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West African mixed farming systems as meta-ecosystems: A source-sink modelling approach

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ABSTRACT

Nutrient availability is a major limitation of the production of West African mixed farming systems. The fertility of these systems was traditionally sustained by fallowing, and nutrient transfers by livestock from savanna to croplands. However, demographic growth and socio-economic constraints require the agro-ecological intensification of these systems. To understand how agricultural practices and landscape management affect crop production, we built a meta-ecosystem model of nitrogen stocks and fluxes, and we examined different scenarios of fallow management with or without livestock.

Our results suggest that crop production is highly dependent on the source-sink dynamics of nitrogen. Without livestock, maximum crop production is obtained for an intermediate duration of fallowing, highlighting a trade-off between space devoted to production (cropland) and space devoted to fertility restoration (fallow). In presence of livestock, crop production is maximum for a shorter duration of fallowing; it is markedly higher with than without livestock. This result highlights the positive roles of livestock and fallows as pumps (vectors) of nitrogen from savanna rangeland to cropland, and from fallow land to cropland, respectively. However, it also highlights the negative relationship between livestock presence and fallowing, suggesting that the optimal configuration of livestock and fallow management is highly context-dependent.

Overall, we argue that the meta-ecosystem approach is particularly relevant for the study of agro-ecosystems characterized by high spatial heterogeneity. This work can be seen as a first step toward an alternative approach, integrating tools from theoretical ecology for the study of agro-ecosystems which functioning strongly depends on spatial organisation.

1. Introduction

In dry to sub-humid West-Africa, most farms are traditional mixed systems combining crop and livestock production. For a long time, West-African mixed farming systems (WAMFS) were relatively well adapted to the population needs, in the context of subsistence agriculture (Garrity et al., 2012; Jalloh et al., 2012; Sebastian., 2014). However, WAMFS are currently facing important demographic, social, economic and environmental changes (Jalloh et al., 2013). Over the last century, the increase in agricultural production has been achieved mainly by cropland expansion. This led to a gradual disappearance of fallowing and not cultivated areas, a key component of traditional mixed farming systems. This degradation of the natural vegetation and landscape, particularly pregnant in more semi-arid and arid regions, tends to expand to more humid climate area, the new breadbasket of West-Africa countries. These changes are threatening biomass production and soil fertility, mainly through a decrease of carbon and mineral nutrient stocks in soils (Schlecht et al., 2006; UNEP, 2008). In turn, this decrease compromises the sustainability of the whole farming system, with potentially dramatic social and economic consequences. These perspectives have fostered research on fertility management aimed at defining innovative practices that ensure sustainable farming in sub-Saharan Africa (Rufino et al., 2007).

Increasing exogenous inputs of mineral nutrients and organic matter

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to soils may seem to be the best response to the decrease of soil fertility; however, applying fertilizers is often prohibitive and risky for local farmers. Moreover, the use of exogenous fertilizers is increasingly recognized as a non-sustainable option, mainly because fertilizer production itself is not sustainable in the long run (Tilman et al., 2002). Many soils of WAMFS are lixisols (IUSS Working Group WRB: World Reference Base for Soil Resouces, 2006). These nutrient-poor, highly erodible soils are subject to the formation of slaking crusts and to important losses of nutrients through leaching (Smaling et al., 1999). Therefore, crop production in these systems is likely to be particularly sensitive to nutrient loss at the landscape level. The soil capacity to prevent nutrient loss, also referred to as nutrient retention capacity, depends on the efficiency of nutrient recycling, which is driven by soil and ecosystem functioning (Barot et al., 2007; Boudsocq et al., 2009) within the spatial components of the landscape, and on nutrient transfers between these components.

Since crop production in WAMFS is frequently limited by nutrient availability, we argue that a better understanding of the cycling and transfers of nutrients across agricultural landscapes may help determine spatial organizations maximizing crop production. The key role of nutrient cycling at both ecosystem (Aerts and Chapin, 1999) and meta-ecosystem levels (Loreau et al., 2003) for primary production has been highlighted in theoretical ecology. For example, primary production in a given ecosystem may widely depend on processes that maintain fertility in the other ecosystems connected to it through source-sink dynamics (Loreau et al., 2013).

As agro-ecosystems are mosaics of subsystems forming networks of patches connected by fluxes of nutrients, agro-ecosystems are meta-ecosystems (Loreau et al., 2003). In these landscapes, the productivity of crop fields depends on (1) local nutrient cycling within a subsystem, (2) transfers of nutrients between the connected subsystems, and therefore on (3) nutrient balance within each connected subsystem. Therefore, a better spatial organization of the mosaic of landscape subsystems and a better management of nutrient fluxes between subsystems may help increase crop production and its sustainability.

We tackle these issues using a modelling approach focusing on WAMFS of the Guineo-Sudanian biome (Le Houérou, 2009) at the beginning of intensification processes, when the surface of savanna is still large enough to provide non-limiting rangeland for livestock. WAMFS are highly spatially structured landscapes with two distinct cultivated subsystems surrounding the dwellings, namely, the "compound ring" (intensive crop fields) and the "bush ring" (extensive crop fields), and two non-cultivated subsystems, namely, fallows in the bush ring, and savanna (Fig. 1a).

Fluxes of nutrient between these subsystems, and the subsequent connectivity, are well documented (Diarisso et al., 2015; Manlay et al., 2004b; Prudencio., 1993). These fluxes mainly rely on livestock movements, crop harvest and on active spreading by farmers of household wastes close to dwellings. Moreover, these factors all vary across the seasons. Therefore, livestock and land-use management (e.g. the proportion of non-cultivated versus cultivated areas) represent the main driving-forces to optimize nutrient retention and nutrient transfers between subsystems, hence, crop production at the landscape scale.

To assess how livestock and land-use management can qualitatively affect the optimization of crop production, we developed and analysed a "minimal" (sensu Mooij et al., 2010) mathematical model of nutrient stocks and fluxes in a WAMFS. More specifically, we examined how three "driving forces", namely, the extent of fallow in space and time, the presence/absence of livestock, and the compound ring:bush ring surface ratio, affect crop production at the landscape level. We used the model to identify the optimal spatial organization for crop production, and the mechanisms by which these three driving-forces, individually or in combination, affect crop production.

2. Model

In this section, we describe the mathematical model that we built for our study. We focus on the well-documented case study in Guineo-Sudanian West Africa (Le Houérou, 2009): the village of Sare Yero Bana, in the High Casamance region of Senegal (N 12.81917, W 14.89024) (Manlay et al., 2002). All the parameters used in the model, their values, dimensions and their definitions are referenced in Appendix 2. The equations of the subsystems models for each season and transition event during the year are summarized in Appendix 3.

2.1. Spatio-temporal structure of the model

In the following sections, we first present the spatial structure of the model. Then we detail the two time scales considered in the model: the year (annual cycle), and the multi-year duration of the cropland/fallow rotation cycle.

2.1.1. Spatial structure

As for many agro-ecosystems of West Africa, the landscape at Sare Yero Bana is structured in subsystems that are spatially organized in concentric rings around the dwellings (Manlay et al., 2004b). The compound ring (Fig. 1a) is the closest to the dwellings and is permanently cropped with staple crops such as cereals (pearl millet *Pennisetum glaucum* L., maize *Zea mays* L., sorghum *Sorghum bicolor* L. Moench). The compound ring benefits from organo-mineral inputs as household wastes and livestock manure. Surrounding the compound ring is the bush ring, which is managed more extensively, and alternates cropping for cash (e.g., groundnut *Arachis hypogea*, a legume; Manlay et al., 2002) and fallow (which consists in a succession of plants dominated by Combretaceae and including nitrogen-fixing species; Manlay et al., 2002).

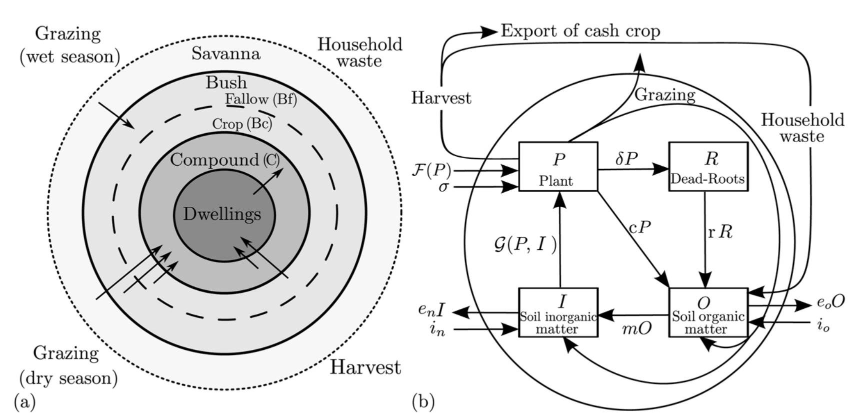

Fig. 1. (a) Representation of the fluxes occurring between the rings over a year in the whole agro-ecosystem. (b) Model of the nitrogen cycle in a generic subsystem of the agro-ecosystem. Representation of all stocks and fluxes occurring over a year. See Appendix 1 and 2 for the description of variables and parameters, respectively.

Table 1
Summary of active fluxes depending on the rings and the instant in the annual cycle. Empty boxes symbolize an absence of flux, × an active flux, $\times_0$ and $\times_1$ are fluxes active during the cropland/fallow and the fallow/cropland shifts, respectively. c: crop; bf: bush-fallow; bc: bush-crop.

	Rain season nT to nT + τ			Harvest at nT + τ			Dry season nT + τ to (n+1)T			Sowing/clearing at (n+1)T		
	comp. crop (c)	bush crop (bc)	fallow (bf)	comp. crop (c)	bush crop (bc)	fallow (bf)	comp. crop (c)	bush crop (bc)	fallow (bf)	comp. crop (c)	bush crop (bc)	fallow (bf)
Harvest γ				×	×	×						
Sowing σ										×	×	$\times_0$
Fallow transfer δ											$\times_1$	$\times_1$
Biological fixation i_p		×	×									
Growth G	×	×	×									
Losses e_n	×	×	×				×	×	×			
Losses e_o	×	×	×									
Household waste	×						×					
Degradation r		×	×					×	×			
Degradation c							×	×	×			
Mineralization m	×	×	×				×	×	×			
Deposition i_n	×	×	×				×	×	×			
Deposition i_o	×	×	×				×	×	×			
Grazing			×				×	×	×			
Night corralling			×				×					

The compound and bush rings are surrounded by permanently uncultivated savanna and used as rangeland for livestock. There is thus an intensification of cropping practices from the savanna to the dwellings.

Since we focus on crop production, the nutrient dynamics is explicitly represented in the bush and compound rings only. In the model, the compound and the bush rings are considered as subsystems which areas are denoted by α_c and α_b, respectively. The dwellings and the savanna are simply considered as nutrient sources or sinks. We define sources and sinks accordingly to Loreau et al. (2013), where a source (respectively a sink) subsystem is an exporter (respectively an importer) of nutrient within the whole agro-ecosystem. The savanna is assumed to be a non-limiting source of nutrient; Section 4.4 discusses this assumption. The compound and bush subsystems are connected to each other and to the other spatial entities by different fluxes, that gives the model of the agro-ecosystem the form of a meta-ecosystem model.

2.1.2. Annual cycle

Agricultural practices change over the seasons. Over one year, a short wet season (4-5 months), corresponding to the growing period for plants, alternates with a long dry season (7-8 months). The wet season is characterized by erratic rains amounting annually to circa 1100 mm (Ardoin-Bardin, 2004). In our model, a year starts at the beginning of the wet season. In the sequel, T denotes the number of days in a year, τ the number of days in a wet season and n represents the number of years considered since year 0 . The wet season of year n starts at day $nT + 1$ with sowing, and ends at day $n\,T + \tau$ with the harvest, which initiates the transition between the two seasons. The dry season lasts from day $n\,T + \tau$ to day $(n + 1)T$.

2.1.3. Crop-fallow cycle

The crop-fallow rotation is an agricultural practice that runs at the time scale of several years. It affects the spatial and temporal organizations of the agro-ecosystem and generates a particular set of nutrient fluxes. The "rotation" is defined as the succession of one cropping period followed by one fallow period. If L denotes the duration (in years) of the rotation and L_c the duration of the cropland period, then $L_f = L - L_c$ is the duration of the fallow period.

The bush subsystem includes multiple crop fields and fallow lands. To account for this heterogeneity and to ensure that the cultivated part of the bush ring is constant over time, the bush subsystem is split into L subunits of the same area that will alternatively be in a state of cropland or fallow. At each instant, among the L subunits, L_c and L_f subunits are in states of cropland and fallow, respectively. With this mathematical trick, L (respectively L_c and L_f) represents both the duration (in years) of a rotation (respectively a cropping period and a fallow period) and the total number of subunits (respectively the number of subunits that are in a state of cropland and the number of subunits that are in a state of fallow). Thus, the proportions of cropland $\frac{L_c}{L}$ and fallow $\frac{L_f}{L}$ are considered constant over a simulation.

For instance, a rotation duration of $L = 20$ years and a cropland period duration of $L_c = 15$ years implies a fallow period duration of $L_f = 5$ years. In that case, the bush subsystem is split into 20 subunits with at any time during the rotation, 15 subunits in a state of cropland and 5 in a state of fallow. The proportion of subunits in a state of cropland is constant and equal to $\frac{15}{20}$.

2.2. Compound and bush subsystems

The same generic model is used to represent the compound and bush subsystems (Fig. 1b). This model focuses on the cycle of nitrogen (N), which is usually considered as the main limiting nutrient for crop production in Guineo-Sudanian West Africa (Pieri, 1992; Rufino et al., 2006; Smaling et al., 1999). Though some processes that are specific to N (such as the biological N fixation) are taken into account in the model, adapting the model to phosphorus, which is the other main nutrient limiting primary productivity in these agro-ecosystems (Brouwer and Powell., 1998) would be easy. The subsystem model considered is a N stocks and fluxes model composed of several interconnected N compartments. Fluxes of N between compartments within the subsystem and between the different subsystems depend on the subsystem and on the season (Table 1). The different compartments and fluxes of one subsystem are presented in the following paragraphs. N stocks and fluxes are expressed respectively in kgN per hectare (kgN ha^{-1}), and in kgN per hectare of the subsystem they belong to and per day (kgN ha^{-1} day^{-1}).

2.2.1. Nitrogen compartments

Each subsystem is composed of three compartments: the plant (P), the soil organic fraction (O) and the soil inorganic fraction (I), to which a fourth compartment, the dead roots of woody plants (R), is added in the case of the bush ring (Fig. 1b).

The P compartment represents the quantity of nitrogen contained in the plant (both the aboveground and underground parts) per surface unit (kgN ha^{-1}). Each subsystem is assumed to contain one type of plant. In fallow, possible changes in digestibility and palatability of plants over time are not considered. For simplicity, we assume that in the compound subsystem and the cropland subunits of the bush subsystem, the plant compartment P contains live crop biomass during the wet season, and crop residues (straw, litter, dead-roots) during the dry season. The O and I compartments represent the quantities of nitrogen under organic and inorganic forms contained in the first 30 cm of soil per surface unit (kgN ha^{-1}), respectively. The R compartment represents the quantity of nitrogen contained in the belowground part of the woodyplants growing in the bush subsystem during fallow periods.

For a subunit j (with $1 \leq j \leq L$) of the bush subsystem, the compartments P, O, I and R are denoted P_j, O_j, I_j and R_j respectively, and are expressed in kgN per hectare of the subunit j [kgN (ha of bush subunit j)$^{-1}$]. Within the bush subsystem, the mean biomass of fallow plants (in kgN per hectare of fallow) is denoted P_{bf} and the mean biomass of crop plants (in kgN per hectare of bush crop) P_{bc}. See equations (10) and (11) in Appendix 1 for details.

Within the compound subsystem, the compartments P, O and I are simply denoted P_c, O_c and I_c. They are expressed in kgN per hectare of compound ring [kgN (ha of compound)$^{-1}$].

2.2.2. Intra-subsystem fluxes

The model includes five intra-subsystem fluxes (Fig. 1b) that connect the different nitrogen compartments to each other:

- the growth of the plant compartment P through the uptake of inorganic nitrogen coming from I (growth function G) and the biological fixation of atmospheric N in the case of legumes (growth function F) during the wet season
- the decay of the plant compartment P into soil organic matter O at rate c during the dry season (this process is considered negligible during the wet season)
- the transfer of nitrogen located in roots from the plant compartment P (only for woody plants) to the dead root compartment R (parameter δ), which only occurs in the bush subsystem during the shift from fallow to cropland after clearing (cf. 2.3.3). We indeed assume that roots die only when the fallow is cleared at the end of the fallow
- the decay of the dead-root compartment R which decomposes into soil organic matter O at rate R, which only occurs in the bush subsystem since R compartment is specific to it
- and the mineralization of organic matter O into inorganic nitrogen I at rate m.

Intra-subsystem fluxes are all linear and proportional to the amount stored in the compartment they originate from, except for plant growth function G (1). G is a modified logistic function with a carrying capacity K and a growth rate u proportional to the stock of inorganic nitrogen I:

$$G(P, I) = uI\frac{K-P}{K}P \tag{1}$$

In the fallow subsystem, the carrying capacity is the plant biomass at equilibrium in absence of herbivore (May and McLean, 2007). In cultivated subsystems, the carrying capacity represents the maximum stand biomass at the end of the wet season. In addition to the assimilation of soil inorganic nitrogen I through the plant growth function G (1), atmospheric N is assimilated by legumes through symbiotic fixation: groundnut in cropland subunits of the bush subsystem, and by wild species (as *Piliostigma, Indigofera spp*,…) in fallow subunits. We assume that the function F (2) describing the atmospheric N fixation is logistic, with a carrying capacity similar to that of G, and with a biological fixation rate i_p:

$$F(P) = i_p\frac{K-P}{K}P \tag{2}$$

To account for the variations of fertility in cultivated subunits of the bush subsystem, the carrying capacity K is reset every year. In each cultivated subunit j of the bush subsystem, the carrying capacity K_j (3) is assumed proportional to the value of the compartment I at the beginning of the wet season:

$$K_j = \min(\omega I_j(\mathrm{nT}), K_{\max}), \tag{3}$$

ω being a constant parameter and $K_{\max}$ the maximum carrying capacity in absence of limitation by soil inorganic nitrogen. In the fallow subunit j of the bush subsystem, $K_j = K_{bf}$.

2.2.3. Inputs and outputs of nitrogen from and to the outside

In addition to the intra-subsystem fluxes, there are also some inputs and outputs of nitrogen entering or exiting the agro-ecosystem. We have represented the inputs of nitrogen through dry and wet atmospheric depositions of mineral (parameter i_n) and organic (parameter i_o) nitrogen.

Sowing is considered as an additional punctual input of nitrogen that occurs at the beginning of the wet season. At this instant, the stock in the P compartment of the compound and bush subsystems is initialized at a value σ (in kgN ha^{-1}), except for the fallow subunits of the bush ring that were already fallow the year before. σ is the quantity of nitrogen contained in seeds sown per hectare. When shifting from cropland to fallow, the nitrogen stock in the seed bank from which fallow vegetation develops is spontaneously present in the environment. Losses of nitrogen from the compartments O and I passively occur through erosion, leaching, volatilization and denitrification. In the model, the parameters e_o and e_n account for the overall loss rates of organic and mineral nitrogen, respectively.

2.3. Inter-subsystems fluxes

The compound and bush subsystems are finally connected to each other through inter-subsystems fluxes. Two types of nitrogen fluxes connect the subsystems, namely, the spreading of household wastes from dwellings and the excretion of nitrogen by livestock. Household wastes are spread in the compound subsystem. They mainly originate from crops harvested in both the compound and the bush subsystem, and therefore generate an indirect flux of nitrogen from the bush to the compound subsystem. Livestock generates fluxes of nitrogen between subsystems, and between the savanna and the subsystems, by ingesting nitrogen through grazing during the day, and by excreting nitrogen during day and during night corralling through urine and faeces. Each of these fluxes is detailed in the following paragraphs.

2.3.1. Harvest and recycling fluxes

Crops from the compound subsystem fulfil most staple food needs of villagers, the rest coming from a small part of crops produced by the bush subsystem (Vigan, 2013). The rest of the crops produced by the bush subsystem is exported outside the village. Therefore, there is no exportation of nitrogen through the crop produced in the compound subsystem, whereas most of the nitrogen of the crop produced in the bush subsystem is exported from the agro-ecosystem.

The parameter γ represents the share of harvested plant, and the parameter ϵ represents the share of harvested cash crop that is exported from the agro-ecosystem. The quantity of crop $V(n)$ brought to the dwellings after the harvest for a year n is therefore:

$$V(n) = \underbrace{\alpha_c\gamma_c P_c(nT+\tau^-)}_{\text{from compound subsystem}} + \underbrace{\frac{L_c}{L}\alpha_b\gamma_{bc}(1-\epsilon)P_{bc}(nT+\tau^-)}_{\text{from bush subsystem (cropland subunits)}} \tag{4}$$

where $nT+\tau^-$ is the time just before $nT+\tau$, at the end of the wet season, before the harvest. A share λ_v of $V(n)$ is recycled in the agro-ecosystem and spread during the year in the compound subsystem as organic amendment. We assume that the spreading is constant over the year, and that the entire quantity $V(n)$ for year n is consumed within the following year. Thus, the daily quantity of nitrogen spread in the compound subsystem from day $nT+\tau+1$ to day $(n+1)T+\tau$ is given by $\frac{\lambda_v V(n)}{T}$.

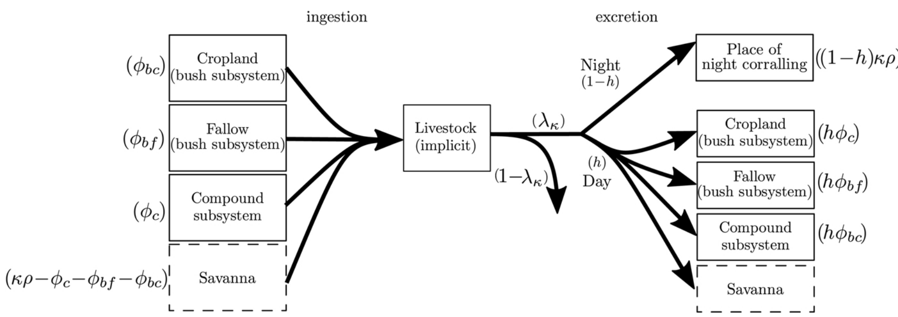

Fig. 2. Representation of livestock-induced nitrogen fluxes. For the sake of simplicity, only one cropland subunit and one fallow subunit of the bush subsystem are represented. The place of night corralling is the fallow during the wet season or the compound subsystem during the dry season.

2.3.2. Livestock-driven fluxes

We assume that livestock grazing follows a Monod function characterized by the half-saturation constant for feed ingestion κ_κ (in kgN ha^{-1}) and a maximal grazing rate $g_{\max}$ (in day^{-1}). A herd of κ TLU (TLU stands for Tropical Livestock Unit, corresponding to an average animal of 250 kg of live weight) that graze on a field containing P kgN ha^{-1} of palatable plant will ingest $g_{\max}\frac{P}{\kappa_\kappa + P}\kappa\psi$ kgN per day, where ψ is the quantity of nitrogen (in kgN) per TLU that we assume constant.

The quantity of nitrogen ingested by livestock per day in each subsystem will finally depend on the season, the subsystem, the area of the subsystem, the available plant biomass, the palatability coefficient of the plants, the time spent in the subsystem, the half-saturation Monod constant κ_κ for feed ingestion and the maximal grazing rate $g_{\max}$.

During the wet season the livestock is kept away from crops, graze in fallows and in the savanna and is corralled at night in fallows. The quantity of nitrogen ingested by the livestock per day in the fallow is therefore given by $\zeta_{\text{wet}} g_{\max}\frac{b_{\text{bf}}P_{\text{bf}}}{\kappa_\kappa + b_{\text{bf}}P_{\text{bf}}}\kappa\psi$ (in kgN day^{-1}) where ζ_{wet} is the percentage of time spend by the livestock in fallows, the other part of the day being spent in savanna or corresponding to the night, and b_{bf} is the palatability coefficient of the fallow plants. In this quantity, the part coming from the fallow subunit j of the bush ring is given by:

$$\phi_{\text{wet}}^j = \zeta_{\text{wet}} g_{\max}\frac{b_{\text{bf}}\frac{1}{L_f}P_j}{\kappa_\kappa + b_{\text{bf}}P_{\text{bf}}}\kappa\psi \text{ kgNday}^{-1} \tag{5}$$

During the dry season the livestock grazes all over the landscape, and is corralled in the compound subsystem at night. The concentration of nitrogen contained in the palatable plants in the bush and compound rings, that we denote P_{tot}, is given by:

$$P_{\text{tot}} = \frac{\frac{L_f}{L}\alpha_b b_{\text{bf}}P_{\text{bf}} + \frac{L_c}{L}\alpha_b b_{\text{bc}}P_{\text{bc}} + \alpha_c b_c P_c}{\alpha_b + \alpha_c} \quad \text{kgN} \quad (\text{ha of bush + compound})^{-1} \tag{6}$$

where b_{bc} and b_{bf} are the palatability coefficients of the plants in the cropland part of the bush ring and in the compound ring, respectively. The quantity of nitrogen ingested by the livestock per day in the bush and compound rings is therefore given by $\zeta_{\text{dry}} g_{\max}\frac{P_{\text{tot}}}{\kappa_\kappa + P_{\text{tot}}}\kappa\psi$ (in kgN day^{-1}) where ζ_{dry} is the percentage of time spend by the livestock on the bush and compound rings, the other part being spend in savanna or corresponding to the night. In this quantity, the part coming from the compound subsystem is:

$$\phi_{\text{dry}}^c = \zeta_{\text{dry}} g_{\max}\frac{\frac{\alpha_c b_c P_c}{\alpha_b + \alpha_c}}{\kappa_\kappa + P_{\text{tot}}}\kappa\psi \quad \text{kgNday}^{-1} \tag{7}$$

and the part coming from the subunit j (cropland or fallow) of the bush subsystem is:

$$\phi_{\text{dry}}^j = \zeta_{\text{dry}} g_{\max}\frac{\frac{1}{L}\frac{\alpha_b b_j P_j}{\alpha_b + \alpha_c}}{\kappa_\kappa + P_{\text{tot}}}\kappa\psi \quad \text{kgNday}^{-1} \tag{8}$$

with $b_j = b_{bc}$ for a cropland subunit j of the bush subsystem and $b_j = b_{bf}$ for a fallow subunit j of the bush subsystem. We assume that feed requirements of livestock is always met and remain constant over time. Hence, a fixed *per-capita* quantity ρ of nitrogen has to be ingested daily (in kgN TLU^{-1} day^{-1}), which amounts to a total quantity $\kappa\rho$ (in kgN day^{-1}).

The savanna is a feed reservoir exploited only when cultivated areas cannot fulfil livestock requirements. In this case, the complement of feed provided by the savanna is given by $\kappa\rho - \sum_{j=1}^{L}(1-\theta_j)\phi_{\text{wet}}^j$ (in kgN day^{-1}) during the wet season and by $\kappa\rho - \phi_{\text{dry}}^c - \sum_{j=1}^{L}\phi_{\text{dry}}^j$ (in kgN day^{-1}) during the dry season, where $\theta_j = 1$ when the subunit j is under cropping and $\theta_j = 0$ when the subunit j is under fallowing. The presence of livestock in the agro-ecosystem induces additional losses due to metabolic constraints: a percentage λ_κ of the feed ingested is excreted, the rest being used for growth and reproduction. We assume that livestock biomass is kept constant and that N allocated to growth and reproduction is exported outside the agro-ecosystem (for instance, through the sale of meat). A proportion ν of the excreted nitrogen returns to the soil as urine (compartment I); the remaining part $(1-\nu)$ returns to the soil as organic nitrogen (compartment O) through the deposition of faeces. Overall, livestock transfers nitrogen from savanna to the bush subsystem during the wet season, and to the compound subsystem during the dry season. Animals feed exclusively during the day but excrete almost equally during day and night (Manlay et al., 2004c). Thus, night corralling generates a net transfer from feeding grounds to the corral. The parameter h represents the proportion of excretion that occurs during the day, when livestock is grazing, and $(1-h)$ is the proportion of excretion that occurs during the night, when livestock is corralled. Consequently, the quantity of nitrogen excreted during one day in a subsystem (or subunit j of a subsystem) only depends on the quantity ϕ of nitrogen ingested during this day in this subsystem (or subunit j of a subsystem): it equals $h\lambda_\kappa\phi$ (in kgN day^{-1}). During the night, the quantity of nitrogen excreted in the corral (fallow during the wet season and compound during the dry season) is constant and equals $(1-h)\lambda_\kappa\kappa\rho$ (in kgN day^{-1}). See Fig. 2 for a schematic representation of livestock-induced nitrogen fluxes.

2.3.3. Fallow-cropland shifts

Fallow-cropland shifts occur at the beginning of the wet season, at time nT. These shifts do not lead to spatial transfers of nutrients, but they change the distribution of nitrogen among the compartments of the bush subsystem. When shifting from fallow to cropland, the compartment R of the concerned bush subunit is updated at the beginning of the wet season to account for the transfer of the roots of senescent fallow biomass to soil organic matter. Plant stems are cleared and exported outside the agro-ecosystem before the sowing and the woody part of the roots (percentage δ) of fallow biomass is transferred to the dead roots compartment R:

$$R_j(\text{nT}) = R_j(\text{nT}^-) + \delta P_j(\text{nT}^-) \tag{9}$$

where nT^- is the time just before nT, at the end of the dry season, before the sowing and the fallow clearing. We assume that R decays exponentially (Manlay et al., 2004c) at rate *r* and fuels the soil organic matter compartment *O* during the years following the shift. According to Manlay et al. (2004c), more than 95% of dead woody roots are degraded after two years.

2.4. Validation of the model

The comparison to Sare Yero Bana data is described in Appendix 4. The effect of each parameter of the model on the bush, the compound and the total crop productions was examined through a sensivity analysis, described in Appendix 5.

3. Simulations

Crop production depends on available nitrogen. According to the meta-ecosystem theory (Gravel et al., 2010; Loreau et al., 2003), crop production should depend on net inputs of nitrogen into the agro-ecosystem, and on how these inputs are transferred to the subsystems that produce crop. Thus, to identify strategies optimizing crop production, we first need to understand what governs the intensity of the nitrogen inputs into the agro-ecosystem, and then, how these fluxes to cropland subunits and to the compound subsystem are implemented.

3.1. The “Fallow Pump” and the “Livestock Pump” as the two main sources of nitrogen.

Two “ecological pumps”, resulting from source-sink dynamics within the agro-ecosystem should have a major influence on the input of nitrogen to the agro-ecosystem, namely the “Fallow Pump” and the “Livestock Pump” (Fig. 3). These terminologies are used by reference to the “whale pump” that brings nutrients from deep to shallower waters in the oceans (Roman and McCarthy, 2010).

Fallow land is a source of nitrogen for the bush subsystem because it hosts N_2-fixing legumes. In addition, fallow efficiently retains soil inorganic nitrogen because leaching is lower than in other subsystems, due to a higher soil cover by plant biomass (Pieri, 1992; Serpantié and Ouattara, 2001). Therefore, fallow subunits accumulate nitrogen, which is then transferred to cropland subunits when fallow subunits are cleared and cultivated. This net input of nitrogen to the agro-ecosystem is referred to as the “Fallow Pump”. On the other hand, livestock transfers nitrogen from grazed savanna, to the bush and compound subsystems, where it is corralled overnight. This overall input of nitrogen to the agro-ecosystem is referred to as the “Livestock Pump”.

Fallow and livestock management drive how these two pumps influence the overall input conservation of nitrogen in the agro-ecosystem (Fig. 3). In addition, within the agro-ecosystem, livestock management influences how nitrogen is transferred to subsystems producing crop. Indeed, through grazing and night corralling, animals generate source-sink dynamics between fallow subunits and crop fields subunits within the bush subsystem, and between the bush subsystem and the compound subsystem. These source-sink dynamics vary across seasons.

We first studied the system in absence of livestock to understand how to optimize crop production with the Fallow Pump alone. Then, we studied the system in presence of livestock, to understand the effect of the Livestock Pump, the effect of the source-sink dynamics due to livestock, and the interaction between the Fallow and the Livestock Pumps.

3.2. Test of the effect of the pumps

We performed two distinct studies. For all the simulations, we assumed that the total area of the agro-ecosystem was constant and equal

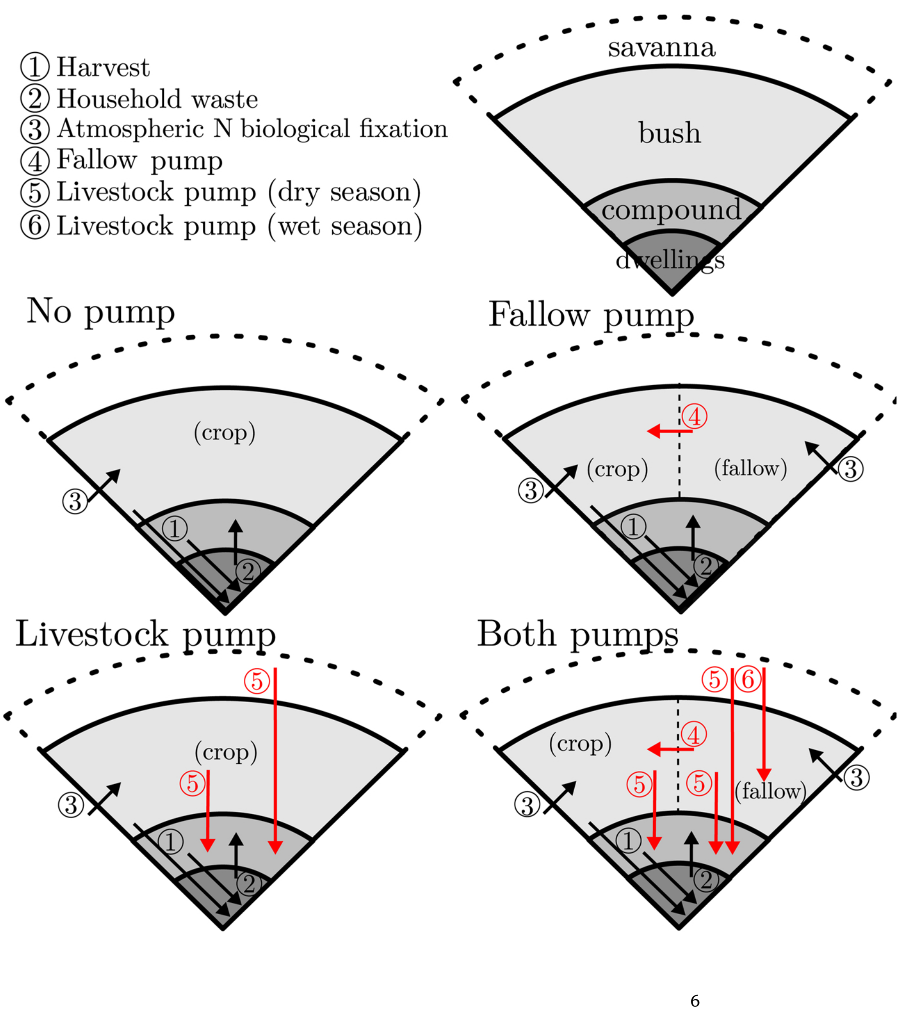

Fig. 3. Representation of the fluxes occurring between the rings depending on agricultural practices and livestock management. From top to bottom, left to right, without Fallow and Livestock Pumps, with Fallow but no Livestock, with Livestock and no Fallow, with both Fallow and Livestock Pump. The arrows in red represent fluxes due to pumps.

to 200 ha, which is roughly the size of the agro-ecosystem of Sare Yero Bana. This surface does not include the surrounding savanna, which is assumed to be infinite. We performed simulations with and without ($\kappa = 0$ TLU) livestock. Simulations with livestock were run with $\kappa = 410$ TLU, which is consistent with the herbivory pressure observed in Sare Yero Bana (Vigan, 2013). The first study we performed focuses on the impact of the fallow extent on the biomass of crop harvested at the end of the wet season in the bush and the compound subsystems. More precisely, we tried to assess the consequences of (1) an increase in the duration of rotation (L = 10, 20, 50 and 100 years), and of (2) an increase in the cropland ratio ($0 \leq \frac{L_c}{L} \leq 1$). For this first study, we assumed a constant ratio $\alpha_c : \alpha_b$ of 1:3, 50 ha of compound and 150 ha of bush, as observed recently in Sare Yero Bana by Vigan (2013).

In a second study, we examined how the fraction of the agro-ecosystem occupied by the compound subsystem $\frac{\alpha_c}{(\alpha_c + \alpha_b)}$, hereafter named the "compound ratio", influences the biomass of crop harvested at the end of the wet season in the bush and the compound subsystems, fallow extent being fixed. There is no variation in spatial organization and practices within one simulation.

Simulations were performed with R (R Core Team, 2016) by using the Runge-Kutta method of the R package "deSolve" (Soetaert et al., 2010) that enables to numerically integrate systems of ordinary differential equations. Each simulation (one simulation per set of parameters tested) was performed over 300 years, which was enough to reach the periodic equilibrium of the system. The R package containing all the necessary functions to simulate the model is available on github (https://github.com/AnneBisson/EwocR_2.git).

4. Results and discussion

4.1. Managing the Fallow Pump to maximize crop production: the effect of cropland ratio and rotation duration

Fig. 4a depicts the impact of the cropland ratio $\frac{L_c}{L}$ and the rotation duration L (the colour of the line varies from light to dark as the rotation duration L increases) on crop production in the bush subsystem (i.e. the sum of crop production in all the cropland subunits of the bush subsystem), in absence of livestock. Both affect the Fallow Pump and its effect on crop production in the bush subsystem, with consequences for crop production in the compound subsystem.

Regardless of the rotation duration, when the cropland ratio increases from 0 to 1, crop production in the bush subsystem increases from 0 to a maximum π_{max}, then decreases and finally slightly re-increases when the cropland ratio reaches 1.

The humpback shape of the curves is consistent with previous results obtained with a simpler mathematical model by Robertson (1994) and Mobbs and Cannell (1995) in their study of a generic *Sorghum bicolor Acacia Senegal* agro-system. In our model, as in the model of the latter, this humpback curve results from a trade-off between the increase in crop production due to the increase in the cultivated area, and the decrease of the restoration of soil fertility by fallow. Indeed, as the cropland ratio increases, the cultivated area increases, entailing an increase in crop production. However, the decrease of fallow leads to a loss of fertility that translates into lower yields, which finally leads to a decrease of crop production at the subsystem level. In our model, the cropland ratio that leads to π_{max} varies with the rotation duration, with the overall maximal production (3233 kgN yr^{-1}) reached for a rotation duration of 50 years and a cropland ratio of 0.67. The observation of a crop production without fallow higher than with few years of fallow suggests that short fallow time does not restore soil fertility enough in terms of nitrogen stock to compensate for the cropping area reduction it demands. This trend is consistent with other studies (Aweto, 1981; Brand and Pfund, 1998; Roder et al., 1997); it is even an assumption in some fallow models (Aweto, 2012). In the first years of fallow, soil fertility decline is usually thought to result from an inadequate vegetation cover during the early succession of natural vegetation recovery, but the model suggests an alternative explanation. In simulations, the inflection results from slow restoration of the soil organic nitrogen stock during the very first years of fallowing and to a much lower growth rate of fallow than cropped plants (0.005 and 0.01 ha kgN^{-1} y^{-1}, respectively). As a result, the net balance of nitrogen after a short fallow time is negative: the impact of the Fallow Pump is thus negative. According to our simulations, the number of years of fallow (4 years) beyond

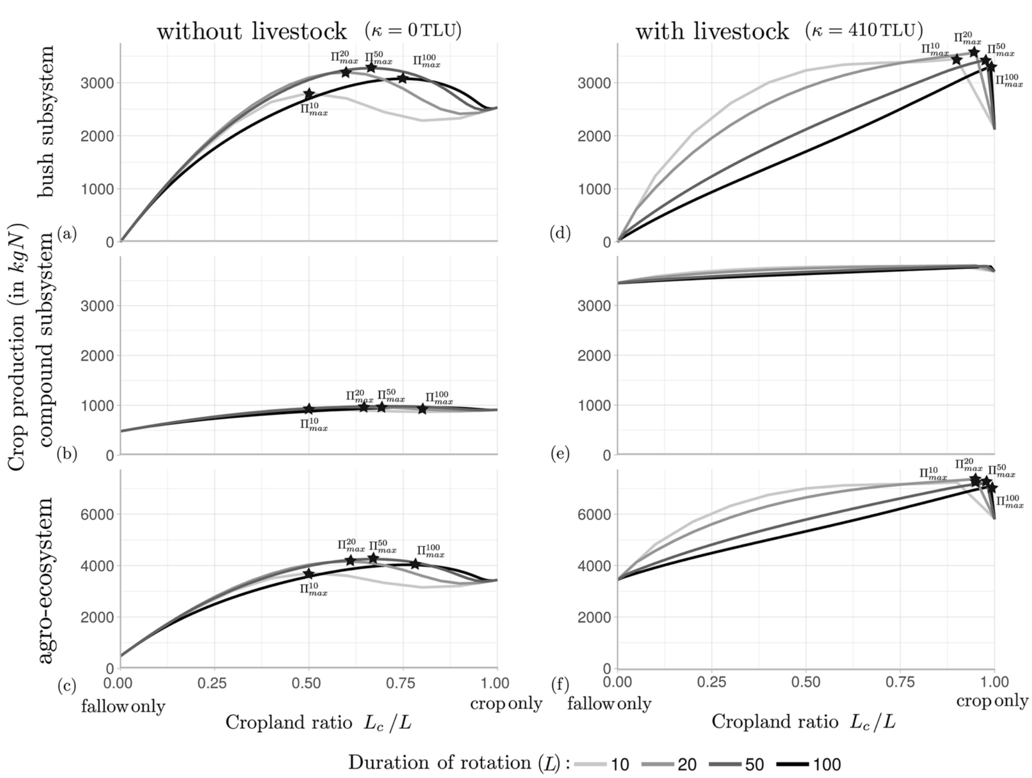

Fig. 4. Crop production (in kgN) in the bush subsystem, the compound subsystem and the whole agro-ecosystem for different rotation durations and cropland ratios without (a, b and c) and with (d, e and f) livestock ($\kappa = 410$ TLU) and for a compound and bush subsystems area of 50 and 150 ha, respectively. The colour of the line varies frop light to dark as the duration L increases. Each line results from several simulations with different cropland ratios but a same rotation duration after 300 years of simulations. Black stars point the scenario where the maximal bush production Π_{max} is reached for each duration of rotation (10, 20, 50 and 100 years). The cropland ratio $\frac{L_c}{L}$ represents the ratio of crop duration over rotation duration. It varies from 0 (all bush subunits are fallow) to 1 (all bush subunits are crop).

which fallow has a positive impact on productivity is independent of the rotation duration (Fig. 4a). On the other hand, if the fallow period is long enough, dead-roots (R) and soil organic matter (O) accumulations reach a maximum. Once this maximum is reached, from a biogeochemical point of view it is no more profitable to maintain fallowing.

The comparison between curves of Fig. 4a shows that the cropland ratio leading to the maximal crop production π_{max} increases with the rotation duration. Among the different rotation duration scenarios, the highest crop production is reached for an intermediate rotation duration π^{50}_{max}. This is because crop production is driven by the combination of two mechanisms. First, for short rotation durations, fallow duration is too short to restore soil fertility. Second, for long rotation durations, large accretion in soil organic and mineral nitrogen during prolonged fallowing does not balance declining yields at the end of longer cropping periods. For a given cropland ratio indeed, a longer rotation duration translates into longer cropping duration and not just longer fallow duration.

Fig. 4b-c shows that the increase in crop production in the compound subsystem and in the agro-ecosystem as the whole is correlated to the increase in crop production in the bush subsystem. Indeed, the redistribution of fertilizing household wastes to the compound subsystem generates a source-sink dynamics from the bush to the compound subsystem, because part of these wastes comes from crop production in the bush subsystem. As a consequence of this simple source-sink dynamics, the trends observed in the compound subsystem (Fig. 4b) and in the whole agro-ecosystem (Fig. 4c) are similar to the trends observed in the bush subsystem (Fig. 4a).

Fig. 5 represents the balance of N fluxes (in kgN ha^{-1} y^{-1}) of the compound subsystem and the bush subsystem (crops and fallow) over the last year of a 300 years simulation without (0 TLU) and with (410 TLU) livestock for three cases of the simulations represented in Fig. 4, corresponding to a cropland ratio $\frac{L_c}{L}$ = 0.25, 0.5 and 0.75, respectively. Without livestock, biological fixation represents the main source of nitrogen for the agro-ecosystem. Looking at the three detailed cases, N fixation decreases in cropland subunits as the cropland ratio increases. On the other hand N fixation in fallows is maximal for an intermediate value of cropland ratio ($\frac{L_c}{L}$ = 0.5).

4.2. Managing the Livestock Pump to maximize crop production

Fig. 4d-f depicts the impact of increasing the cropland ratio $\frac{L_c}{L}$ and the rotation duration L on crop production in the bush subsystem, in the compound subsystem, and in the whole agro-ecosystem, respectively, in the presence of livestock.

The activation of the Livestock Pump strongly modifies the functioning of the agro-ecosystem. Strikingly, crop production of the whole agro-ecosystem increases sharply (Fig. 4f), mainly driven by the increase in crop production in the compound subsystem (Fig. 4e). This gain of production highlights the Livestock Pump as the main importer of nitrogen to the agro-ecosystem, through a source-sink dynamics from the savanna to the compound ring. In addition, within the agro-ecosystem, livestock generates source-sink dynamics between the subunits of the bush subsystem, and between the bush and the compound subsystems. These dynamics strongly affect the way the gain in nitrogen from the Livestock Pump is transferred to crop production in the compound subsystem.

During the wet season, livestock mainly grazes in the savanna and is corralled at night in the fallow subunits where it does not graze and where it excretes some of the nitrogen ingested during the day. Hence, the Livestock Pump fuels the fallow subunits only. The gain of nitrogen adds up to the Fallow Pump and is transferred to the cropland subunits and crop production when fallow subunits are cleared and cultivated. During the dry season, the situation drastically changes. Livestock grazes both in the savanna and in the agro-ecosystem and is corralled at night in the compound subsystem, where it excretes nitrogen. Hence, the Livestock Pump fuels the compound subsystem. The variation of range in N balance (Fig. 5) in the compound ring shows how the inputs of N by livestock leads to significant losses of N.

The Livestock Pump has a positive effect on crop production in the compound subsystem (Fig. 4e). However, it may or may not have a positive effect on crop production in the bush subsystem, depending on the management of the Fallow Pump (Fig. 4d). In the case of short rotation durations ($\leq$ 20 years, see Appendix 4) the Livestock Pump has a positive effect on the stock of nitrogen in the fallow subunits, regardless of the cropland ratio $\frac{L_c}{L}$. Through fallow to cropland conversion, this fertility is transferred to the cropland subunits and increases crop production in the bush subsystem.

On the other hand, for longer rotation durations, the Livestock Pump has a positive effect on crop production of bush subsystem only for high cropland ratios (e.g., $\frac{L_c}{L} > 0.8$ for $L = 100$ years, as depicted in Fig. 4). The reason is that for lower cropland ratios, the quantity of feed provided by fallow covers a large part of the requirement of livestock during the dry season. Therefore, livestock mostly grazes in the bush subsystem and transfers the ingested nitrogen to the compound

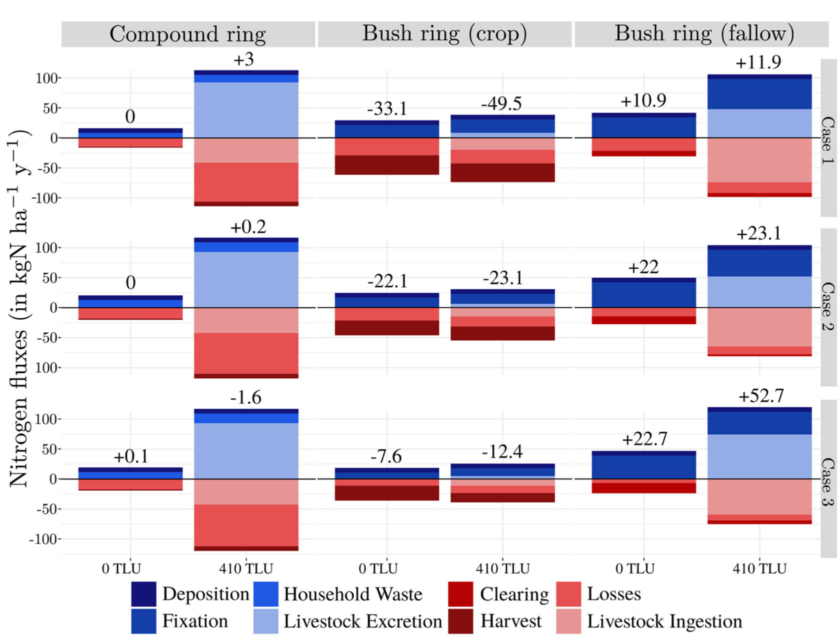

Fig. 5. Balance of N fluxes (in kgN ha^{-1} y^{-1}) at the scale of the compound subsystem, bush subsystem (crops and fallow) over the last year of a 300 years simulation without (0 TLU) and with livestock (410 TLU). The number above each histogram indicates the balance. In these simulations, total bush and compound areas are 150 and 50 ha, respectively. The duration of a rotation is 20 years, which corresponds to 20 plots; results in bush subsystems (cropland and fallow) are a mean of plot in cropland and fallow, respectively. Three cases are simulated with a different duration of cropping (5, 10 and 15 years, respectively). Data from this figure are available in Appendices 4 and 5 .

subsystem during night corralling. This mechanism has two main effects, (1) it weakens the Livestock Pump since there is less transfer from savanna to the agro-ecosystem during the dry season, and (2) it increases the source-sink dynamics from the bush to the compound subsystem. As a result, crop production in the bush subsystem is lower in the presence than in the absence of livestock.

With livestock, the maximum crop production is always reached for $L_c = L - 1$, which corresponds to the shortest possible fallow ratio. Fallows must at least exist in its minimum form to allow livestock corralling and the functioning of the Livestock Pump. As a result, the negative effect of too short fallow without livestock is no longer observed because in addition to the weak effect of restoring fertility, livestock corralling in fallows during the wet season concentrates nutrient in fallows. Finally, fallows tend to annihilate the Livestock Pump since the agro-ecosystem is less dependent on nutrients from the savanna.

4.3. Managing spatial organization to maximize crop production

The connectivity introduced by livestock between the bush and the compound subsystems leads to an interdependency of these two compartments of the landscape. Given this interdependency, crop production of the whole agro-ecosystem is expected to depend on the fraction of the whole agro-ecosystem occupied by the compound subsystem referred to hereafter as the "compound ratio". The influence of the compound ratio on crop yield (in kgN ha^{-1}) and total crop production (in kgN) in each subsystem and at the whole agro-ecosystem level is examined (Fig. 6), in presence of livestock. We assumed a rotation duration of 20 years, and a cropland ratio of 0.25, that is 5 years of cropland followed by 15 years of fallow. This scenario is similar to the situation in Sare Yero Bana (Manlay et al., 2004b,a).

For this scenario, both the yield and the total production follow a humpback curve when the compound ratio increases. The optimal total production is obtained for a compound ratio of 0.3, whereas the optimal yield is obtained for a compound ratio of 0.25. This mismatch results from the fact that sub-optimality of the yield when the ratio increases is overbalanced by the increase in total cropland area, which increases the production at the agro-ecosystem level. In fact, increasing the compound ratio has both a positive and negative effect on the total production. The positive effect arises from the increase in the area devoted to crop production. The negative impact results from the dilution of the source-sink effect: when the compound ratio increases, the source (the bush subsystem) decreases and the sink (the cropland subsystem) increases in size. Therefore, the flux of nitrogen imported by livestock from bush to cropland decreases and is diluted over an increasing area of cropland.

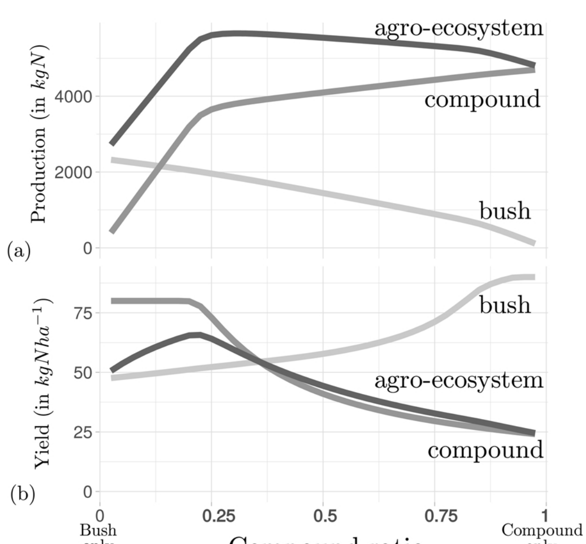

Fig. 6. Crop production (in kgN) and crop yield (in kgN ha^{-1}) in bush and compound subsystems and in the whole agro-ecosystem as a function of the share of the compound subsystem in the whole agro-ecosystem. Each line results from several simulations with different cropland ratios but a same rotation duration after 300 years of simulations. The size of livestock is 410 TLU for an agro-ecosystem of 200 ha.

4.4. The hidden gain from savanna

In the model, a fraction of the nitrogen ingested by livestock exits the agro-ecosystem through meat exportation. Over a year, livestock intakes 14.9 tN (the quantity of nitrogen ingested by 410 TLU, that is $\rho\kappa T$) and excretes 11.9 tN trough urine and faeces ($\lambda_\kappa \rho\kappa T$). A fraction of the consumed nitrogen comes from the fallow subunits of the bush subsystem where livestock grazes during the dry season, the rest coming from the savanna. The proportion of time spent feeding in the fallow versus the savanna determines the respective contribution of these two sources. Our model assumes that livestock always fulfils its nitrogen requirement. It first consumes what is available in the agro-ecosystem, then satisfies its nitrogen requirements with nitrogen from the savanna. Thus, if the cropland ratio increases within the bush subsystem and/or if the compound ratio increases, the area of land occupied by fallow decreases, entailing a higher contribution of savanna as a source of nitrogen. Assuming a herd of 410 TLU, for a cropland ratio of 0.25 and a rotation duration of 20 years, the savanna provides 50% of the nitrogen ingested by livestock (7045 kgN that represents about 1300 ha of savanna considering numbers given by Powell et al. (1996) for Sahelian areas or by Abbadie et al. (2006) for Lamto savanna). With the same rotation duration and a cropland ratio of 0.75, the savanna represents more than 70% of the nitrogen ingested by livestock, becoming the main source of nitrogen for the agro-ecosystem. This dependency on savanna raises the question of the sustainability of crop production in the agro-ecosystems of West Africa, where agriculture is encroaching on savanna. In this context, savanna area may become a limiting resource, constraining the size of livestock herds and thus, the net input of nitrogen to the agro-ecosystem (Vayssières et al., 2015). In addition to this decrease of the Livestock Pump, the agriculture evolution in a demographic growth context generally comes together with a shortening of the rotation duration and an increase in the cropland ratio, which reduces the N source provided by legumes in fallows, and thus, decreases the Fallow Pump. The reduction of N source could be offset by an increase of legume-cereal crop rotation or intercropping as it is the case in the groundnut basin. There is an other limit according to Liebig's law: the availability of P, which can only be increased by the application of mineral fertilizers, or by the possible (but not yet certain) increase of P by the deep root systems of the trees (need for agroforestry). Some farmers facing such a reduction of accessible savanna manage to maintain large herds of livestock by feeding animals with exogenous supplementation (Audouin et al., 2015). Doing so, they maintain the Livestock Pump, but they replace economical and ecological costless nitrogen provided by savanna by economical and ecological costly nitrogen.

To take into account this cost, our modelling work calls for an explicit representation of the savanna as a finite source of nitrogen, and an explicit representation of the dynamics of nitrogen in livestock. Such improvement would allow (1) assessing whether the nutrient provisioning by savanna is sustainable or not, (2) measuring the livestock production and its possible limitations due to nutrient availability, and (3) exploring the potential of other sources of nitrogen such as mineral fertilizers to improve the agro-ecosystem production. Unlike for traditional agro-ecosystems where savanna is not limiting, we hypothesize that in agro-ecosystems with increasingly limited land in the future (Jayne et al., 2014), new tensions and new trade-offs occur between crop production in the bush versus compound subsystems, and between meat and crop productions. Such situations are likely to occur more often as local human population densities increase, with a subsequent increasing need for croplands.

5. Conclusion

Crop production in WAMFS depends on complex dynamics of nitrogen through the different compartments of the agricultural landscape. Despite this complexity, our model, with its “meta-ecosystem” approach, shows that the optimization of crop production relies mainly on a good management of the Fallow Pump and the Livestock Pump that represent the main inputs of nitrogen into the agro-ecosystem. Management must take into account the interaction between these two ecological pumps to optimize the global input of nitrogen, as well as the role of the livestock as a driving-force to optimize the transfer of this nitrogen flux to the agro-ecosystem's subsystems that produce crop.

More precisely, our results suggest that the Livestock Pump represents a higher input of nitrogen to the agro-ecosystem than the Fallow Pump, and that the Fallow Pump tends to interact negatively with the Livestock Pump. Thus, crop production is optimal when agricultural practices and spatial organizations are such that the agro-ecosystem contains livestock and has a relatively low area devoted to fallow.

In addition, our results stress the fact that livestock reinforces the source-sink dynamics between the bush and compound subsystems, that is, between the extensive and intensive part of the agro-ecosystem. This source-sink dynamics is required to transfer the benefit of the Fallow Pump to the productive compound subsystem.

A corollary to these results is that crop production by WAMFS is highly dependent on the Livestock Pump and therefore on the savanna as an external source of nitrogen. The optimal practices suggested by our model hold as long as savanna extension is enough not to be a limiting source of nitrogen to livestock. This assumption was likely relevant in traditional WAMFS, but it should be reconsidered in the context of agriculture extensification where cropland is encroaching on savanna. In this new context, our model could be regarded as a “null model”. This null model could serve as a corner stone to help understand how fertility transfers will evolve according to new management strategies and spatial organization, and to help propose new management practices that will ease the transition towards a more sustainable agriculture.

Acknowledgements

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Appendices

A.1 Table of variables

Table 2

Within the bush subsystem, the mean biomass of fallow plants (in kgN per hectare of fallow) is expressed by

$$P_{\text{bf}} = \frac{1}{L_f}\sum_{j=1}^{L} P_j(1-\theta_j) \quad \text{kgN (ha of fallow)}^{-1} \tag{10}$$

and the mean biomass of crop plants (in kgN per hectare of bush crop) is

$$P_{\text{bc}} = \frac{1}{L_c}\sum_{j=1}^{L} P_j\theta_j \quad \text{kgN(ha of bush crop)}^{-1} \tag{11}$$

Table 2
Variables used in the model. E.v. is for Estimated value.

Variable	Eq.	Unit	Description
P		kgN ha^{-1}	Quantity of N contained in the plant biomass per hectare of a generic subsystem
O		kgN ha^{-1}	Quantity of N contained in the soil organic fraction per hectare of a generic subsystem
I		kgN ha^{-1}	Quantity of N contained in the soil inorganic fraction per hectare of a generic subsystem
R		kgN ha^{-1}	Quantity of N contained in the dad roots of woody plants per hectare of a generic subsystem
X_c		kgN (ha of c)$^{-1}$	Quantity of N contained in the stock X, with $X \in P, O, I$, per hectare of compound ring
X_j		kgN (ha of b unit j)$^{-1}$	Quantity of N contained in the stock X, with $X \in P, O, I, R$, per hectare of subunit j of the bush ring
P_{bf}	(10)	kgN (ha of bf)$^{-1}$	Quantity of N contained in the plant biomass per hectare of bush fallow
P_{bc}	(11)	kgN (ha of bc)$^{-1}$	Quantity of N contained in the plant biomass per hectare of bush crop
P_{tot}	(6)	kgN (ha of b and c)$^{-1}$	Quantity of N contained in the palatable plants per hectare of bush + compound ring
θ_j		-	Current state of the subunit j of the bush ring: $\theta_j(t)=1$ means that the subunit j is under cropping at time t, $\theta_j(t)=0$ means that the subunit j is under fallowing at time t.
K_j	(3)	kgN (ha of b unit j)$^{-1}$	Carrying capacity of the subunit j of the bush ring
G	(1)	kgN ha^{-1} day^{-1}	Growth function of the plant compartment P through the uptake of inorganic N
F	(2)	kgN ha^{-1} day^{-1}	Growth function of the plant compartment P through the atmospheric N biological fixation
ϕ		kgN day^{-1}	Quantity of N ingested by the livestock per day in a generic subsystem
ϕ_{wet}^j	(5)	kgN day^{-1}	Quantity of N ingested by the livestock per day in a subunit j of the bush ring during the wet season
ϕ_{dry}^j	(8)	kgN day^{-1}	Quantity of N ingested by the livestock per day in a subunit j of the bush ring during the dry season
ϕ_{dry}^c	(7)	kgN day^{-1}	Quantity of N ingested by the livestock per day in a the compound ring during the dry season
$V(n)$	(4)	kgN	Quantity of crop N brought back to the dwellings after the harvest of a year n

A.2 Table of parameters

Table 3

Table 3
Parameters used in the model. E.v. is for Estimated value. AS is for Sensitivity Analysis.

Param.	Value	Range (AS)	Dimensions	Description and source
u_c	$5\,10^{-3}$	0.0035–0.0065	ha kgN^{-1} day^{-1}	Rate of mineral N uptake by Plant in compound subsystem – E.v.
K_c	80	56–104	kgN ha^{-1}	Carrying capacity (cereals) – Manlay et al. (2002)
c_c	0.01	0.007–0.013	day^{-1}	Decomposition rate of crop residues – E.v.
m_c	$1\,10^{-4}$	$7\,10^{-5}$–0.00013	day^{-1}	Mineralization rate by microorganisms – E.v.
e_{oc}	$2\,10^{-4}$	0.00014–0.00026	day^{-1}	Organic N loss rate – Pieri (1992)
e_{nc}	0.003	0.0056–0.0104	day^{-1}	Mineral N loss rate – Pieri (1992)
u_{bc}	0.01	0.0035–0.0065	ha kgN^{-1} day^{-1}	Rate of mineral N uptake by plants in cropland subunits of bush subsystem – E.v.
$K_{\max}$	90	63–117	kgN ha^{-1}	Maximum Groundnut carrying capacity – Manlay et al. (2002)
ω	2.5	1–5	–	constant parameter in the expression of $K_{\max}$ – E.v.
i_{pbc}	$2\,10^{-2}$	0.014–0.026	day^{-1}	Biological N fixation by groundnut–Ndiaye (1986)
c_{bc}	$1\,10^{-2}$	0.007–0.013	day^{-1}	Decomposition rate of crop residues – E.v.
m_{bc}	$1\,10^{-4}$	$7\,10^{-5}$–$1.3\,10^{-4}$	day^{-1}	Mineralization rate by microorganisms – E.v.
e_{obc}	$2\,10^{-4}$	0.00014–0.00026	day^{-1}	Organic N loss rate –Pieri (1992)
e_{nbc}	$5\,10^{-3}$	0.0035–0.0065	day^{-1}	Mineral N loss rate – Pieri (1992)
u_{bf}	$5\,10^{-5}$	0.0035–0.0065	ha kgN^{-1} day^{-1}	Rate of mineral N uptake by plants in fallow subunits of bush subsystem – E.v.
K_{bf}	350	245–455	kgN ha^{-1}	Carrying capacity (fallow) – Manlay et al. (2002)
i_{pbf}	$6\,10^{-4}$	0.0042–0.0078	day^{-1}	Biological N fixation by plants – Buerkert and Hiernaux (1998)
c_{bf}	$8\,10^{-4}$	0.00056–0.00104	day^{-1}	Plant mortality during dry season – Buerkert and Hiernaux (1998)
m_{bf}	$1\,10^{-4}$	10^{-5}–0.00013	day^{-1}	Mineralization rate by microorganisms – E.v.
e_{obf}	$2\,10^{-4}$	0.00014–0.00026	day^{-1}	Organic N loss rate – Buerkert and Hiernaux (1998)
e_{nbf}	$1\,10^{-3}$	0.0007–0.0013	day^{-1}	Mineral N loss rate – Buerkert and Hiernaux (1998)
λ_κ	80	60–95	%	Percent of N intake excreted by livestock – Manlay et al. (2004b)
κ	410	0–1000	TLU	Size of livestock – Manlay et al. (2004a)
ψ	8	–	kgN TLU^{-1}	Quantity of N per TLU – Guerin and Roose (2015)
ν	0.5	0–1		Fraction of N excreted as urine – De Leeuw and Tothill (1911), Buerkert and Hiernaux (1998)
h	53	45–65	%	Percent of N excreted by livestock during day – Manlay et al. (2004b)
ρ	0.1	0.07–0.13	kgN TLU^{-1} day^{-1}	Feed Requirements – De Leeuw and Tothill (1911)
K_κ	30	21–39	kgN ha^{-1}	Monod constant demi-saturation – E.v.
$g_{\max}$	0.5	–	day^{-1}	Maximal grazing rate of the livestock – E.v.
ζ_{dry}	0.4	0.3–0.5	%	Percentage of time spend by the livestock on the bush and compound rings during the dry season, the other part being spend in savanna or corresponding to the night –E.v.
ζ_{wet}	0.2	0.15–0.25	%	Percentage of time spend by the livestock on fallows during the wet season, the other part of the day being spend in savanna or corresponding to the night – E.v.
b_c	1	0.7–1.3	–	Plant "palatability" in compound subsystem – E.v.
b_{bf}	1	0.7–1.3	–	Plant "palatability" in fallow subunits (bush subsystem) – E.v.
b_{bc}	0.08	0.0056–0.0104	–	Plant "palatability" in cropland subunits (bush subsystem) – E.v.
i_n	0.02	0.014–0.026	kgN ha^{-1} day^{-1}	Mineral N deposition (dry and wet) – Buerkert and Hiernaux (1998), Delon et al. (2010)
i_o	0.001	0.0007–0.0013	kgN ha^{-1} day^{-1}	Organic N deposition (dry and wet) – Buerkert and Hiernaux (1998), Delon et al. (2010)
d	0.0027	0.00189–0.00351	day^{-1}	Post-fallow decomposition of woody roots – Manlay et al. (2004b)
σ	1	–	kgN ha^{-1}	Sowing density – E.v.
λ_V	70	0–100	%	Recycling of household waste by village – Manlay et al. (2004b)
γ_c	10	0–100	%	Harvest – Manlay et al. (2004b)
γ_{bc}	60	0–100	%	Harvest – Manlay et al. (2004b)
δ	0.5		–	Fraction of roots from tree species in fallow plots – Manlay et al. (2004c)
ϵ	55	%	%	Harvest exported out of village – Manlay et al. (2004b)
α_b	150	0- 200	ha	Area of Bush subsystem – Manlay et al. (2004b)
α_c	50	200–a_b	ha	Area of Compound subsystem –Manlay et al. (2004b)
T	365	–	day	Number of days per annual cycle
τ	120	–	day	Number of days in the wet season
n	–	–		Index of annual cycle, number of the current year
nT^-	–	–	day	Index of the day at the beginning of the wet season before the sowing and fallow clearing
nT	–	–	day	Index of the day at the beginning of the wet season after the sowing and fallow clearing
$nT+\tau^-$	–	–	day	Index of the day at the end of the dry season before the harvest
$nT+\tau$	–	–	day	Index of the day at the end of the dry season after the harvest
L	–	10–100	year	Duration of the Crop/Fallow rotation cycle and number of subunits in the bush ring
L_c	–	0–L	year	Duration of the cropping period and number of subunits in the bush ring that are in a state of cropland
L_f	–	0–L	year	Duration of the fallow period and number of subunits in the bush ring that are in a state of fallow

A.3 System of differential equations

All the parameters used in the model, their values, dimensions and their definitions are referenced in Appendix 2. Stocks and fluxes are expressed in kgN ha^{-1} and kgN ha^{-1} day^{-1}, respectively. The equations of the subsystems models for each season and transition event during a year n are presented hereafter.

A.3.1 Beginning of the wet season, shifts, sowing and carrying capacity: at time nT

The state shifts (from fallow to cropland subunit and conversely) and the sowing are discrete events that occur at time nT, at the beginning of the wet season. When they occur, the following variables are updated.

State shifts

Shifts from cropland to fallow:

$\theta_j(t) = 0, \quad \forall\ t \in [\mathrm{nT}, (n+1)T)$ if $\theta_j((n-1)T) = 1$ and $\theta_j((n-L_c)T = 1$

Shifts from fallow to cropland:

$\theta_j(t) = 1, \quad \forall\ t \in [\mathrm{nT}, (n+1)T)$ if $\theta_j((n-1)T) = 0$ and $\theta_j((n-L_c)T = 0$

In these cases, the root compartment R is also updated in the following way:

$R_j(\mathrm{nT}) = R_j(\mathrm{nT}) + \delta P_j(\mathrm{nT})$

where nT^- is the time just before nT, at the end of the dry season, before the sowing and the fallow clearing.

Sowing

In the compound and bush subsystems, the stock in the P compartment is initialized at a value σ (being the quantity of sown seeds expressed in kgN ha^{-1}), except for the fallow subunits of the bush subsystem that were already in the state of fallow the year before:

Compound subsytem: $P_c(nT) = \sigma,$

Cropland subunits of the Bush subsystem: $\mathrm{P}_j(nT) = \sigma, \quad \forall_j$ such that $\theta_j(nT) = 1,$

Fallow subunits of the Bush subsystem: $P_j(nT) = \sigma, \quad \forall_j$ such that $\theta_j(nT) = 0$ and $\theta_j((n-1)T) = 1.$

Carrying capacity

In the bush subsystem

$$K_j = \begin{cases} \min(\omega I_j(\mathrm{nT}, K_{\max}) & \text{if } \theta_j(\mathrm{nT}) = 1 \\ K_{\mathrm{bf}} \quad \text{if } \theta_j(\mathrm{nT}) = 0 \end{cases}$$

A.3.2 Wet season: from nT to nT + τ

In the compound subsystem:

$$\begin{cases} \frac{dP_c}{dt} = \underbrace{u_c \frac{K_c - P_c}{K_c} P_c I_c}_{\text{growth}} \\ \frac{dO_c}{dt} = \underbrace{-m_c O_c}_{\text{mineralization}} + \underbrace{i_o}_{\text{atmospheric deposition}} - \underbrace{e_{oc} O_c}_{\text{losses}} + \underbrace{\frac{\lambda_v}{\alpha_c T} V(n-1)}_{\text{recycling from dwellings}} \\ \frac{dI_c}{dt} = \underbrace{m_c O_c}_{\text{mineralization}} - \underbrace{u_c \frac{K_c - P_c}{K_c} P_c I_c}_{\text{uptake by P}} + \underbrace{i_n}_{\text{atmospheric deposition}} - \underbrace{e_{nc} I_c}_{\text{losses}} \end{cases} \tag{12}$$

In the bush subsystem, for each subunit j from 1 to L:

$$\begin{cases} \frac{dP_j}{dt} = \underbrace{u_j \frac{k_j - P_j}{k_j} P_j I_j}_{\text{growth}} + \underbrace{i_{pj} \frac{k_j - P_j}{k_j} P_j}_{\text{biological fixation}} - \underbrace{(1-\theta_j) \frac{L}{\alpha_b} \phi^j_{wet}}_{\text{grazing}} \\ \frac{dR_j}{dt} = - \underbrace{r R_j}_{\text{degradation of R}} \\ \frac{dO_j}{dt} = - \underbrace{m_j O_j}_{\text{mineralization}} + \underbrace{i_o}_{\text{atmospheric deposition}} - \underbrace{e_{oj} O_j}_{\text{losses}} + \underbrace{r R_j}_{\text{degradation of R}} + \\ \qquad \underbrace{(1-\theta_j)\lambda_\kappa (1-\nu) \left(h \frac{L}{\alpha_b} \phi^j_{wet} + (1-h)\kappa\rho \frac{L}{\alpha_b(L_f)} \right)}_{\text{excretion}} \\ \frac{dI_j}{dt} = \underbrace{m_j O_j}_{\text{mineralization}} - \underbrace{u_j \frac{K_j - P_j}{K_j} P_j I_j}_{\text{uptake by P}} + \underbrace{i_n}_{\text{atmospheric deposition}} - \underbrace{e_{nj} I_j}_{\text{losses}} + \\ \qquad \underbrace{(1-\theta_j)\lambda_\kappa \nu \left(h \frac{L}{\alpha_b} \phi^j_{wet} + (1-h)\kappa\rho \frac{L}{\alpha_b(L_f)} \right)}_{\text{excretion}} \end{cases} \tag{13}$$

Different values are assigned to the parameters u_j, K_j, i_{pj}, m_j, e_{oj} and e_{nj} depending on whether the subunit j is being cultivated during the current year or not.

$x_j = x_{bc}$ if the subunit j is cultivated or $x_j = x_{bf}$ if the subunit j lies in fallow (with $x = u$, K, i_p, m, e_o and e_n).

A.3.3 Harvest: at time $nT + \tau$

At harvest, the plant compartment of the cultivated part of the agro-ecosystem (in the compound and bush subsystems) are updated as follows:

$$\text{Compound subsystem: } P_c(nT + \tau) = (1 - \gamma_c)P_c(nT + \tau^-)$$

$$\text{Cropland subunits of Bush subsystem: } P_j(nT + \tau) = (1 - \gamma_{bc})P_j(nT + \tau^-), \quad \forall j \text{ such that } \theta_j = 1$$

where $nT + \tau^-$ is the time just before $nT + \tau$, at the end of the wet season, before the harvest. The quantity $V(n)$ of crop brought back to the dwellings after the harvest of the year n is updated at this time:

$$V(n) = \underbrace{\alpha_c \gamma_c P_c(nT + \tau^-)}_{\text{from Compound subsystem}} + \underbrace{\frac{L_c}{L}\alpha_b \gamma_{bc}(1 - \epsilon)P_{bc}(nT + \tau^-)}_{\text{from cropland subunits of Bush subsystem}}$$

A.3.4 Dry Season: from $nT + \tau$ to $(n + 1)T$

In the compound subsystem:

$$\begin{cases} \frac{dP_c}{dt} = -\underbrace{c_c P_c}_{\text{degradation of crop residues}} - \underbrace{\frac{1}{\alpha_c}\phi^c_{dry}}_{\text{grazing}} \\ \frac{dO_c}{dt} = \underbrace{c_c P_c}_{\text{degradation of crop residues}} - \underbrace{m_c O_c}_{\text{mineralization}} + \underbrace{i_o}_{\text{atmospheric deposition}} - \underbrace{e_{oc} O_c}_{\text{losses}} + \underbrace{\frac{\lambda_v}{\alpha_c T}V(n-1)}_{\text{recycling from dwellings}} + \underbrace{\lambda_\kappa(1-\nu)\left(h\frac{1}{\alpha_c}\phi^c_{dry} + (1-h)\frac{\kappa\rho}{\alpha_c}\right)}_{\text{excretion}} \\ \frac{dI_c}{dt} = \underbrace{m_c O_c}_{\text{mineralization}} + \underbrace{i_n}_{\text{atmospheric deposition}} - \underbrace{e_{nc} I_c}_{\text{losses}} + \underbrace{\lambda_\kappa \nu \left(h\frac{1}{\alpha_c}\phi^c_{dry} + (1-h)\frac{\kappa\rho}{\alpha_c}\right)}_{\text{excretion}} \end{cases} \tag{14}$$

In the bush subsystem, for each subunit j from 1 to L:

$$\begin{cases} \frac{dP_j}{dt} = -\underbrace{c_j P_j}_{\text{degradation of crop residues}} - \underbrace{\frac{L}{\alpha_b}\phi^j_{dry}}_{\text{grazing}} \\ \frac{dR_j}{dt} = -\underbrace{r R_j}_{\text{degradation of R}} \\ \frac{dO_j}{dt} = \underbrace{c_j P_j}_{\text{degradation of crop residues}} - \underbrace{m_j O_j}_{\text{mineralization}} + \underbrace{i_o}_{\text{atmospheric deposition}} - \underbrace{e_{oj} O_j}_{\text{losses}} + \underbrace{r R_j}_{\text{degradation of R}} + \underbrace{\lambda_\kappa(1-\nu)h\frac{L}{\alpha_b}\phi^j_{dry}}_{\text{excretion}} \\ \frac{dI_j}{dt} = \underbrace{m_j O_j}_{\text{mineralization}} + \underbrace{i_n}_{\text{atmospheric deposition}} - \underbrace{e_{nj} I_j}_{\text{losses}} + \underbrace{\lambda_\kappa \nu h\frac{L}{\alpha_b}\phi^j_{dry}}_{\text{excretion}} \end{cases} \tag{15}$$

Different values are assigned to the parameters c_j, m_j and e_{nj} depending on whether the subunit j is being cultivated during the current year or not. $x_j = x_{bc}$ if the subunit j is cultivated or $x_j = x_{bf}$ if the subunit j lies in fallow (with $x = c$, m, and e_n),

A.4 Balance of fluxes, comparison to Sare Yero Bana data

Tables 4 and 5 describe the balances of N fluxes (in kgN ha^{-1} y^{-1}) at the scale of the compound subsystem and the bush subsystem (crops and fallow) over the last year of a 300 years simulation without and with livestock for a duration of a rotation of 20 years.

The model is designed to be simple enough to provide a mechanistic understanding of the way agricultural practices influence crop production. Therefore, it is set up to be qualitatively rather than quantitatively predictive. Yet, the comparison of the main outputs to data from Sare Yero Bana shows a rather good fit (case 1 of Table 5 presented in Appendix 4). More precisely, N fluxes related to livestock and harvest are close to field data from Manlay et al. (2004a,b) in both the cropland subunits of the bush subsystem and the compound subsystem. On the other hand, N fluxes related

Table 4
Balance of N fluxes (in kgN ha^{-1} y^{-1}) at the scale of the compound subsystem, bush subsystem (crops and fallow) over the last year of a 300 years simulation without livestock. In these simulations, total bush and compound areas are 150 and 50 ha, respectively. The duration of a rotation is 20 years, which corresponds to 20 plots; results in bush subsystems (crop and fallow) are a mean of plot in crop and fallow, respectively. Three cases are simulated with a different duration of cropping (5, 10 and 15 years, respectively).

Without Livestock	Compound ring		Bush ring (Crop)		Bush ring (Fallow)	
	In	Out	In	Out	In	Out
Case 1: (L_c = 5) area (ha)	50		37.5		112.5	
Harvest/household waste[a]	8.6	1.5		32.2		0
Livestock-mediated fluxes	0	0	0	0	0	0
Losses[b]		14.6		29.3		21.8
Atmospheric deposition [c]	7.6		7.6		7.6	
Biological fixation [d]			21.5		34.1	
Clearing						9
Sowing	1	1.2	1	1.8		
Total	17.3	17.2	30.1	63.3	41.7	30.8
Balance	0		−33.1		10.9	
Case 2: (L_c = 10) area (ha)	50		75		75	
Harvest/household waste[a]	12.9	1.8		24.6		0
Livestock-mediated fluxes	0	0	0	0	0	0
Losses[b]		18.2		21.6		14.7
Atmospheric deposition[c]	7.6		7.6		7.6	
Biological fixation[d]			16.8		42.1	
Clearing						13.0
Sowing	1	1.4	1	1.4		
Total	21.5	21.4	25.4	47.5	49.7	27.7
Balance	0		−22.1		22	
Case 3: (L_c = 15) area (ha)	50		112.5		37.5	
Harvest/household waste[a]	11.7	1.7		14.8		0
Livestock-mediated fluxes	0	0	0	0	0	0
Losses[b]		17.2		11.4		6.9
Atmospheric deposition[c]	7.6	0	7.6		7.6	
Biological fixation[d]			10.8		39.0	
Clearing						17.0
Sowing	1	1.4	1	1.4		
Total	20.3	20.2	19.4	27.0	46.6	23.8
Balance	0.1		−7.6		22.7	

[a] Harvest take into account staple crop for the consumption of the village (compound ring) and exports of cash crop outside the agro-ecosystem (bush ring).
[b] Losses due to erosion, leaching, volatilization and denitrification.
[c] Dry and atmospheric depositions of mineral and organic N.
[d] Biological fixation from N-fixing Plant association with *Rhizobium*.

to livestock in the fallow subunits of the bush subsystem are of the same order of magnitude, but they are largely higher. This overestimation may be mainly due to simplifying assumptions regarding livestock dynamics and grazing behaviour. For instance, all the plants present in the fallows were assumed palatable. In reality, fallows contain unpalatable species (Ickowicz and Mbaye, 2001), in particular in late successional states, while a share of palatable biomass is left due to tainting by urine and trampling during browsing (Manlay et al., 2004c). Overestimating the livestock-induced fluxes in fallow tends to reduce livestock-induced fluxes from savanna, which may explain the underestimation of crop production in the compound subsystem.

The abundance of legumes in fallows is poorly documented. Some *Acacia spp.* and annual legumes are present but there is no precise estimate of the amounts of N they fix. However, the order of magnitude for biological N fixation fluxes (50.4 kgN ha^{-1} yr^{-1}) in our model is consistent with Cleveland et al. (1999) who gave the range of value 16-44 kgN ha^{-1} yr^{-1} for tropical savannas.

Table 5
Balance of N fluxes (in kgN ha^{-1} y^{-1}) at the scale of the compound and the bush subsystem (crops and fallow) over the last year of a 300 years simulation with livestock. In these simulations, total bush and compound areas are 150 and 50 ha, respectively. The duration of a rotation is 20 years (corresponding to 20 plots); results in bush subsystems (crop and fallow) are a mean of plots in crop and fallow, respectively. Three cases are simulated with a different duration of cropping. The case 1 represents the closest scenario of the agro-ecosystem of Sare-Yero-Bana, Senegal in 2000. Between brackets are given aggregated data calculated from (a) (Manlay et al., 2004b,a), (b) (Buerkert and Hiernaux, 1998; Delon et al., 2010), (c) Ndiaye (1986) or (d) (Cleveland et al., 1999).

With Livestock	Compound ring In	Compound ring Out	Bush ring (Crop) In	Bush ring (Crop) Out	Bush ring (Fallow) In	Bush ring (Fallow) Out
Case 1: (L_c = 5)						
area (ha)	50(35)		37.5(70)		112.5(117)	
Harvest/household waste [a]	12.5(63)[a]	7.3(15)[a]		31.1(56)[a]		
Livestock-mediated fluxes	92.7(146)[a]	41.3(59)[a]	8.5(12)[a]	20(21)[a]	47.8(3)[a]	74.2(7)[a]
Losses [b]		65.1		22.7		17.9
Atmospheric deposition [c]	7.6 (4-8)[b]		7.6 (4-8)[b]		7.6 (4-8)[b]	
Biological fixation [d]			22.3(15-68)[c]		50.3(16-44)[d]	
Clearing						6.4
Sowing	1	0.1	1			
Total	117	114	39.4	88.8	105	94
Balance	3		−49.5		11.6	
Case 2: (L_c = 10)						
area (ha)	50		75		75	
Harvest/household waste [a]	16.1	7.5		23.1		
Livestock-mediated fluxes	93.1	42.2	6.3	14.8	51.9	64.9
Losses [b]		68.1		16.8		13.1
Atmospheric deposition [c]	7.6		7.6		7.6	
Biological fixation [d]			16.7		44.5	
Clearing						3.04
Sowing	1	0.1	1	0.1		
Total	117.8	117.8	31.5	54.7	104.1	81.0
Balance	0.2		−23.1		23.1	
Case 3: (L_c = 15)						
area (ha)	50		112.5		37.5	
Harvest/household waste [a]	16.1	7.5		15.4		
Livestock-mediated fluxes	93.3	42.6	4.8	11.4	74.2	59.5
Losses [b]		69.6		12.2		9.7
Atmospheric deposition [c]	7.6		7.6		7.6	
Biological fixation [d]			13.1		37.8	
Clearing						6.08
Sowing	1	0.1	1	0.1		
Total	116.9	116.8	27.1	44.6	119.3	66.6
Balance	−1.6		−12.4		52.7	

[a] Harvest take into account staple crop for the consumption of the village (compound ring) and exports of cash crop outside the agro-ecosystem (bush ring).
[b] Losses due to erosion, leaching, volatilization and denitrification.
[c] Dry and atmospheric depositions of mineral and organic N.
[d] Biological fixation from N-fixing Plant association with *Rhizobium*.

A.5 Sensitivity analysis

The sensitivity analysis was performed using the Morris method that is implemented in the package "sensitivity" (Pujol et al., 2017). The analysis of the Morris graph makes it possible to distinguish:

- the parameters whose effects are negligible: points close to the origin (0,0);
- the parameters whose linear effect is important: points located to the right of the abscissa axis;
- the parameters whose effects are non-linear or include interaction with other factors: points located at the top of the y-axis (from Faivre et al., 2013).

The effect of each parameter of the model on the bush, the compound and the total crop productions was examined. This sensitivity analysis (Fig. 7) shows that factors such as the surface of the bush subsystem α_b and the size of livestock κ are among the most influential factors. Some other parameters such as the harvest percentages (γ) and the plant parameter related to the level of atmospheric N biological fixation in crop subunits of the bush subsystem (ω) are influential too, but to a lesser extent. This result is not surprising, since these parameters are directly linked to the inputs/outputs balance of the system. The importance of the parameter h, which represents the percentage of N excreted by livestock during the day (Manlay et al., 2004b) suggests that livestock management is a key driver in the system. It calls for the consideration of other types of livestock management in future studies performed with our model. For instance, in-barn livestock systems based on feed imports from outside the ecosystem are practiced when landscape is dominated by crops and when rangelands surfaces are insufficient to feed large livestock herds. Imported feeds represent new source of N inputs that may compensate the loss of N spatial transfer from rangelands to croplands (Audouin et al., 2015).

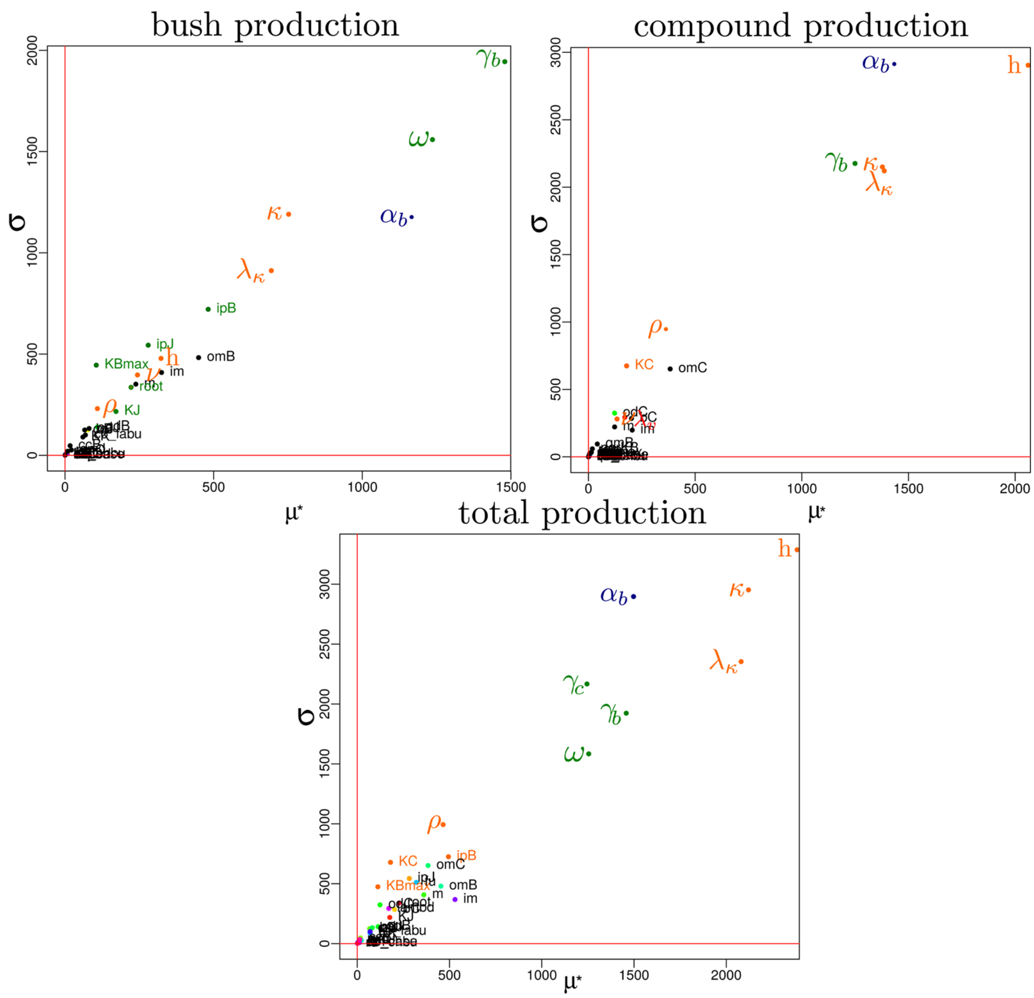

Fig. 7. Morris method results on bush, compound and total crop production. mean, μ, and standard deviation, σ, of the finite distribution of elementary effects associated with the parameters of the model. Parameter α_b is the proxy for the bush:compound surface ratio as the size of the agro-ecosystem stays unchanged. See appendix 2 for description and definition of the parameters.

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