossiter-Rachor et al. (2017) clearly showed that *Andropogon gayanus* an invasive African grass species in Australian savannas is able to inhibit nitrification and has a preference for NH_4^+. Wang and Macko (2011) studies on grass preferences of Southern African savannas according a rainfall gradient also showed that grasses in humid areas tend to preferentially use NH_4^+ relative to NO_3^-. Some ongoing experiments seem to confirm a preference of grasses for NH_4^+ (Barot, personal communication). As existing data did not allow to determine plant preference for NH_4^+ *versus* NO_3^- with certainty, I studied coexistence by scanning different combinations of plant preference from cases in which plants only take up NH_4^+ to cases in which plants only take up NO_3^-. **I found that a differential uptake of trees in the open and under tree canopy influences conditions of coexistence.** Their stimulation of nitrification under their canopy suggests a certain affinity for NO_3^-. But they also would benefit from the high availability of NH_4^+ in the open, only if they prefer NH_4^+ in the open. Houlton et al. (2007) found through their experiment in tropical forests that plants can show a certain plasticity in their preference for NH_4^+ depending on the more accessible N form in dry and wet sites. Although some studies support the idea of the existence of a trade-off in the uptake of NH_4^+ and NO_3^- (Maire et al., 2009), plants expressing an exploitative strategy tend to use both NH_4^+ and NO_3^- (Grassein et al., 2015).

Different plant preference for different chemical N forms can play a major role in the coexistence of plant species. Some studies showed that N partitioning into organic and mineral N forms (NH_4^+ and NO_3^-) can facilitate coexistence (McKane et al., 2002; Miller and Bowman, 2002). **My results show that tree-grass coexistence occurs when trees and grasses have different preferences for** NH_4^+ ***versus*** NO_3^-**.** Boudsocq et al. (2012) demonstrated by modelling that plants can coexist if their preferences for NH_4^+ *versus* NO_3^- are sufficiently different. This coexistence is not expected for a strict preference for NH_4^+ *versus* NO_3^-. Tavernier (2003) found that under controlled conditions, an optimal growth of Lamto savanna grasses was obtained with a mixed uptake of 75% NH_4^+ and 25% NO_3^-. This is in accordance with some studies indicating that a mixture of NH_4^+ and NO_3^- is often more beneficial for plant growth (Konnerup and Brix, 2010) because both mineral N forms tend to be available to some extent.

In my model, plant preference is considered as a fixed value although it is a multifactorial parameter that can involve many environmental and physiological conditions (Britto and Kronzucker,

2013), which suggests that plant preference for NH_4^+ *versus* NO_3^- is plastic. It could be interesting for further models to include this plasticity for example as a function of the NH_4^+ and NO_3^- availabilities or the seasonality and the soil water content.

Most plants have the capacity to form symbiotic mycorrhizal associations (Brundrett, 2002). Plants strongly benefit from this association because it enhances nutrient acquisition (Lambers et al., 2006). This could influence NH_4^+ and NO_3^- uptake by plants and tree-grass competition for N. The current model includes horizontal soil root proliferation in the open but does not consider mycorhizae. This is due to the lack of information about fungi and mycorrhizae in the Lamto savanna, and should be fully studied through new empirical studies.

5.4 Mineral N partitioning as mechanism of coexistence in the Lamto savanna

Mechanisms of coexistence through niche partitioning appear as a stabilizing mechanism (Barot and Gignoux, 2004). According to Chesson theories, species coexistence can be due to both different niches that stabilize coexistence and the decrease of fitness differences that slows down exclusion (Chesson, 2000). Tree and grass differences arising from nitrification control by plants lead to stabilizing niche differences promoting intraspecific competition relative to interspecific competition (Adler et al., 2013; Barot and Gignoux, 2004). The results of Chapter 4 show that spatial heterogeneity in nitrification can promote tree-grass coexistence. **Interactions between plants and microbial communities locally create NH_4^+ rich patches in the open and NO_3^- rich patches under tree clumps, which causes a spatial heterogeneity in the availability of NH_4^+ and NO_3^-. Tree-grass coexistence occurs in our case when grasses prefer NH_4^+ and trees prefer NO_3^-. These feedbacks based on nitrification control spatially separate the mineral N resource by increasing the availability of their preferred N form, which can reduce the competition between trees and grasses for N acquisition and can promote their coexistence (Amarasekare, 2003). Consequently, this spatial heterogeneity induces a niche partitioning through different preferences for NH_4^+ and NO_3^-.**

The notion of niche differentiation to explain outcomes of competition has long been studied (Chase and Leibold, 2003). In the Lamto savanna, the different effects of plants on nitrification may lower niche overlap and therefore interspecific competition (Adler et al., 2013). These different plant preference for NH_4^+ and NO_3^- create some niche complementarity that can facilitate coexistence (Silvertown, 2004). This result is supported by studies predicting that species that differ in their resource use are more likely to coexist (Holt, 2008; Pacala and Tilman, 1994). Although the capacity to inhibit nitrification is likely to have evolved to overcome N limitation, trees and grasses have developed two complementary strategies (inhibition and stimulation) that allow them to coexist. In most cases, niche differentiation is induced by a certain plasticity in their resource use (Aerts et al., 1991; Casper and Jackson, 1997). Plasticity in resource use can be involved in niche complementarity as weaker competitors respond to the presence of the superior competitor by taking up the less-used resource (Hector et al., 1999).

Moreover, classical resource competition theory suggests that when species compete for the same resource, the species able to reduce resource availability the most outcompetes all others (Tilman, 1982). If we consider NH_4^+ and NO_3^- as two distinct resources, our results are consistent with Tilman's R* theories (Tilman, 1982, 1985) suggesting that the coexistence of two species is not possible on fewer than two resources. Mineral N partitioning enables the coexistence of two types of plants on two distinct resources that firstly represent a single N resource and then are linked by nitrification: the NO3- availability depends on the NH_4^+ availability. The nitrification rate is strongly influential in this mechanism because reducing or increasing this rate diminishes the impact of spatial heterogeneity. N is only present in a unique form and could lead to exclusion (results of Chapter 3).

In the Lamto savanna, it is known that fire is determinant in the tree-grass dynamics (Gignoux et al., 2006). An experiment of fire exclusion resulted in an increase of woody cover (Abbadie et al., 2006) and ultimately the exclusion of grasses. My study shows that mineral N partitioning is also relevant in the functioning of the Lamto savanna, but clearly this new coexistence mechanism likely acts in interaction with fire. Although fire is important for tree-grass coexistence, the intensity of fire partly depends on the biomass of grasses that in turn depends on their N uptake. Consequently, tree-grass coexistence likely depends on these interactions between fire and mineral N partitioning resulting from feedbacks between these two mechanisms.

5.5 Effects of spatial tree distribution and horizontal soil exploration on tree-grass coexistence

I also show that spatial tree distribution can influence niche partitioning. Most savanna landscapes display clustered tree distributions because tree clumping increases their chances to escape fire and to recruit new individuals (Barot et al., 1999; Hochberg et al., 1994). Intraspecific aggregation can reduce interspecific competition relative to intraspecific competition (Pacala and Levin, 1997; Stoll and Prati, 2001). This can promote coexistence by impeding the better competitor to exclude lower competitors.

The results of Chapters 4 and 5 show the influence of horizontal soil exploration by tree roots outside their canopy projection on N fluxes and also on tree-grass coexistence. The proliferation of tree roots in the open strengthens interspecific competition relative to intraspecific competition (Pacala and Levin, 1997; Stoll and Prati, 2001), which tends to reduce the effect of spatial heterogeneity. Horizontal fluxes resulting from horizontal soil exploration increases the competitive ability of trees for N, which increases competitive interactions between trees and grasses for N acquisition in the open and decreases chances of coexistence. These horizontal fluxes can homogenize the N availability between these two patches (Barot et al., 2015, 2014), and ultimately enhance exclusion.

5.6 Can mineral N partitioning as a coexistence mechanism be expected in other savannas?

NH_4^+ and NO_3^- partitioning is a newly described mechanism that can be applied to all African savannas that have plant species able to alter nitrification. BNI capacity has been identified in *Brachiara humidicola* and *Sorghum bicolor* (Subbarao et al., 2013) and seems to be common in African perennial grasses (Lata et al., 2004; Rossiter-Rachor et al., 2009; Subbarao et al., 2009). Most perennial tussock grass species of West African savannas seem to have the same impact on N cycling. A potential ability of grasses to inhibit nitrification has been mentioned in a sudanian savanna (Yé et al., 2015). In northern Australian and South American savannas where African grasses have been introduced as pasture species, they became invasive (D'Antonio and Vitousek, 1992; Rossiter-Rachor et al., 2017), which could be due to their capacity to influence nitrification. Indeed, it has been showed that they strongly modify soil N cycle and the high N-use efficiency of these African grasses relative to native species seem to be linked to their ability to inhibit nitrification (Rossiter-Rachor et al., 2009). Compared to native grasses, *Andropogon gayanus* lowers nitrification rates, which suggests that this capacity is likely restricted to native African perennial grasses.

Contrary to the Lamto savanna, East African savannas experience a high pressure of large herbivores and host N-fixing trees (Sankaran et al., 2008). These mechanisms can differently influence soil N cycling. Savannas with N-fixing trees increase their N availability but switch to P-limited systems (Boutton and Liao, 2010; Ludwig et al., 2004). These features provide important N inputs through symbiotic fixation and animal dungs, and hence strongly impact N cycling. However, some studies found no significant difference between leguminous and non leguminous species on N turnover rates (Becker et al., 2017). Besides, experiments have been performed in Hwange savanna in Zimbabwe (an example of savanna driven by herbivores and N fixation) to measure nitrification enzyme activity under dominant grass and tree species. Preliminary results (Lata and Barot, personal communication) shows that NH_4^+ concentration is higher under grasses than under trees while NO_3^- concentration is higher under trees than under grasses. But the nitrification rate is higher under grasses than under trees (Fig. 5.1). Even if the results are for the moment difficult to interpret, they suggest that this savanna has a very different functioning from that of the Lamto savanna. Complementary studies are needed to fully test the possibility that the partitioning of the N resource can play a role in the coexistence between trees and grasses in Hwange savannas. To determine whether the mechanism based on the competition for N can be influential in other savannas (including savannas from South America, India, Australia,...), a global assessment of nitrification inhibition by savanna grasses is firstly needed to test the scope of BNI capacity in other savannas. Then, if BNI occurs in other savannas, it is also important to know how trees respond to it, and whether nitrification is stimulated under trees in others savannas. Finally, new parameterization and adjustments should be performed in new models to test the robustness of my results to other mechanisms (N fixation, herbivores, ...). At the present time, existing data are insufficient to generalize our results to other savannas. But, even if this inhibition has not been assessed in other savanna types, mineral N partitioning could play an important role in the tree-grass coexistence of all West African humid savannas that have virtually the same grass and tree species as the Lamto savanna.

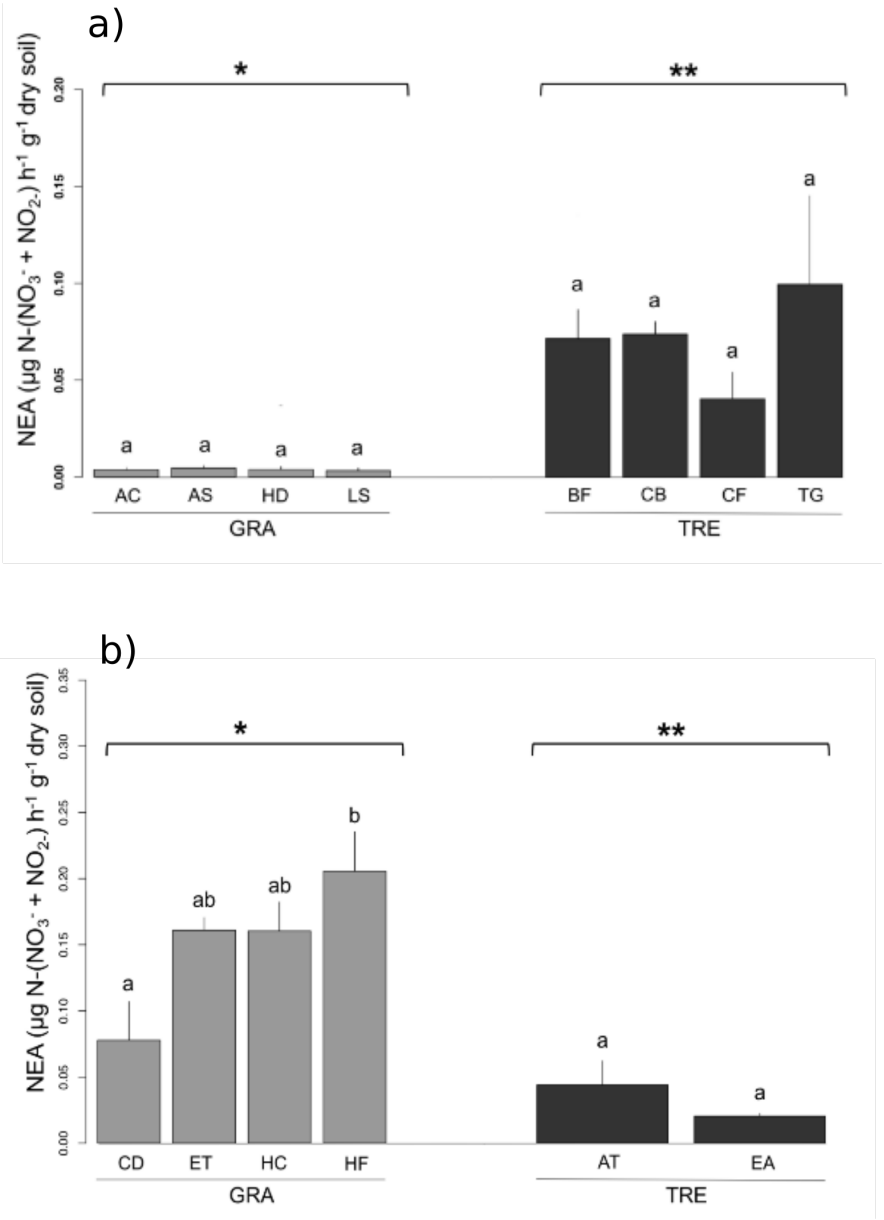

Figure 5.1 – Nitrifying Enzyme Activity according plant types (trees and grasses) in a) the Lamto savanna and b) Hwange savanna. Grasses (GRA): AC (*Andropogon canaliculatus*), AS (*Andropogon schirensis*), HD (*Hyparrhenia diplandra*), LS (*Loudetia simplex*), CD (*Cynodon dactylon*), ET (*Eragrotis trichoflora*), HC (*Heteropogon contortus*), HF (*Hyparrhenia filipendula*) and Trees (TRE): BF (*Bridelia ferruginea*), CB (*Cussonia barteri*), CF (*Crossopteryx febrifuga*), TG (*Terminalia glaucescens*), AT (*Acacia tortilis*), EA (*Erythrophleum africanum*) (Srikanthasamy, 2018)

The process of denitrification contributes to the release of nitrous oxide (N_2O) produced from NO_3^-. The capacity of trees to stimulate nitrification (Srikanthasamy et al., 2018), increases NO_3^- availability, which can increase NO_3^- losses by denitrification. Indeed, Srikanthasamy et al. (2018) found that denitrification is 9 times higher under trees than under grasses, which can also increase N_2O emissions. An increase of tree cover in similarly functioning savannas could thus accelerate global warming as N_2O is an efficient greenhouse gas (more than CO_2). However, the current rising CO_2 levels is likely involved in the currently observed increase of woody cover in savannas (Blaser et al., 2014), by increasing the competitive ability of trees *versus* grasses because trees are C_3 plants while grasses are C_4 plants. These processes leading to bush encroachment should interact with tree-grass competition

for N. The replacement of grasses by trees could potentially affect mineral N partitioning by reducing spatial heterogeneity. Results of Chapter 3 show that increasing woody cover can induce large N losses (through denitrification and leaching of NO_3^-), which can ultimately change the system from a more N conservative to a less conservative system. The assessment of plant impact on nitrification in other savannas could lead to different N_2O emissions depending on savannas and could therefore show the contribution of savannas in the release of N_2O emissions. But if nitrification stimulation is common to tree species in most savannas, increasing woody cover could enhance greenhouse effect and thus intensify global warming. Some studies showed that bush encroachment tends to particularly involve trees having the ability to fix N symbiotically (Boutton and Liao, 2010; Eldridge et al., 2011), which should impact N cycling. Becker et al. (2017) found no apparent effects of N-fixing trees on greenhouse gas compared to no fixing trees. But this should be further studied to assess N losses through denitrification and N_2O emissions. Changes in fire regimes resulting from woody encroachment and low grass biomass should decrease N losses through biomass burning. This could lead to complex feedbacks impacting mineral N partitioning.

5.7 Perspectives

Overall, I have shown in my PhD thesis that the partition of the N resource under the forms of NH_4^+ and NO_3^- between trees and grasses could play an important role for both tree-grass coexistence and the N budget of savannas. Obviously, these processes interact with already-identified mechanisms that are influential for savanna dynamics and for their N cycle. A huge work remains to be achieved to study these interactions, both by new experiments and new models.

5.7.1 Empirical studies

Lata (Lata et al., 2004, 1999) was the first to identify the capacity of savanna grasses to inhibit nitrification in the Lamto savanna but little is know about the existence of this capacity in other savannas. A global assessment of this BNI capacity in other savannas is thus needed to test the generality of the partitioning of mineral N resource in other savannas. A recent project coordinated by Lata will consist in assessing the frequency of this capacity among savanna grasses of all savannas. It will allow to know if BNI capacity is widespread among other savanna grasses and if it is linked to particular environmental conditions. In the case of savannas exhibiting nitrification inhibition, it would be interesting to know how trees respond to it and if the stimulation of nitrification by trees is common in other savannas.

Empirical studies are also needed to determine the plant preference for NH_4^+ *versus* NO_3^- by comparing different treatments for trees and grasses: (1) plants growing only with NO_3^-, (2) plants growing only with NH_4^+ and (3) plants growing with both NH_4^+ and NO_3^- using ^{15}N labelling.

An experiment of N fertilization by increasing total mineral N availability could also be interesting to test its effects on BNI activity and nitrification stimulation by trees and how this influences tree and grass preference for NH_4^+ *versus* NO_3^- and ultimately tree and grass biomass and tree-grass coexistence.

Finally, *in situ* measurements of fluxes such as NO_3^- losses by leaching and denitrification at temporal and spatial (in the open and under tree canopy) scales, and an estimation of horizontal fluxes through the quantity of N absorbed by tree roots in the open, are also needed to parameterize models.

5.7.2 Modelling studies

Vertical niche separation

Walter (1971) suggested that vertical niche separation through different rooting depths can facilitate tree-grass coexistence. In the Lamto savanna, trees and grasses have an overall superficial rooting profile (Mordelet et al., 1997). However, there is some field evidence that grass roots are mainly in the 30 cm of the soil while trees roots cannot extend until more than 60 cm of depth (Fig. 5.2). In my model, I considered that tree and grass roots overlap in the same soil layers, i.e., between 0 and 30 cm. In future studies, it could be interesting to build a modified version of the two-patch model including the ability of trees to take up resources deeper than 30 cm. Because NO_3^- is more prone to leaching and thus can easily reach deeper soil layers, extending tree roots deeper can increase their N uptake by trees and thus can reduce the impact of NO_3^- leaching. The current model takes into account the horizontal soil exploration by trees. Coupling horizontal and vertical soil exploration should allow determining a trade-off for trees in their soil exploration and emphasizing the better strategy that favors their N acquisition and contributes to tree-grass coexistence. The existence of deeper tree roots could explain that they have "chosen" in Lamto a strategy consisting to stimulate nitrification: this would increase their competitive ability for N against grasses in the open.

Effect of disturbances

Fire and herbivores are key actors of important disturbance-mediated coexistence mechanism that affects tree demography (Higgins et al., 2000; Sankaran et al., 2004). As I wrote above, mineral N partitioning should interact with disturbance-based mechanisms to explain tree-grass coexistence. It could be interesting to build individual-based models to take into account mechanisms based on both resource competition and disturbance e.g. the effects of fire and herbivores on plant demography (Higgins et al., 2000; Van Langevelde et al., 2003). Such models should allow testing the feedbacks between the partition of mineral N, fire and herbivores and also assessing the influence of both types of mechanisms, i.e. N partitioning and plant demography, on the competition between trees and grasses.

As many savannas, the Lamto savanna climate is strongly seasonal (Abbadie et al., 2006). These seasonal variations also impact N cycling, as during the dry season the activity of microorganisms is relatively low, which reduces mineralization and nitrification processes (Srikanthasamy, 2018). A model including the effects of seasonality and fire-induced changes could therefore be very enriching.

Evolution of the capacity of plant to control nitrification

Because of the N limitation in the Lamto savanna, grasses have developed strategies to secure their N uptake. The capacity of grasses to inhibit nitrification also strongly influences ecosystem properties by reducing N losses, which can increase primary production (Boudsocq et al., 2009). It could be interest-

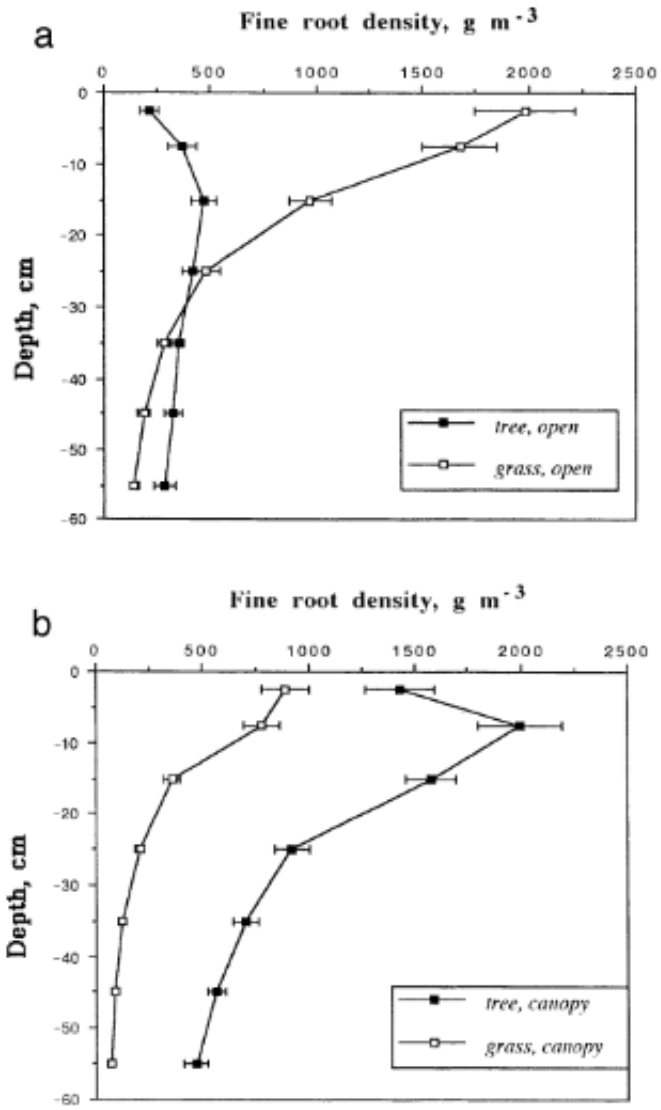

Figure 5.2 – Vertical distribution of tree and grass root densities in the open (a) and under tree canopy (b) (from (Mordelet et al., 1997))

ing to study the evolution of the ability of plants to control (inhibit or stimulate) nitrification through an adaptive dynamics modelling approach (Fussmann et al., 2007). This would allow determining the general conditions under which the evolution can lead to diverse strategies for N acquisition and studying the co evolution between the capacity of plants to control nitrification and the preference of plants for NH_4^+ *versus* NO_3^-.

Conclusion

Firstly, my study allows to test the effects of nitrification control by trees and grasses and how these effects influence tree-grass competition for N. This allows to address the impacts of plant preference on plant dynamics and N budget. This suggests that the influence of mineral N partitioning on tree-grass coexistence depends on the capacity of plants to inhibit or stimulate nitrification and their preferences for NH_4^+ *versus* NO_3^-. Besides, the effects of the spatial heterogeneity created by plants can be influenced at least by: the horizontal soil exploration by trees and the percentage of tree cover, already implemented in my study. My study suggests the existence of a new mechanism based on N partition that could be determinant in the coexistence between trees and grasses and thus could contribute to the maintenance of savannas, at least in West African humid savannas.

Despite the theoretical approach of my study, my models could also deal with practical issues in agroecosystems. The current agricultural practices and the use of fertilizers have modified agricultural systems towards high-nitrifying environments (Subbarao et al., 2013). This causes large losses of N through leaching and denitrification as N is more available in the NO_3^- form and lowers N-use efficiency (Subbarao et al., 2013). The capacity of grasses to inhibit nitrification can be an interesting alternative to lower N fertilizer inputs as such a capacity better conserves N and thereby reduces N losses. The models developed in my study can be adjusted for agrosystems to test the competitive ability of crops and nitrification inhibiting grasses for N acquisition and could be used as a decision-making tool for the management of agricultural systems. Moreover, it could particularly be applied in models of agroforestry mixing grasses and trees, as in Brazil.

Bibliography

Abbadie, L. (2006). Nitrogen inputs to and outputs from the soil-plant system. In *Lamto: structure, functioning, and dynamics of a savanna ecosystem*, pages 255–275. New York: Springer.

Abbadie, L., Gignoux, J., Le Roux, X., and Lepage, M. (2006). *Lamto: structure, functioning, and dynamics of a savanna ecosystem*. New York: Springer.

Adler, P. B., Fajardo, A., Kleinhesselink, A. R., and Kraft, N. J. (2013). Trait-based tests of coexistence mechanisms. *Ecology letters*, 16(10):1294–1306.

Aerts, R., Boot, R., and Van der Aart, P. (1991). The relation between above-and belowground biomass allocation patterns and competitive ability. *Oecologia*, 87(4):551–559.

Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: a synthesis. *Ecology letters*, 6(12):1109–1122.

Ashton, I. W., Miller, A. E., Bowman, W. D., and Suding, K. N. (2010). Niche complementarity due to plasticity in resource use: plant partitioning of chemical n forms. *Ecology*, 91(11):3252–3260.

Barot, S., Bornhofen, S., Boudsocq, S., Raynaud, X., and Loeuille, N. (2015). Evolution of nutrient acquisition: when space matters. *Functional ecology*, 30(2):283–294.

Barot, S., Bornhofen, S., Loeuille, N., Perveen, N., Shahzad, T., and Fontaine, S. (2014). Nutrient enrichment and local competition influence the evolution of plant mineralization strategy: a modelling approach. *Journal of Ecology*, 102(2):357–366.

Barot, S. and Gignoux, J. (2004). Mechanisms promoting plant coexistence: can all the proposed processes be reconciled? *Oikos*, 106(1):185–192.

Barot, S., Gignoux, J., and Menaut, J.-C. (1999). Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. *Ecology*, 80(6):1987–2005.

Becker, J. N., Gütlein, A., Sierra Cornejo, N., Kiese, R., Hertel, D., and Kuzyakov, Y. (2017). Legume and Non-legume Trees Increase Soil Carbon Sequestration in Savanna. *Ecosystems*, 20(5):989–999.

Bever, J. D., Westover, K. M., and Antonovics, J. (1997). Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology*, 85(5):561–573.

Blaser, W. J., Shanungu, G. K., Edwards, P. J., and Olde Venterink, H. (2014). Woody encroachment reduces nutrient limitation and promotes soil carbon sequestration. *Ecology and evolution*, 4(8):1423–1438.

Boudsocq, S., Lata, J.-C., Mathieu, J., Abbadie, L., and Barot, S. (2009). Modelling approach to analyse the effects of nitrification inhibition on primary production. *Functional Ecology*, 23(1):220–230.

Boudsocq, S., Niboyet, A., Lata, J. C., Raynaud, X., Loeuille, N., Mathieu, J., Blouin, M., Abbadie, L., and Barot, S. (2012). Plant preference for ammonium versus nitrate: a neglected determinant of ecosystem functioning? *The American Naturalist*, 180(1):60–69.

Boutton, T. and Liao, J. (2010). Changes in soil nitrogen storage and δ15n with woody plant encroachment in a subtropical savanna parkland landscape. *Journal of Geophysical Research: Biogeosciences*, 115(G3).

Britto, D. T. and Kronzucker, H. J. (2013). Ecological significance and complexity of N-source preference in plants. *Annals of botany*, 112(6):957–963.

Brundrett, M. C. (2002). Coevolution of roots and mycorrhizas of land plants. *New phytologist*, 154(2):275–304.

Casper, B. B. and Jackson, R. B. (1997). Plant competition underground. *Annual review of ecology and systematics*, 28(1):545–570.

Chase, J. M. and Leibold, M. A. (2003). *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press.

Chesson, P. (2000). General theory of competitive coexistence in spatially-varying environments. *Theoretical population biology*, 58(3):211–237.

D'Antonio, C. M. and Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual review of ecology and systematics*, 23(1):63–87.

Eldridge, D. J., Bowker, M. A., Maestre, F. T., Roger, E., Reynolds, J. F., and Whitford, W. G. (2011). Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters*, 14:709–722.

Fussmann, G. F., Loreau, M., and Abrams, P. A. (2007). Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology*, 21:465–477.

Gignoux, J., Barot, S., Menaut, J.-C., and Vuattoux, R. (2006). Structure, long-term dynamics, and demography of the tree community. In *Lamto: structure, functioning, and dynamics of a savanna ecosystem*, pages 335–364. Springer.

Grassein, F., Lemauviel-Lavenant, S., Lavorel, S., Bahn, M., Bardgett, R. D., Desclos-Theveniau, M., and Laîné, P. (2015). Relationships between functional traits and inorganic nitrogen acquisition among eight contrasting european grass species. *Annals of botany*, 115(1):107–115.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M., Diemer, M., Dimitrakopoulos, P., Finn, J., Freitas, H., Giller, P., Good, J., et al. (1999). Plant diversity and productivity experiments in european grasslands. *science*, 286(5442):1123–1127.

Higgins, S. I., Bond, W. J., and Trollope, W. S. (2000). Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology*, 88(2):213–229.

Hochberg, M. E., Menaut, J. C., and Gignoux, J. (1994). The influences of tree biology and fire in the spatial structure of the west african savannah. *Journal of Ecology*, 82:217–226.

Holt, R. D. (2008). Theoretical perspectives on resource pulses. *Ecology*, 89(3):671–681.

Houlton, B. Z., Sigman, D. M., Schuur, E. A., and Hedin, L. O. (2007). A climate-driven switch in plant nitrogen acquisition within tropical forest communities. *Proceedings of the National Academy of Sciences*, 104(21):8902–8906.

Konnerup, D. and Brix, H. (2010). Nitrogen nutrition of *Canna indica*: effects of ammonium versus nitrate on growth, biomass allocation, photosynthesis, nitrate reductase activity and n uptake rates. *Aquatic Botany*, 92(2):142–148.

Lambers, H., Shane, M. W., Cramer, M. D., Pearse, S. J., and Veneklaas, E. J. (2006). Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Annals of botany*, 98:693–713.

Lata, J.-C., Degrange, V., Raynaud, X., Maron, P.-A., Lensi, R., and Abbadie, L. (2004). Grass populations control nitrification in savanna soils. *Functional Ecology*, 18(4):605–611.

Lata, J.-C., Durand, J., Lensi, R., and Abbadie, L. (1999). Stable coexistence of contrasted nitrification statuses in a wet tropical savanna ecosystem. *Functional Ecology*, 13(6):762–768.

Lata, J.-C., Guillaume, K., Degrange, V., Abbadie, L., and Lensi, R. (2000). Relationships between root density of the african grass *Hyparrhenia diplandra* and nitrification at the decimetric scale: an inhibition–stimulation balance hypothesis. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1443):595–600.

Ludwig, F., De Kroon, H., Berendse, F., and Prins, H. H. (2004). The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology*, 170(1):93–105.

Maire, V., Gross, N., da Silveira Pontes, L., Picon-Cochard, C., and Soussana, J.-F. (2009). Trade-off between root nitrogen acquisition and shoot nitrogen utilization across 13 co-occurring pasture grass species. *Functional Ecology*, 23(4):668–679.

McKane, R. B., Johnson, L. C., Shaver, G. R., Nadelhoffer, K. J., Rastetter, E. B., Fry, B., Giblin, A. E., Kielland, K., Kwiatkowski, B. L., Laundre, J. A., et al. (2002). Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, 415(6867):68–71.

Miller, A. E. and Bowman, W. D. (2002). Variation in nitrogen-15 natural abundance and nitrogen uptake traits among co-occurring alpine species: do species partition by nitrogen form? *Oecologia*, 130(4):609–616.

Mordelet, P., Abbadie, L., and Menaut, J.-C. (1993). Effects of tree clumps on soil characteristics in a humid savanna of west africa (lamto, côte d'ivoire). *Plant and Soil*, 153(1):103–111.

Mordelet, P. and Le Roux, X. (2006). Tree/grass interactions. In *Lamto: structure, functioning, and dynamics of a savanna ecosystem*, pages 139–161. New York: Springer.

Mordelet, P., Menaut, J.-C., and Mariotti, A. (1997). Tree and grass rooting patterns in an african humid savanna. *Journal of Vegetation Science*, 8(1):65–70.

Pacala, S. W. and Levin, S. A. (1997). Biologically generated spatial pattern and the coexistence of competing species. In *Spatial ecology: the role of space in population dynamics and interspecific interactions*, pages 204–232. Princeton University Press, Princeton, NJ.

Pacala, S. W. and Tilman, D. (1994). Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *The American Naturalist*, 143(2):222–257.

Rossiter-Rachor, N., Setterfield, S., Douglas, M., Hutley, L. B., Cook, G., and Schmidt, S. (2009). Invasive *Andropogon gayanus* (gamba grass) is an ecosystem transformer of nitrogen relations in australian savanna. *Ecological Applications*, 19(6):1546–1560.

Rossiter-Rachor, N. A., Setterfield, S. A., Hutley, L., McMaster, D., Schmidt, S., and Douglas, M. M. (2017). Invasive *Andropogon gayanus* (gamba grass) alters decomposition and nitrogen fluxes in an australian tropical savanna. *Scientific reports*, 7:11705.

Sankaran, M., Ratnam, J., and Hanan, N. (2008). Woody cover in african savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography*, 17(2):236–245.

Sankaran, M., Ratnam, J., and Hanan, N. P. (2004). Tree–grass coexistence in savannas revisited–insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology letters*, 7(6):480–490.

Silvertown, J. (2004). Plant coexistence and the niche. *Trends in Ecology & evolution*, 19(11):605–611.

Srikanthasamy, T. (2018). *Impact du couvert arboré et herbacé sur le cycle de l'azote: Cas de la savane de Lamto*. PhD thesis, Paris 6.

Srikanthasamy, T., Leloup, J., N'Dri, A. B., Barot, S., Gervaix, J., Koné, A. W., Koffi, K. F., Le Roux, X., Raynaud, X., and Lata, J.-C. (2018). Contrasting effects of grasses and trees on microbial n-cycling in an african humid savanna. *Soil Biology and Biochemistry*, 117:153–163.

Stoll, P. and Prati, D. (2001). Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology*, 82(2):319–327.

Subbarao, G., Ito, O., Sahrawat, K., Berry, W., Nakahara, K., Ishikawa, T., Watanabe, T., Suenaga, K., Rondon, M., and Rao, I. M. (2006). Scope and strategies for regulation of nitrification in agricultural systems—challenges and opportunities. *Critical Reviews in Plant Sciences*, 25(4):303–335.

Subbarao, G., Nakahara, K., Hurtado, M. d. P., Ono, H., Moreta, D., Salcedo, A. F., Yoshihashi, A., Ishikawa, T., Ishitani, M., Ohnishi-Kameyama, M., et al. (2009). Evidence for biological nitrification inhibition in brachiaria pastures. *Proceedings of the National Academy of Sciences*, 106(41):17302–17307.

Subbarao, G., Sahrawat, K. L., Nakahara, K., Rao, I. M., Ishitani, M., Hash, C., Kishii, M., Bonnett, D., Berry, W., and Lata, J.-C. (2013). A paradigm shift towards low-nitrifying production systems: the role of biological nitrification inhibition (BNI). *Annals of botany*, 112(2):297–316.

Tavernier, V. A. M. (2003). *Interactions entre structures racinaires et cycle de l'azote en zone de savane africaine*. PhD thesis, Paris, Institut national d'agronomie de Paris Grignon.

Tilman, D. (1982). *Resource competition and community structure*. Princeton university press.

Tilman, D. (1985). The resource-ratio hypothesis of plant succession. *The American Naturalist*, 125(6):827–852.

Van Langevelde, F., Van De Vijver, C. A., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A. K., Hearne, J. W., Stroosnijder, L., Bond, W. J., et al. (2003). Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, 84(2):337–350.

Walter, H. (1971). *Ecology of tropical and subtropical vegetation*. Edinburgh: Oliver Boyd.

Wang, L. and Macko, S. A. (2011). Constrained preferences in nitrogen uptake across plant species and environments. *Plant, cell & environment*, 34(3):525–534.

Yé, L., Abbadie, L., Bardoux, G., Lata, J. C., Nacro, H. B., Masse, D., de Parseval, H., and Barot, S. (2015). Contrasting impacts of grass species on nitrogen cycling in a grazed Sudanian savanna. *Acta Oecologica*, 63:8–15.