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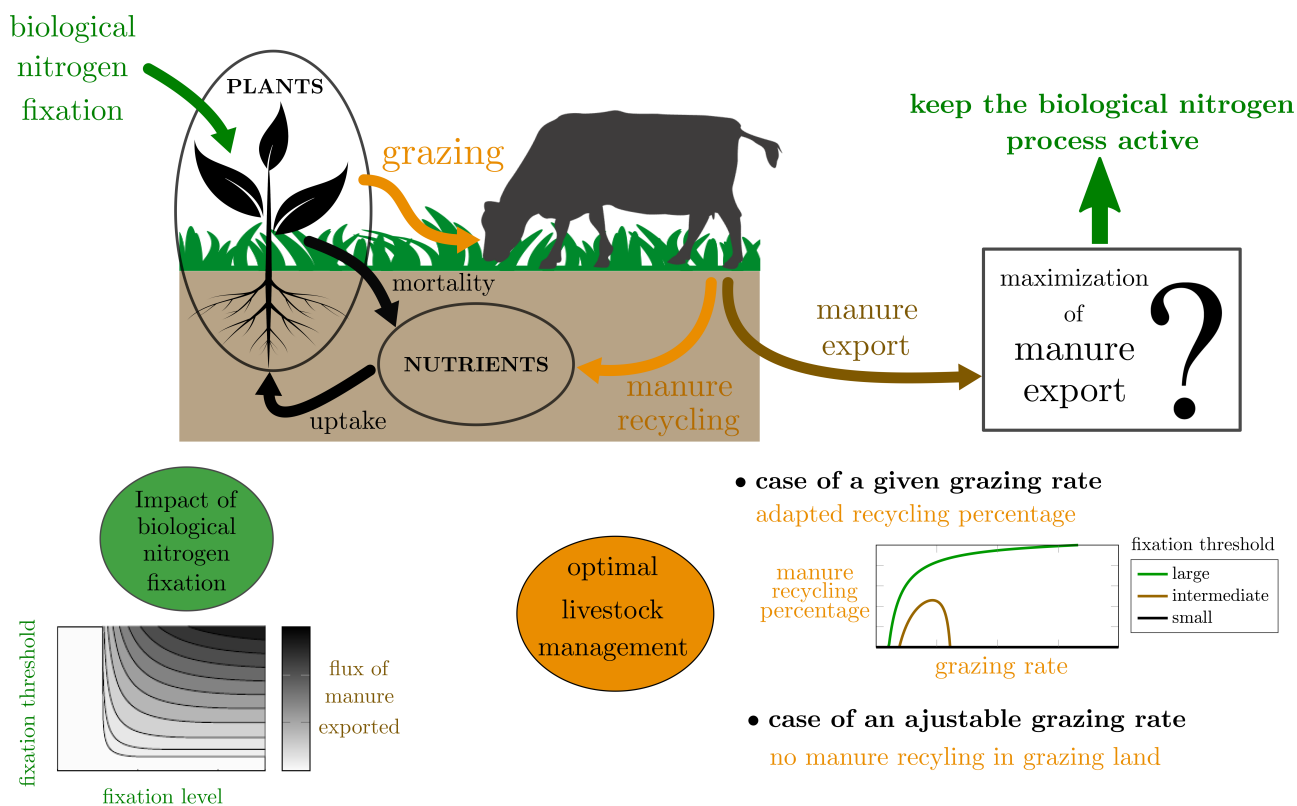
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Graphical Abstract

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Highlights

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- Adding nitrogen fixing plants in grazing land increase the optimal value of manure transfer
- When grazing rate is high, recycling part of the manure on the grazing land is necessary to maximize the flux of exported manure
- The maximal flux of exported manure is reached when all the produced manure is transferred and the grazing rate adapted accordingly
- To maximize the flux of exported manure, the process of biological nitrogen fixation must be kept active

Impact of biological nitrogen fixation and livestock management on the manure transfer from grazing land in mixed farming systems

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ABSTRACT

Soil fertility in mixed farming systems relies on the manure produced by livestock and its recycling in the entire system. In the particular case of crop-livestock system with grazing area, the proper functioning of the system also depends on the presence of nitrogen-fixing plants in the area where livestock grazes (the grazing land). In this paper, we study the impact of biological nitrogen fixation (BNF) and livestock management on the flux of manure exported outside the grazing land. We address this issue using a modeling approach. We consider a plant-soil model composed of a set of nonlinear ordinary differential equations that represents the grazing land. We assume that the manure produced by the grazing livestock can be partially exported as a fertilizer outside of this area. Through the mathematical analysis of the model, and analytical and numerical optimization, we then determine the optimal livestock management in terms of grazing rate and manure recycling percentage that lead to the maximal flux of exported manure. We focus more precisely on the role of nitrogen-fixing plants and their impact on the optimal livestock management. When grazing rate is high and the capacity of plants to fix nitrogen is important, we showed that it is necessary to recycle some of the manure produced by the livestock in the grazing land to maximize the flux of exported manure. On the contrary, if we can optimize both the grazing rate and the manure recycling percentage, then it is better to transfer all the produced manure and to adapt the grazing rate accordingly to minimize nitrogen losses from the soil. Finally, to maximize the flux of exported manure, it is also necessary to bring the system to a state in which the plants fix nitrogen. In this way, we can benefit from the nitrogen fixation which provides an additional input of nitrogen in the system.

1. Introduction

In a world facing an increasing food demand, the optimization of crop production is essential. The objective is to increase the food crop production while preserving resources and protecting the environment, which involves reducing the use of chemical fertilizers, optimizing their use and finding sustainable alternatives [66]. In particular, the development of sustainable agriculture requires closing (as much as possible) the nutrient cycles [32]. Nutrients have to be conserved or recycled in the system to reduce the use of synthetic fertilizers and ensure a long-term agricultural production [58]. A way to close nutrient cycles is to link crop and livestock production [68, 2, 18] which can be done at the scale of a plot, of a farm, or of a territory [3, 60, 31]. Indeed, while the fodder needed for the livestock is provided by the crops, the fertilizer needed for the crops can come from the livestock manure.

In some parts of the world, the evolution of agriculture tends to the specialization of agriculture and the separation of crop and livestock production. Nutrient cycles have thus been disrupted, with the additional consequences of increased use of synthetic fertilizers and greater pollution


of water bodies and soils due to poor management of livestock effluents [25]. Yet, if distributed properly, animal manure can be used to fertilize both forage and food crops. The objective is to combine the “*economic benefits of specialization at farm level and environmental benefits of integrating cropping and livestock systems at regional level*” [7]. Several papers propose strategies to manage such systems, that are called “Integrated crop-livestock systems” [34], taking into account several constraints such as the travel cost for instance [46, 28].

However, farming systems that combine crop and livestock production on the same farm are still present in many parts of the world [24]. In these systems, called “mixed farming systems”, soil fertility supporting crop production mainly relies on the manure produced by livestock [51] and its recycling in the entire system. Mixed farming systems have several agronomic, economic and environmental advantages [33, 7, 60]. They improve the soil quality [60], reduce the use of external inputs (chemical fertilizers, biocides, etc.), increase the nutrient use efficiency [33] and facilitate the management of weeds [36]. Moreover, when managed appropriately, mixed farming system can also lead to higher yields [7], which explains the interest of the scientific community in such systems. The proper functioning of mixed farming systems depends on the nutrient transfer by livestock, but also on the presence of nitrogen-fixing plants in area where it graze, which provide the bulk of the nitrogen supply when other inputs of nitrogen (atmospheric deposition, rock weathering) are low (e.g [12, 49]).

To maximize crop production in mixed farming sys-

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tems, it is essential to optimize the management of livestock [58], and thus the amount and deposition strategy of manure, both in time and space. In a previous paper [6], we considered a meta-ecosystem model composed of two subsystems to represent a crop-livestock system with a grazing area: one subsystem for the grazing land and another for the cropland, with the livestock represented as a simple nutrient flux. In this model, the plants grazed by the livestock are partly recycled within the grazing land, the other part being exported to the cropland. The objective of the paper was to determine the optimal livestock management (in terms of grazing rate and manure recycling percentage on the grazing land) that leads to the maximal plant production. We first showed that to maximize the crop production, we have to maximize the flux of nutrients exported by the livestock from grazing land to cropland. We then found that maximizing the flux of exported nutrients requires exporting all nutrients ingested by livestock, regardless of the value of the grazing rate. In other words, recycling some of the manure in the grazing land does not result in increased crop production.

However, in that paper, the plants considered in the grazing land were not capable of fixing atmospheric nitrogen. Yet nitrogen-fixing plants are naturally present in grazing land, especially in nitrogen-poor soils. It represents an important part of the external nitrogen inputs [51], and should therefore not be neglected. In the present paper, nitrogen fixing plants have been added in the grazing land subsystem of the model. Based on the results of our previous paper [6], the objective is to assess how nitrogen fixation can increase the flux of nutrients exported by the livestock in order to maximize the crop production at the scale of the meta-ecosystem. We will see how the optimal livestock management is modified compared to the results obtained in the case without nitrogen-fixing plants.

The paper is organized as follows. In section 2, the equations of the model are given. Specific paragraphs dedicated to the choice of the nitrogen fixation function and to the parameters related to the livestock management are also included. Then, the optimization problem under consideration is introduced in section 3 with a paragraph dedicated to the model assumptions. In section 4, the dynamics of the model is studied (existence and stability of the equilibrium points) and the impact of the fixation function on the system dynamics is assessed. The optimisation problem is then addressed in section 5. Finally, section 6 is dedicated to the discussion.

2. Model

On a farm scale, we consider a grazing area (the grazing land) on which some nitrogen-fixing plants grow, and on which livestock graze. One part of the manure produced by the livestock is recycled on the grazing land, the other part is exported outside (see Figure 1). The objective is to determine the optimal livestock management (in terms of grazing rate and manure recycling percentage) that leads to the maximal flux of exported manure (denoted T in the

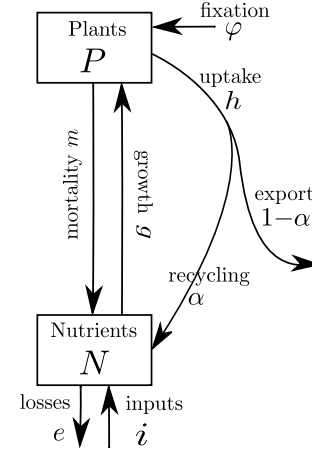


Figure 1: Model of the nitrogen cycle in a grazing land. Representation of all stocks and fluxes presents in the model. See Table 1 for the parameters description and units.

sequel), based on a modelling approach (see section 3).

2.1. Model equations

The model we consider for the grazing land is composed of a set of nonlinear ordinary differential equations. It is the one that was introduced in [6] to which we added a fixation flux (see Figure 1). It is composed of two compartments: the plant compartment P and the nitrogen compartment N . Three types of fluxes are taken into account in the model: plant related fluxes, abiotic fluxes and livestock related fluxes.

Plants assimilate nitrogen from the nitrogen compartment N at a growth rate $g(P, N)$ and from the atmosphere by fixation at a rate $\varphi(N)$. The mortality of plants recycles nitrogen back to the N compartment at a rate m . Nitrogen enters the grazing land through dry deposition of mineral nitrogen (input flux i). Losses of nitrogen are mainly due to erosion, leaching, volatilization and denitrification (loss rate e).

Livestock is represented implicitly in the model, through the parameters h and α (see paragraph 2.3). The parameter h represents the uptake rate, that is the rate at which the plants are uptaken to feed the livestock. The flux of nitrogen ingested by the livestock and that will be transformed into manure is thus given by hP . This flux is separated in two parts in the model: one percentage α is recycled in the grazing land, the other part (percentage $(1 - \alpha)$) is exported with the livestock when it leaves the grazing land.

The equations of the grazing land are finally given by:

$$(\mathcal{M}) \begin{cases} \frac{dN}{dt} = -g(N, P)P - eN + i + mP + ahP \\ \frac{dP}{dt} = g(N, P)P + \varphi(N)P - mP - hP \end{cases} \quad (1)$$

The growth function g is a modified logistic function with a maximal growth rate rN that depends on the available nitrogen, and a carrying capacity K :

$$g(N, P) = rN \left(1 - \frac{P}{K}\right) \quad (2)$$

name	unit	description
P	[M] [L] ⁻²	Stock of nitrogen in the plant compartment
N	[M] [L] ⁻²	Stock of nitrogen in the inorganic nitrogen compartment
P^*, N^*	[M] [L] ⁻²	values of P and N at equilibrium
$g(N, P)$	[M] [L] ⁻² [T] ⁻¹	growth function of plants
$\varphi(N)$	[M] [L] ⁻² [T] ⁻¹	function of nitrogen fixation by plants
r	[L] ² [M] ⁻¹ [T] ⁻¹	nitrogen uptake rate of plants
K	[M] [L] ⁻²	carrying capacity of plants
f	[M] [L] ⁻² [T] ⁻¹	fixation level, i.e maximal fixation rate
N_b	[M] [L] ⁻²	fixation threshold, i.e value of nitrogen stock below which the plants fix nitrogen
λ	[L] ² [M] ⁻¹	parameter of the sigmoid fixation function
m	[T] ⁻¹	mortality rate of plants
e	[T] ⁻¹	losses rate (ex: leaching) of inorganic nitrogen
i	[M] [L] ⁻² [T] ⁻¹	input flux of inorganic nitrogen
s	[L] ²	surface of the sub-system
h	[T] ⁻¹	grazing rate in grazing land
α	unitless	fraction of uptake by livestock recycled into grazing land
$1-\alpha$	unitless	fraction of manure exported outside grazing land
T	[M] [L] ⁻² [T] ⁻¹	flux of produced manure that is exported outside grazing land: $T = (1 - \alpha)hP$ (see eq. (3))

Table 1

Nomenclature of model parameters, variables and functions with the associated units. [M], [L] and [T] stand for the units of Mass, Length and Time respectively. In the paper, the mass M values are expressed in kilograms of nitrogen kgN, the surface (i.e the square of the length [L]²) in ha and the time [T] in days.

The expression of the nitrogen fixation function φ is discussed in section 2.2.

The flux of manure exported outside the grazing land at equilibrium is finally given by:

$$T = (1 - \alpha)hP^* \text{ (kgN.ha}^{-1}.\text{d}^{-1}\text{)} \quad (3)$$

where P^* is the quantity of nitrogen in the plant compartment (of the grazing land) at equilibrium.

All stocks and fluxes are expressed in kgN.ha⁻¹ and in kgN.ha⁻¹.d⁻¹ respectively. It implies that some of the model parameters include conversion coefficients. The units and significance of all the model parameters are summarized in Table 1. The ranges of model parameter values found in literature are given in appendix C, in Table 6.

2.2. Nitrogen fixation functions

Nitrogen fixation has an energetic cost that plants have to support [48]. This can explain why most nitrogen-fixing plants use this capacity only when they really need it, that is when there is not enough nitrogen in the soil. In model (1), the nitrogen fixation term $\varphi(N)P$ should therefore be decreasing with respect to N as it is generally done in the literature [35]. In the present paper, we consider the two following fixation functions and study the model (1) for the different cases:

- Constant nitrogen fixation function

$$\varphi(N) = f, \forall N > 0. \quad (4)$$

We denote (\mathcal{M}_c) the model (1) when $\varphi(N)$ is given by (4). The case $f = 0$ has already been studied

in [6]: the associated system is denoted (\mathcal{M}_0) in the sequel.

This first fixation function is not decreasing with N , but the study of (\mathcal{M}_c) is a preliminary step that is then used for the study of the system with the decreasing and discontinuous nitrogen fixation (5).

- Discontinuous nitrogen fixation function

$$\varphi(N) = \begin{cases} f & \text{if } 0 \leq N < N_b \\ 0 & \text{if } N_b \leq N \end{cases} \quad (5)$$

In the sequel, we denote (\mathcal{M}_d) the system (1) associated with the discontinuous fixation function (5).

With such a function, the plant fix only if the quantity of nitrogen N in the soil is smaller than the threshold N_b . Beyond this threshold, fixation does not occur. This function has also the advantage to be the limit case of a smoother sigmoid fixation function of the form $\varphi(N) = \frac{f}{1 + e^{\lambda(N - N_b)}}$, $\forall N > 0$. Indeed, when λ goes to $+\infty$, the sigmoid function goes to the discontinuous function (5). So, if λ is large enough, we can expect to get similar results with the discontinuous function (5) and the sigmoid function.

2.3. Livestock management parameters

The impact of livestock on the grazing land is represented in the model through the parameters h and α .

- The parameter h is the grazing rate, that is the rate at which the plants are uptaken to feed the livestock. In the case of grazing livestock, it takes into account the size of the herd (livestock biomass per surface unit), the type of livestock (and therefore their capacity to ingest nitrogen) and the time spent on the grazing land. For example, a same value of h may either represent a big herd of livestock that do not stay all year along in the grazing land or a small herd of livestock that stay all year along in the grazing land.
- The parameter α represents the percentage of the flux of produced manure that is recycled in the grazing land. The percentage $(1 - \alpha)$ corresponds to the part that is exported. The parameter α depends on the daily time spent by the livestock (day/night) on the grazing land, and on the metabolism of the livestock.

Note that when α equals to 0, it necessarily means that the livestock do not graze on the grazing land. The model considered in this paper must then be interpreted differently. It no longer represents a grazing land, but rather fields of forage crops, part of plant biomass production of which is used to feed livestock, which are kept in separate areas from the fields. In that case, the parameter h does not represent the grazing rate anymore but the uptake rate of plant biomass in the forage crop fields. This brings us to the case of Integrated Crop Livestock System (ICLS) mentioned in the introduction, for which one challenge is to find effective strategies for transferring manure from livestock farms to crop fields [46, 28].

3. Optimization problem

3.1. Statement of the problem

The objective of the study is to assess the impact of biological nitrogen fixation and livestock management on the flux of manure exported outside the grazing land. More precisely, we want to maximize the flux of manure T that is exported outside the grazing land (and that is given by (3)) through an optimal management of the livestock and evaluate the impact of the biological nitrogen fixation on the optimal livestock management. In the model, the livestock is represented by the parameters h (the grazing rate) and α (the manure recycling percentage) described in paragraph 2.3.

In the case where there is no fixation in the grazing land, we showed in [6] that the maximal value of T is reached for $\alpha = 0$ and for a value h_{opt} of h between 0 and $h_{max} = \frac{ri}{e} - m$ (provided that $\frac{ri}{e} - m > 0$). The optimal value $\alpha = 0$ that is obtained in [6] can be explained by the fact that, in absence of fixation ($\varphi(N) = 0$), $T = i - eN^*$ where N^* is the quantity of nitrogen in the nitrogen compartment of the grazing land at equilibrium. T is indeed equal to the difference between nitrogen inputs and outputs in the system. Maximizing T is therefore equivalent to minimizing N^* . That is why it is preferable not to recycle manure in the nitrogen compartment of grazing land ($\alpha = 0$).

We can now wonder if the same conclusion will be drawn in the presence of nitrogen-fixing plants in grazing land, because in that case, there is an additional nitrogen input $\varphi(N^*)P^*$ that appears in the expression of T . In the sequel, we study the impact of fixation on the maximal value T_{max} of T , and on the values α_{opt} and h_{opt} of α and h for which this maximum is reached.

3.2. Assumptions

In the sequel, we only consider the cases where:

$$\frac{i}{e} > \frac{m}{r}. \quad (6)$$

This is the condition for the existence of an optimal value h_{opt} of h that maximizes the transfer T with $\alpha = 0$ [6] in the case without fixation (model (\mathcal{M}_0)). If this condition is not satisfied, T (and P^*) is equal to 0 whatever the value of h . This condition means that the soil has to be sufficiently rich and/or well structured (i high and/or e low) or that the plants have to be sufficiently efficient (m low and/or r high).

For the models with nitrogen-fixing plants (\mathcal{M}_c) and (\mathcal{M}_d) , we also assume that:

$$f < m. \quad (7)$$

This inequality means that the fixation alone can not ensure the growth of the plants (i.e. if $g = 0$, then $\frac{dN}{dt} < 0$).

4. Model analysis

In this section, we study the system (\mathcal{M}_c) with constant fixation function (4) and the system (\mathcal{M}_d) with discontin-

uous fixation function (5). Only the results are given here. The proofs can be found in Appendix A.

4.1. Equilibrium points and stability

Let's start by determining the equilibrium points of both systems and their stability.

4.1.1. Model with constant fixation function

We consider here the system (\mathcal{M}_c) with the constant fixation function defined by (4). By definition, the equilibrium points (N^*, P^*) of system (\mathcal{M}_c) are the solutions of the equations:

$$\begin{cases} -rPN \left(1 - \frac{P}{K}\right) - eN + i + mP + \alpha hP & = 0 \\ P \left(rN \left(1 - \frac{P}{K}\right) + f - m - h\right) & = 0 \end{cases} \quad (8)$$

The trivial equilibrium point E_0 corresponds to the case where there is no plant in the system ($P = 0$). E_0 exists whatever the parameter values and is given by:

$$E_0 = \left(N_0 = \frac{i}{e}, P_0 = 0\right); \quad (9)$$

it is locally stable if and only if $\frac{i}{e} < \frac{m+h-f}{r}$ (see Appendix A).

Let us now consider the case where $P \neq 0$. In that case, if $f + (\alpha - 1)h \neq 0$, and after simple computations, the system (8) can be rewritten:

$$\begin{cases} P & = K \frac{f+rN-m-h}{eN-i} =: F_1(N) \\ P & = \frac{eN-i}{f+(\alpha-1)h} =: F_2(N) \end{cases} \quad (10)$$

Finding the solution of the system of equations (8) amounts to find the intersection points of the curves of F_1 and F_2 which can be done graphically (see Figure 2). We only look for the points with biological significance, that is those located in the positive quadrant (i.e. the space with positive values of both P and N variables). We thus get the following cases:

- if $\frac{i}{e} > \frac{m+h-f}{r}$, then there exists one and only one positive intersection point E_1^f .
- if $\frac{i}{e} < \frac{m+h-f}{r}$, we have to consider different cases. Let denote $s = \frac{e}{f+(\alpha-1)h}$ the slope of F_2 (which is linear with respect to N), and \bar{s} the slope of the straight line that is tangent to the curve of F_1 and that goes through the point $\left(\frac{i}{e}, 0\right)$.
 - If $s < 0$ or $0 < \bar{s} < s$, then there does not exist any intersection point;
 - If $0 < s = \bar{s}$, then there exists one and only one positive intersection point E_1^f ;
 - If $0 < s < \bar{s}$, then there exists two positive intersection points E_1^f and E_2^f .

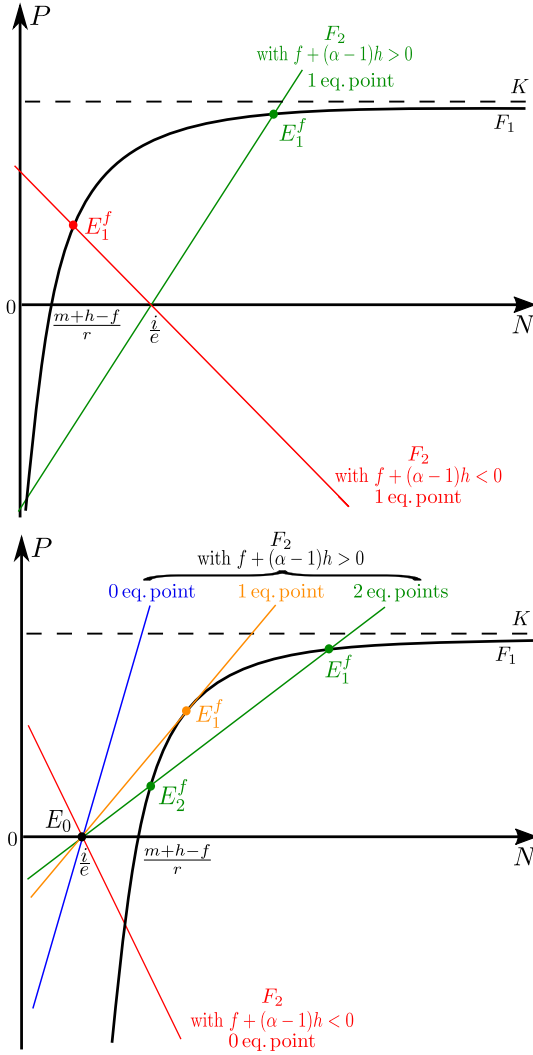


Figure 2: Graphical determination of the positive equilibrium points. Top: case where $\frac{i}{e} > \frac{m+h-f}{r}$ - Bottom: case where $\frac{i}{e} < \frac{m+h-f}{r}$

We can show (see Appendix A) that when they exist, E_1^f is always stable, whereas E_2^f is always unstable.

Finally, there are three cases (see Figure 3):

- case where $\frac{i}{e} > \frac{m+h-f}{r}$ (top of Figure 3): only E_1^f is stable ;
- case where $\frac{i}{e} < \frac{m+h-f}{r}$ and $0 < s \leq \bar{s}$ (bottom of Figure 3, red and yellow lines): bistability between E_0 and E_1^f ;
- case where $\frac{i}{e} < \frac{m+h-f}{r}$ and $s > \bar{s}$ or $s < 0$ (bottom of Figure 3, blue line): only E_0 is stable.

4.1.2. Model with discontinuous fixation function

To analyze and understand the dynamics of (\mathcal{M}_d) , we use the results obtained with the constant fixation function (presented in section 4.1.1). Indeed, the phase plane $\mathcal{D} :=$

$\{(N, P) \in [0, \infty) \times [0, K)\}$ can be divided in two parts that are separated by the vertical straight line $N = N_b$:

- the left part that corresponds to the values of (N, P) such that $0 < N < N_b$ and $P > 0$, is denoted \mathcal{D}_f . On \mathcal{D}_f , the dynamics of (\mathcal{M}_d) is the one of (\mathcal{M}_c) (model (1) with a constant fixation function $\varphi(N) = f$);
- the right part that corresponds to the values of (N, P) such that $N_b < N$ and $P > 0$, is denoted \mathcal{D}_0 . On \mathcal{D}_0 , the dynamics of (\mathcal{M}_d) is the one of (\mathcal{M}_0) (model (1) without fixation, that is with $\varphi(N) = 0$).

The different possible configurations then depend on the position of the stable equilibrium points of (\mathcal{M}_c) and (\mathcal{M}_0) in \mathcal{D} . The stable equilibrium points of (\mathcal{M}_c) (respectively of \mathcal{M}_0) remains stable for the system (\mathcal{M}_d) if they are inside \mathcal{D}_f (respectively \mathcal{D}_0). Some examples of phase portraits of system (\mathcal{M}_d) are given in Figure 4. The phase portraits given in Figure 4a correspond to the cases where $\frac{m+h-f}{r} < \frac{i}{e}$ and $f + (\alpha - 1)h < 0$ (i.e. the function F_2 is a decreasing straight line). In these cases, both systems (\mathcal{M}_0) and (\mathcal{M}_c) have a unique positive stable equilibrium point $E_1 = (N_1, P_1)$ and $E_1^f = (N_1^f, P_1^f)$, which are such that $N_1^f < N_1$. The phase portrait thus depends on the value of N_b . If $N_b < N_1^f$, only E_1 is stable for (\mathcal{M}_d) (left of Figure 4a). If $N_1^f < N_b < N_1$, there is bistability between E_1 and E_1^f (middle of Figure 4a). If $N_1 < N_b$, only E_1^f is stable for (\mathcal{M}_d) (right of Figure 4a). Some interesting configurations appear when the stable equilibrium points of (\mathcal{M}_c) are located in \mathcal{D}_0 and those of (\mathcal{M}_0) in \mathcal{D}_f . In such cases, the solutions converge to a point located on the frontier between \mathcal{D}_f and \mathcal{D}_0 , that is on the vertical straight line $N = N_b$. In the sequel, we denote E_{N_b} this point. An example of such a configuration is shown on Figure 4b.

4.2. Impact of fixation on the system dynamics

The nitrogen fixation functions (4) and (5) are characterized by two parameters: the fixation level f (for both functions), and the fixation threshold N_b (only for the discontinuous fixation function (5)). In this section, we analyze how the dynamics of systems (\mathcal{M}_c) and (\mathcal{M}_d) evolves with respect to the values of f , and of f and N_b respectively.

4.2.1. Impact of a constant fixation function

A simple analysis of the existence and stability conditions of the equilibrium points of (\mathcal{M}_c) (not presented here) leads to the three cases given in Table 2. We have:

- Case A where the grazing rate h is low: in that case, plants survive, whatever the value of the fixation rate f . It is necessary however that $\frac{m}{r} < \frac{i}{e}$ for this case to exist, which is exactly the assumption we made in (6).
- Case B where the grazing rate h has an intermediate value: in that case, if f is too low, plants do not

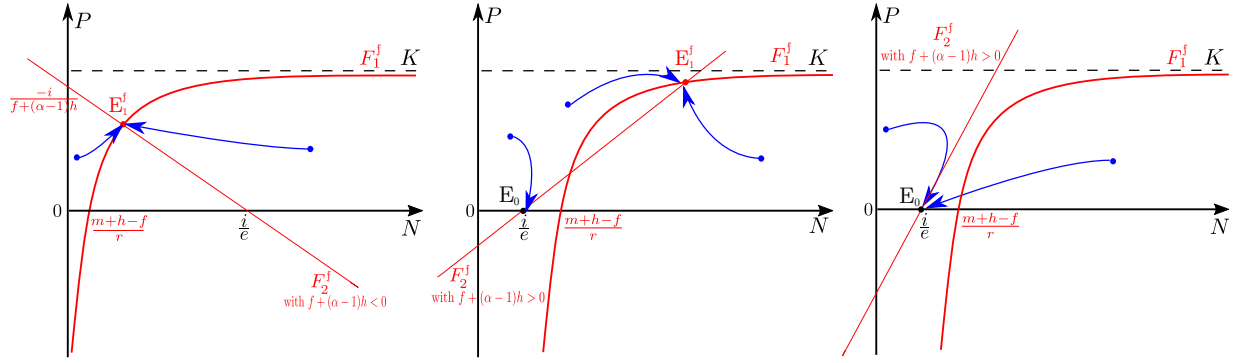


Figure 3: Phase portrait of system (\mathcal{M}_c) . Left: $\frac{i}{e} > \frac{m+h-f}{r}$, E_1^f is stable. Middle: $\frac{i}{e} < \frac{m+h-f}{r}$ and $0 < s \leq \bar{s}$, bi-stability between E_0 and E_1^f . Right: $\frac{i}{e} < \frac{m+h-f}{r}$ and $s > \bar{s}$ or $s < 0$, E_0 stable.

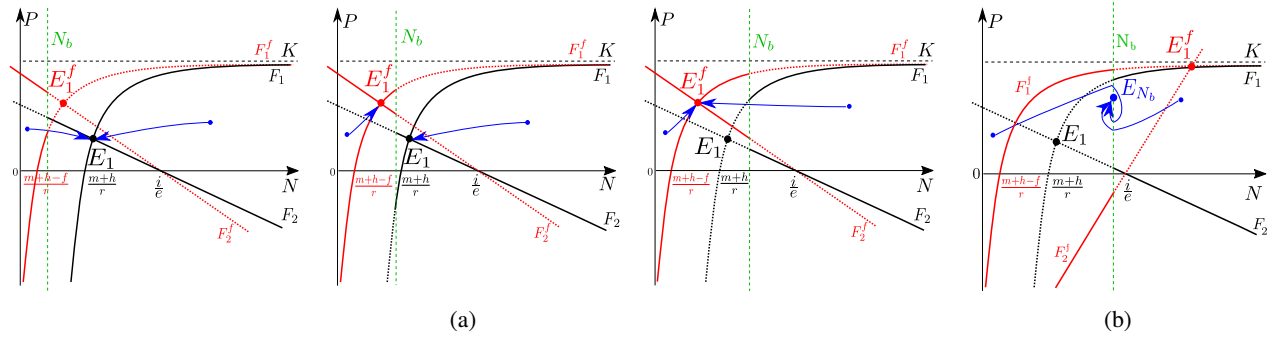


Figure 4: Examples of phase portraits of system (\mathcal{M}_d) . (a) Cases where $\frac{m+h-f}{r} < \frac{m+h}{r} < \frac{i}{e}$. (b) Configuration where some solutions converge towards a point located on the frontier between D_f and D_0 .

manage to survive; if f is high enough, plants settle whatever the conditions.

- Case C where the grazing rate h is high: in that case, if the fixation f is too low, plants can not settle; if f is too high, plants settle whatever the conditions; and if f takes an intermediate value, neither too low, nor too high, there is bi-stability, and plants manage to settle only if the initial conditions are favorable.

4.2.2. Impact of a discontinuous fixation function

To study the evolution of the equilibrium points of (\mathcal{M}_d) with respect to f and N_b , we consider the same three cases (case A, B and C of Table 2) as for system (\mathcal{M}_c) , and make the value of N_b vary. We consider for that a numerical

example, with the following model parameters: $r = 3.0$, $m = 6.3$, $e = 1$, $K = 7$, $i = 3.5$. The numerical study was performed with Matlab [39]. We obtain the results presented on Figure 5:

- Case A is the only case where the system without fixation (\mathcal{M}_0) admits a stable positive equilibrium point. It is also the only case where the plants settle whatever the values of f and N_b are. If the fixation threshold N_b is low, the system reaches an equilibrium state at which the nitrogen fixation is not active. On the contrary, if the fixation threshold N_b is high, the plants are fixing nitrogen at equilibrium. Depending on the level of fixation f , we can obtain some configurations of bistability between E_1 and E_1^f , or

Case	A	B		C		
h	$h \leq \frac{ri}{e} - m$	$\frac{ri}{e} - m < h \leq \frac{1}{\alpha} \left(\frac{ri}{e} - m + \frac{i}{K} \right)$		$\frac{1}{\alpha} \left(\frac{ri}{e} - m + \frac{i}{K} \right) < h$		
f	$m + h - \frac{ri}{e} \leq 0 < f$	$f \leq m + h - \frac{ri}{e}$	$m + h - \frac{ri}{e} < f$	$f \leq f^\circ$	$f^\circ < f \leq m + h - \frac{ri}{e}$	$m + h - \frac{ri}{e} < f$
	E_1^f stable	E_0 stable	E_1^f stable	E_0 stable	bi-stability	E_1^f stable

Table 2

Evolution of the equilibrium points of (\mathcal{M}_c) with respect to the value of f . f° is the value of f for which $s = \bar{s}$.

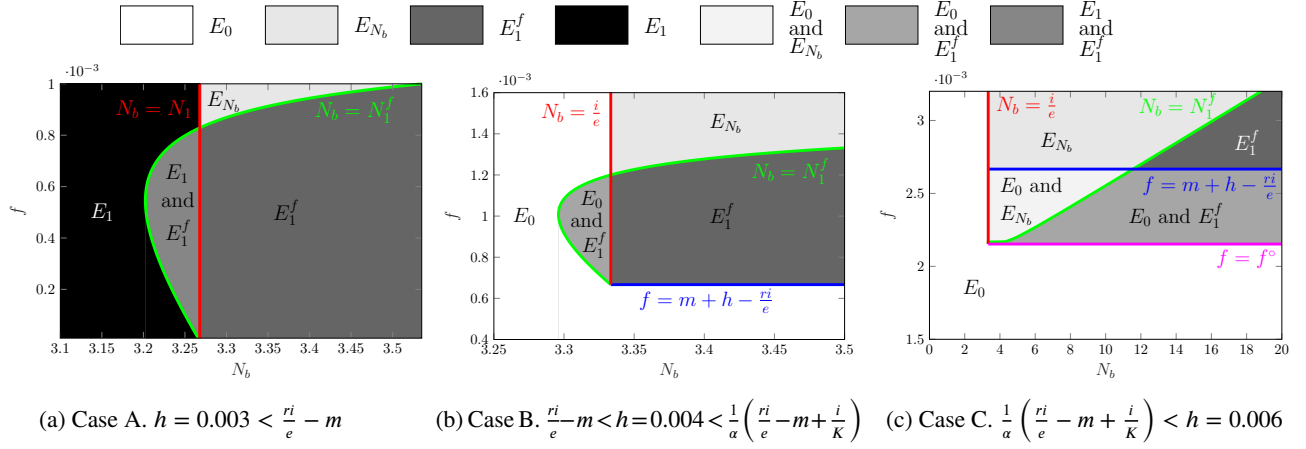


Figure 5: Evolution of the equilibrium points of (\mathcal{M}_d) with respect to f and N_b for the three different cases defined in Table 2 and characterized by the value taken by h . The model parameters have the following values: $r = 0.004$, $m = 0.01$, $e = 0.006$, $K = 80$, $i = 0.02$, $\alpha = 0.7$.

of stabilisation at an intermediate point E_{N_b} located between E_1 and E_1^f .

- In cases *B* and *C*, in order for plants to settle, they must necessarily fix nitrogen at equilibrium. Moreover, both the fixation threshold N_b and the fixation level f have to be sufficiently high for that. Intermediate values of f can lead (depending on the value of N_b) to bi-stability between E_0 and a non negative equilibrium point; in that cases, the initial conditions determine if the plants manage to settle or not.

5. Optimization of the flux of exported manure

In this section, we study the optimization problem introduced in section 3.1. We first consider the maximization of the flux of exported manure T (quantity defined by equation (3)) with respect to α , for a given value of h (section 5.1). This first optimization is performed analytically. In a second time, we look at the optimal values of both parameters α and h for which the transfer T is maximal (section 5.2). This second optimization is performed numerically with Matlab [39].

5.1. Optimization with α

Consider a given value of $h > 0$. The objective of this section is to find the optimal value of α for which T is maximal. This value is denoted α_{opt}^c for the model with constant fixation function (\mathcal{M}_c) and α_{opt}^d for the model with discontinuous fixation function (\mathcal{M}_d).

5.1.1. Model with constant fixation function

First note that, by definition (see equation (3)), T is strictly positive only when there exists a stable equilibrium point (N^*, P^*) such that $P^* > 0$ in the grazing land, that

	unit	description
α_{opt}^0	—	Optimal value of α for which T is maximal for the model without fixation function (\mathcal{M}_0)
α_{opt}^c	—	Optimal value of α for which T is maximal for the model with constant fixation function (\mathcal{M}_c)
α_{opt}^d	—	Optimal value of α for which T is maximal for the model with discontinuous fixation function (\mathcal{M}_d)
h_{opt}^0	d ⁻¹	Optimal value of h for which T is maximal for the model without fixation function (\mathcal{M}_0)
h_{opt}^c	d ⁻¹	Optimal value of h for which T is maximal for the model with constant fixation function (\mathcal{M}_c)
h_{opt}^d	d ⁻¹	Optimal value of h for which T is maximal for the model with discontinuous fixation function (\mathcal{M}_d)

Table 3

Nomenclature of optimization parameters.

is when the equilibrium points $E_1^f = (N_1^f, P_1^f)$ as defined in section 4.1.1 exists. Let denote Ω_α the set of the values of α in $[0, 1]$ for which the system (\mathcal{M}_c) admits such an equilibrium point.

Consider the cases where $\Omega_\alpha \neq \emptyset$ and $f > 0$. We can show (see Appendix B.1) that the function $T : \alpha \in \Omega_\alpha \mapsto T(\alpha) = (1 - \alpha)hP_1^f(\alpha)$ first increases and then decreases with α . More precisely we have, $\forall \alpha \in \Omega_\alpha$:

$$\frac{dT}{d\alpha} \begin{cases} > 0 \text{ if } P_1^f(\alpha) < P^m \\ = 0 \text{ if } P_1^f(\alpha) = P^m \\ < 0 \text{ if } P^m < P_1^f(\alpha) < K \end{cases} \quad (11)$$

with:

$$P^m = K - \sqrt{\frac{eK}{rf}(m + h - f)}. \quad (12)$$

So to maximize the transfer T , there is a compromise to do between (i) increasing the recycling percentage α to increase the plant production P_1^f and therefore the livestock uptake hP_1^f , and (ii) decreasing α to increase the part of livestock uptake that is exported (term $1 - \alpha$ in the expression of T).

Case	(i)	(ii)	(iii)	(iv)	(v)
f	$0 < f \leq \frac{i}{K}$		$\frac{i}{K} < f$		
h	$0 \leq h \leq \frac{r}{e} + f - m$	$\frac{r}{e} + f - m < h$	$0 \leq h \leq \frac{r}{e} + f - m$	$\frac{r}{e} + f - m < h \leq \delta$	$\delta < h$
Ω_α	$[0, 1]$	\emptyset	$[0, 1]$	$[\bar{\alpha}, 1]$	\emptyset
α	$0 \leq \alpha \leq 1$	$0 \leq \alpha \leq 1$	$0 \leq \alpha \leq 1$	$0 \leq \alpha < \bar{\alpha}$	$\bar{\alpha} \leq \alpha \leq 1$
	E_1^f stable	E_0 stable	E_1^f stable	E_0 stable	bi-stability
	$\alpha_m < 1$	-	$\alpha_m < 1$?	-

Table 4

Evolution of the equilibrium points of (\mathcal{M}_c) depending of the values of h and α in the case where $\frac{m}{r} < \frac{i}{e}$. δ is the value of h such that $\bar{s} = \frac{e}{f}$. $\bar{\alpha}$ is the value of α such that $s = \bar{s}$.

P^m is a threshold value for $P_1^f(\alpha)$ under which it is more interesting to increase the recycling percentage α to maximize the value of T and above which, on the contrary, it is better to decrease the value of α . Provided that P^m is positive and reachable, that is if there exists a value $\alpha \in \Omega_\alpha$ such that $P_1^f = P^m$, then P^m is the value of P_1^f for which T is maximal. It is reached for the value α_m of α given by:

$$\alpha_m = 1 - \frac{2f}{h} - \frac{i - Kf}{hP^m}. \quad (13)$$

Finally, the value α_{opt}^c of α for which the function $T : \alpha \in [0, 1] \mapsto T(\alpha) = (1 - \alpha)hP^*$ is maximal on $[0, 1]$ is given by:

$$\alpha_{opt}^c = \begin{cases} \min(\Omega_\alpha) & \text{if } (P^m < 0) \\ & \text{or if } (\alpha_m < \min(\Omega_\alpha) \text{ and } P^m > 0) \\ \alpha_m & \text{if } (\alpha_m \in \Omega_\alpha \text{ and } P^m > 0) \\ 1 & \text{if } (\alpha_m > 1 \text{ and } P^m > 0) \end{cases} \quad (14)$$

where α_m given by (13) and P^m by (12). When $\alpha = \alpha_{opt}^c = \alpha_m$, then $P^* = P^m$ and:

$$T_{max} = T(\alpha_m) = (2P^m - K)f + i. \quad (15)$$

Let us now see how the value of α_{opt}^c does evolve depending on the values of f and h . As previously performed in section 4.2.1, a simple analysis of the existence and stability conditions of the equilibrium points of (\mathcal{M}_c) leads to the 5 possible configurations presented in Table 4.

Among the five configurations, we note that only the configurations (i), (iii) and (iv) lead to a positive maximal value of T . In the other cases, plants never manage to settle in the grazing land, and as a consequence, $T = 0$ whatever the value of α (i.e. $\Omega_\alpha = \emptyset$). In cases (i) and (iii), E_1^f always exists and is stable for all the values of $\alpha \in [0, 1]$. We can moreover show that $\alpha_m < 1$ in that cases. So finally, the optimal value α_{opt}^c of α is either equal to 0 or to α_m depending on the value of h . The case (iv) is more complex as there is bi-stability between E_0 and E_1^f for $\alpha > \bar{\alpha}$. The maximal value of transfer T is therefore obtained for the value $\alpha_{opt}^c \in [\bar{\alpha}, 1]$ of α as defined in (14). However, to be reached, this maximal value of T moreover necessitates the initial conditions in the grazing land subsystem to be favorable. More precisely, the initial concentration of nitrogen in the soil of the grazing land has to be sufficiently high to ensure that the plants are able to settle.

To highlight these results, a numerical example is presented in Figure 6a. Given the following values of model parameters:

$$r = 0.004, m = 0.01, e = 0.006, K = 80, i = 0.02, \quad (16)$$

the value of T is computed for two values of f , and for the ranges of values of α and h given here-after:

- $f = 2.4 \times 10^{-4} < \frac{i}{K} = \frac{0.02}{80} = 2.5 \times 10^{-4}$, $\alpha \in [0, 1]$ and $h \in [0, 0.0043]$: it corresponds to the cases (i) and (ii) of Table 4;
- $f = 6 \times 10^{-4} > \frac{i}{K} = \frac{0.02}{80} = 2.5 \times 10^{-4}$, $\alpha \in [0, 1]$ and $h \in [0, 0.008]$: it corresponds to the cases (iii), (iv) and (v) of Table 4.

This numerical study was performed with Matlab [39].

We first note that when the fixation level f is small compared to the other nitrogen input i (i.e. $f = 2.4 \times 10^{-4} < \frac{i}{K}$, case (i)), the optimal value α_{opt}^c of α first increases and then decreases with h . It is even equal to 0 for small and large values of h . It means that when the fixation is not sufficiently high, if the livestock grazes only a few or on the contrary a lot, it is preferable to export all the produced manure outside of the grazing land. For intermediate values of grazing rate, one part of the produced manure has to be recycled on grazing land.

For a larger value of f ($f = 6 \times 10^{-4} > \frac{i}{K}$, cases (iii) and (iv)), the optimal value α_{opt}^c of α is always increasing with h . It means that if the fixation is high enough, the more the livestock grazes, the smaller the proportion of produced manure that is exported should be (in order to optimize T). Note also that in the case (iv), the optimal value α_{opt}^c never equals to $\bar{\alpha}$ or 1 as it could be a priori (we indeed do not manage to prove the contrary).

To explain that, recall that $T = i + fP^* - eN^*$. To maximize T we thus have to maximize the fixation inputs (term fP^*) and minimize the losses (term eN^*). When the grazing rate h is low, the plant production P^* is the highest (for a given value of α) and so is the fixation term. In that case, it is therefore not necessary to boost the plant growth by recycling. We might as well export everything ($\alpha_{opt}^c = 0$) because in addition, the term hP^* in T can be low (because h is low). When h increases, P^* decreases. To compensate this decrease and maximize T , it can be interesting to increase the recycling percentage α to support

the plant growth and take advantage of the fixation, but it will have some impact on the nutrient losses in the soil that will also increase: indeed both P^* and N^* increase with α . When f is large, we see in figure 6a (Right) that each time we increase a little the value of h , we must jointly increase a little the value of α to maximize the transfer T . Indeed in that case, as the fixation is strong, a small increase of α will increase the fixation term more than the losses term will increase. When the fixation is low this is also true but only for values of h that are not too large: in that cases the value of P^* is sufficiently high to make it worthwhile to support the fixation by increasing the recycling. Then there comes a time when the value of P^* becomes too small, and the increase in fixation is no longer large enough (because f is too small) compared to the increase in losses. In that case it is better to decrease the recycling percentage (i.e. the value of α) as we see on figure 6a (Left).

5.1.2. Model with discontinuous fixation function

Let us now consider the model with discontinuous fixation function (\mathcal{M}_d). We are interested in the variation of the optimal value α_{opt}^d of α depending on the values of f , h and N_b . To study that, we consider the 5 configurations identified for the model with constant fixation function that are given in Table 4, and we make the value of N_b vary. This is done numerically with Matlab [39], on the same numerical example as for the model with constant fixation. The parameter values of the grazing land are thus the ones given in (16). Two values of f : $f = 2.4 \times 10^{-4}$ and $f = 6 \times 10^{-4}$, are considered as in section 5.1.1, which enables to cover all the configurations of Table 4. We then consider several values for N_b . For $f = 2.4 \times 10^{-4}$, N_b takes its value in the set $\{2.8, 2.87, 3.089, 3.218\}$, and for $f = 6 \times 10^{-4}$, in the set $\{2.0, 3.0, 4.75, 7.0\}$. For each value of f and N_b , the optimal value α_{opt}^d is computed numerically for a range of value of h . The results are shown in Fig. 6b.

We first note that for small values of N_b , α_{opt}^d is equal to 0 whatever the value of h : the system (\mathcal{M}_d) indeed behaves as the model without nitrogen fixation (\mathcal{M}_0). Conversely, if the value of N_b is large, the system (\mathcal{M}_d) behaves as the model with constant fixation function (\mathcal{M}_c) and $\alpha_{opt}^d = \alpha_{opt}^c$. For intermediate values of N_b , α_{opt}^d is equal to 0, to α_{opt}^c or to a value between 0 and α_{opt}^c depending on the value of h . Whatever the value of h , α_{opt}^d is always smaller or equal to α_{opt}^c .

In fact, we can mention two additional interesting results that are not shown on figure 6b but that are presented in appendix B.2. First, for a given value of h , if there exists some values of α for which the plants are fixing at equilibrium, then the optimal value α_{opt}^d of α corresponds to such a case (even when there is bi-stability). In other words, to maximize the production of manure, plants have to fix at equilibrium. Secondly, when the value α_{opt}^c of α leads to a stable equilibrium point for the model with discontinuous fixation function (\mathcal{M}_d) (that is when the stable positive equilibrium point of (\mathcal{M}_c) is located inside D_f), then $\alpha_{opt}^d = \alpha_{opt}^c$. It means that, if the optimal equilibrium point of the model

with constant fixation function (\mathcal{M}_c) is also an equilibrium point for the model with discontinuous fixation function (\mathcal{M}_d), then it is the optimal configuration for (\mathcal{M}_d) too, in terms of maximisation of T . Some details about these last two results are given in appendix B.2, where a more detailed (but technical) analysis of the optimisation of T with respect to α in the case of the model with discontinuous fixation function (\mathcal{M}_d) is given.

5.2. Optimization with α and h

Let's now study the maximization of T with respect to both parameters α and h . In the sequel, we denote h_{opt}^c and h_{opt}^d the optimal values of h for systems with constant fixation (\mathcal{M}_c) and discontinuous fixation function (\mathcal{M}_d) respectively. For simplicity, the optimal values of α is still denoted α_{opt}^c and α_{opt}^d as in the preceding paragraph even if they do not depend on h anymore. The optimization is performed numerically with Matlab [39] for both systems.

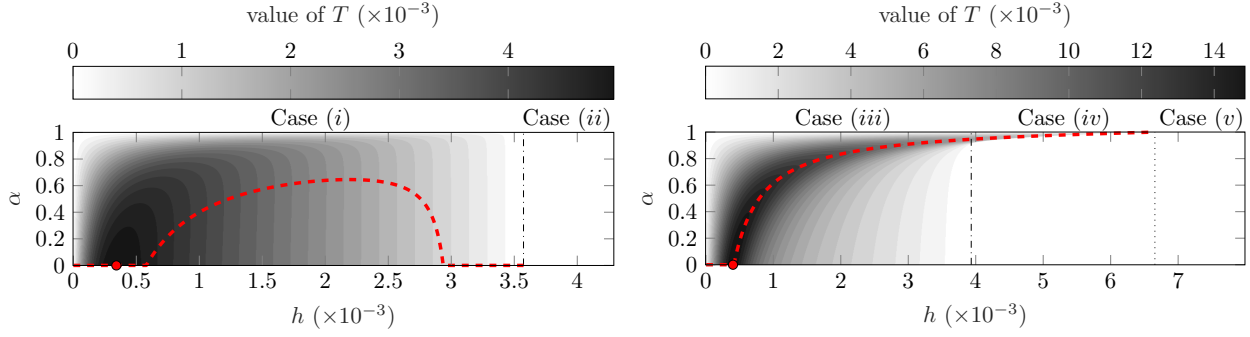
5.2.1. Model with constant fixation function

We consider the same numerical example as in section 5.1.1. The model parameters are thus the one given in (16). The maximal value T_{max} of T has been computed for a range of values of f between 0 and 6.3. The values α_{opt}^c and h_{opt}^c for which this maximum is reached have also been determined. We first note that $\alpha_{opt}^c = 0$ whatever the value of f . The values of h_{opt}^c and T_{max} are given in Figure 7a. T_{max} is always increasing with f , which is logical: the more the plants fix, the greater the amount of nitrogen that can be transferred. The value of h_{opt}^c first decreases and then increases with f .

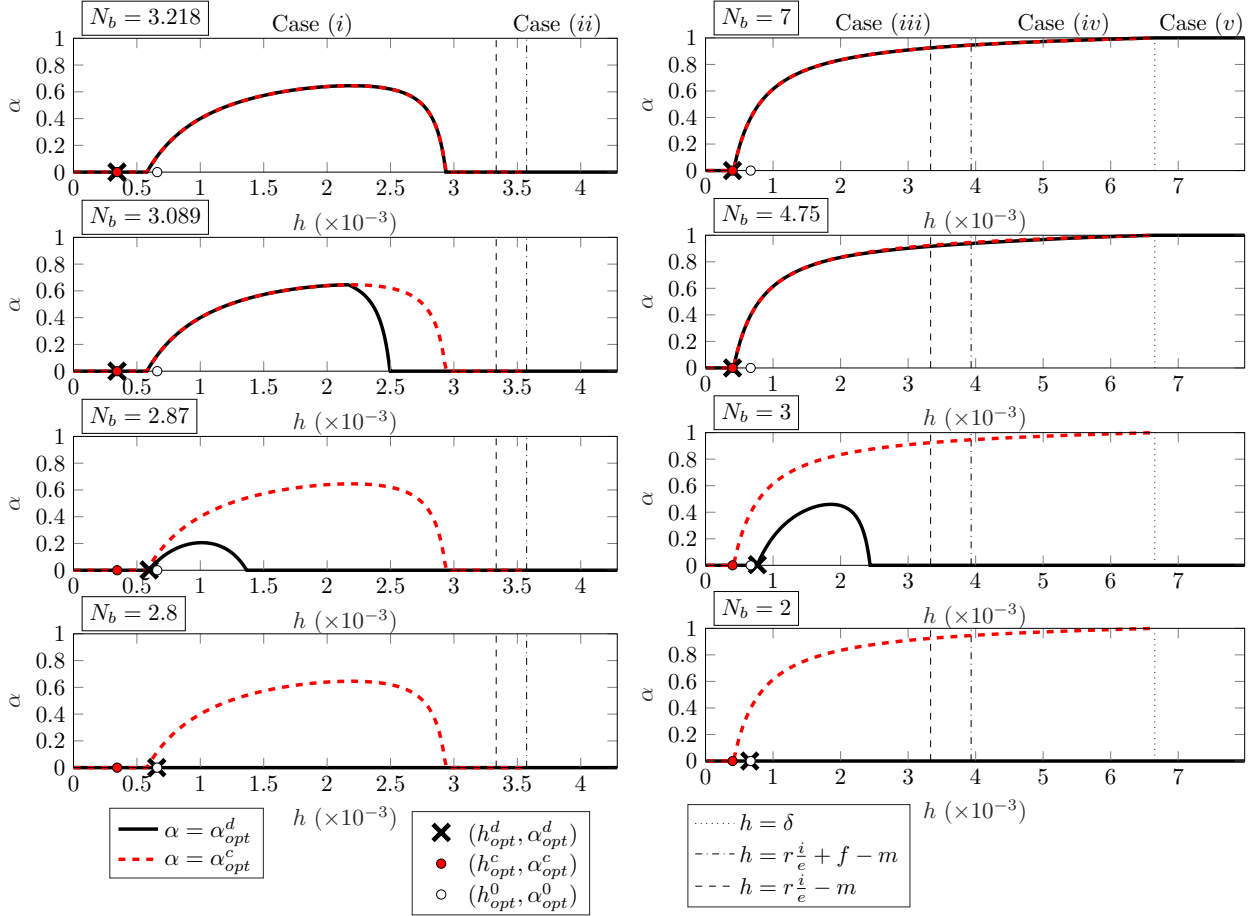
5.2.2. Model with discontinuous fixation function

The same numerical optimization as the one performed for the model with constant fixation function has been done for the model with discontinuous fixation function for a range of values of N_b between 0 and 12. The maximal value T_{max} and the values α_{opt}^d and h_{opt}^d for which this maximum is reached have been determined for each value of f and N_b . As for the model with constant fixation function, the optimal value α_{opt}^d of α is always equal to 0. The values of T_{max} and h_{opt}^d are shown in Figure 7b. We first note that there exists a threshold value of N_b , close to 2.73, below which T_{max} and h_{opt}^d are constant and take the same values as for the model without fixation (\mathcal{M}_0), that is $T_{max} \simeq 0.77$ and $h_{opt}^d \simeq 0.95$. It corresponds to cases where the equilibrium points of (\mathcal{M}_f) are located in D_0 whatever the values of α , f and h . In that cases, only the equilibrium of (\mathcal{M}_0) is reachable and the maximal value of T is therefore equal to the one of (\mathcal{M}_0).

For values of N_b greater than this threshold, there exist some configurations (i.e. some values of α , h and f) for which the equilibrium point of (\mathcal{M}_c) is reachable, that is located inside D_f . We note that in that cases, T_{max} is increasing with N_b and with f , which seems logical as the greater f and N_b , the more the plants can fix. On the other hand, the value of h_{opt}^d decreases with N_b and decreases



(a) Model with constant fixation function. Left: Cases (i) and (ii): $0 < f = 2.4 \times 10^{-4} < \frac{i}{K} = \frac{0.02}{80} = 2.5 \times 10^{-4}$. Right: Cases (iii) to (v): $\frac{i}{K} = \frac{0.02}{80} = 2.5 \times 10^{-4} < f = 6 \times 10^{-4}$



(b) Model with discontinuous fixation function. Left: Cases (i) and (ii): $0 < f = 2.4 \times 10^{-4} < \frac{i}{K} = \frac{0.02}{80} = 2.5 \times 10^{-4}$. Right: Cases (iii) to (v): $\frac{i}{K} = \frac{0.02}{80} = 2.5 \times 10^{-4} < f = 6 \times 10^{-4}$

Figure 6: Optimal value α_{opt} of α with respect to h for the model with constant fixation function (\mathcal{M}_c) and the model with discontinuous fixation function (\mathcal{M}_d) for different values of f , and of f and N_b . The other parameters of the grazing land take the following values: $r = 0.004$, $m = 0.01$, $e = 0.006$, $K = 80$, $i = 0.02$.

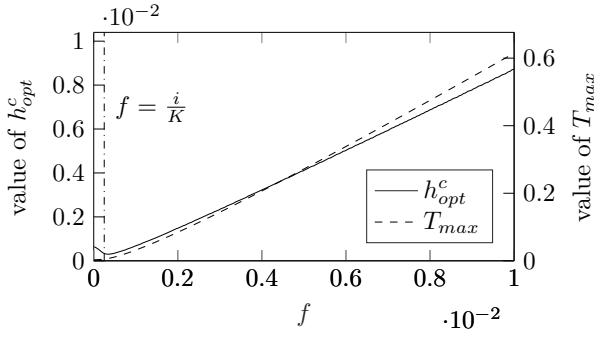
then increases with f , as for the model with constant fixation function. Finally, we can show that to maximize the value of T , we need the plant to be fixing nitrogen at equilibrium. Indeed, the maximal value T_{max} of T is always obtained for some configurations where the plants are fixing at equilibrium.

6. Discussion

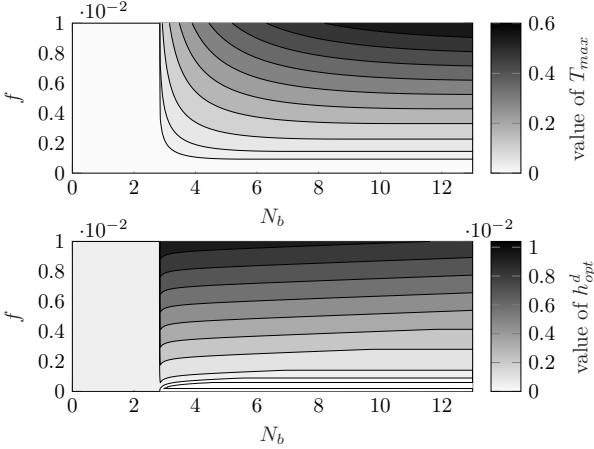
6.1. Optimal livestock management

6.1.1. Recycling vs exportation of the manure

In our previous paper [6], where biological nitrogen fixation was not considered, we showed that to maximize the



(a) Model with constant fixation function.



(b) Model with discontinuous fixation function.

Figure 7: Optimization of T with α and h . The optimal values h_{opt} of h and T_{max} of T are given for the model with constant fixation function (\mathcal{M}_c) and the model with discontinuous fixation function (\mathcal{M}_d) for different values of f , and of f and N_b . The optimal value of α is always equal to 0 (not shown on the figure). The other parameters of the grazing land take the following values: $r = 0.004$, $m = 0.01$, $e = 0.006$, $K = 80$, $i = 0.02$.

flux of nutrients exported by livestock, no manure should be recycled within the grazing land ($\alpha = 0$). With the presence of nitrogen-fixing plants in the grazing land (model studied in the present paper), this result is no longer true. The optimal value of the recycling percentage (parameter α) leads to the best compromise between a high nitrogen fixation flux, and a small soil nitrogen loss flux. It depends on the grazing rate but also on the nitrogen fixation strategy of the plants, which can be very different from one species to another [42, 17]. In particular, we can mention the obligate and facultative fixation strategies [41]. The first one correspond to plants that fix nitrogen whatever the environmental conditions (constant fixation function), whereas the plants with facultative fixation strategy adjust their fixation rate depending on the nitrogen soil concentration (discontinuous fixation function). In both cases, we showed that there are some levels of grazing rates, for which it is preferable to recycle some of the manure produced by the livestock within the grazing land rather than exporting it entirely to maximize the flux of exported manure. Thus, the

manure recycling helps maintain the nitrogen fixation and makes the whole system benefit from an additional source of nitrogen.

To interpret this results in terms of concrete livestock management, recall (see paragraph 2.3) that the recycling percentage (parameter α) and the grazing rate (parameter h) depend on the time spent by the livestock in the grazing land, on the type of livestock and on the size of the herd. Changing the values of these parameters therefore requires adapting the daily route of the herd and/or changing the type of livestock or the size of the herd. For a given type of livestock, both the grazing time and the herd size (per unit area) can be determined so that they correspond to a pair of optimal values of recycling percentage and grazing rate. There are therefore several possibilities to choose from, depending on the needs of the livestock, for example, or the size of the grazing area. From this choice, we can then determine the values of some important parameters of livestock management (see definitions given in [64]): stocking rate, grazing pressure, forage demand, etc. In particular, the stocking rate, defined in [64] as “the number of animals allotted to an area for a given length of time”, is considered as one of the most important decision to take for the grazing land and livestock production management [59, 54, 23].

6.1.2. Optimizing the whole system

If we now look at the optimal management of livestock in terms of both recycling percentage and grazing rate, we are back to the case where it is not worthwhile to recycle some of the manure in the grazing land ($\alpha = 0$). Indeed, in order to maximize the nutrient transfer, it is necessary to maximize inputs through fixation and minimize outputs to the soil. In order to minimize the soil nitrogen outputs, it is better not to add anything to the soil and therefore to export everything. Recall that considering a manure recycling rate equal to 0 implies that the livestock do not graze on the grazing land (see paragraph 2.3) and that the grazing land is therefore a fields of forage crops. With respect to the optimal value of h , that has to be interpreted here as an uptake rate of plant biomass in the forage crop fields since $\alpha = 0$ (see paragraph 2.3), it corresponds to an intermediate value that is neither too high, nor too low, allowing plants in the fields of forage crops to grow sufficiently to transfer a maximum of nutrients out of the system. The higher the capacity of the plants to fix nitrogen, the larger the optimal value of the uptake rate, which highlights again that the system benefits from the nitrogen fixation.

The optimal values of grazing rate and recycling percentage that we have determined in this paper are constant values over time, which assumes that the livestock management is the same throughout the year. Due to the seasonality of crops and climate, this assumption is obviously too strong. In our previous paper [6], we showed that by varying the grazing rate over time, we could achieve a greater crop production at the end of the year. A similar analysis could be performed on the new version of the model with nitrogen fixing plants. The idea is to adapt the grazing and

recycling during the year to meet the needs of the plants, which also change over time. It is a good way to increase Nutrient-use efficiency as advocated in some papers [66].

6.2. Exploitation of the *N*-fixers pump to enrich the system

In the grazing land, *N*-fixers bring some nitrogen from atmosphere to the soil. We propose to use the expression “*N*-fixers pump” to refer to this process, by reference to the “whale pump” that brings nutrients from deep to shallower waters in the oceans [57, 16]. The present study shows that to maximize flux of exported manure from grazing land, the *N*-fixers pump must be kept alive, which implies that the soil nitrogen at equilibrium remains below the plant fixation threshold. It means that the optimal livestock management strategies (optimal recycling percentage and grazing rate) lead to equilibrium states where the plants in the grazing land fix nitrogen and consequently enrich the whole system. It highlights the importance of nutrient inputs in agricultural system and the role of nutrient provider of the *N*-fixers. The *N*-fixers pump has been exploited for a long time, especially in soil with low nitrogen availability [20, 13]. With the advent of synthetic fertilizers, it was tempting to neglect this process in order to improve yields. However, the current ecological context is leading to a rethinking of cropping strategies, with the objective of reducing the use of fertilizers and the associated pollution. Indeed while nitrogen requirements for global food production are increasing, the use of chemical fertilizers contributes significantly to soil, water and air pollution. The exploitation of the *N*-fixers pump should therefore be considered as an interesting alternative to the use of chemical fertilizers. The objective is to optimize the management of agricultural systems to make maximum use of biological nitrogen fixation [62].

Moreover, the *N*-fixers pump is not the only asset of *N*-fixers. In addition to improving soil fertility, these plants “*also aid in solubilizing unsolvable phosphorus (P) in the soil, increasing soil microbial activity, ameliorating the soil physical environment, restoring organic matter, and smothering weeds*” [63, 21] [29].

6.3. Perspectives for the use of the model

6.3.1. Primary succession of nitrogen fixing plants

The model studied in this paper can be used to highlight the concept of primary succession which represents the evolution of the composition (in terms of species) of an ecosystem that develops on a virgin substrate. This concept has been discussed in many papers [45, 11, 67].

In the present paper, the model analysis showed how the ability to fix atmospheric nitrogen of plants allowed them to settle in infertile soils. This analysis supports the view that nitrogen fixers have an advantage in areas with low nitrogen availability [22, 1]. Indeed, such environments are characterized in the model by a low ratio of inorganic nitrogen input flux (parameter i) to inorganic nitrogen output rate (parameter e). The availability of nitrogen in these soils is therefore low, as they receive little input, and do not retain

nutrients. Only nitrogen-fixing plants that have both a high fixation rate (f) and a high fixation threshold (N_b) can colonize such soils (Case C of figure 5). As the plants establish, they contribute to improve the soil structure [47, 29, 63]. The soil will thus retain more nutrients, which results in a decrease of e and an increase of the ratio $\frac{i}{e}$. Moreover, the plants enrich the soil in nitrogen [63, 29], thanks to their ability to fix it. The environment will then become favorable for nitrogen-fixing plants with lower fixation capacities (lower fixation rate and threshold, Case B of figure 5). After the establishment of this second class of plants, the soil quality will further improve [63, 29] to the point where the quality of the soil and the availability in nitrogen will be good enough for any plant to settle, whether it is a nitrogen fixing plant or not (Case A of figure 5).

Note that this interpretation does not take into account the competition between species since only one type of plant is considered in the model. Moreover, it relies upon the assumption that nitrogen is the main limiting factor of primary production. The energetic cost of nitrogen fixation being high [48], the nitrogen-fixing plants may be competitively disadvantaged in soils with high nitrogen availability [22]. However, the present study does not enable us to answer this question: the analysis only show that a larger number of plants can settle in environments with a greater structure and nutrient availability.

Other models have been developed for the study of the primary succession [65, 61]. In [30] for example, the effects of the interaction between nitrogen fixation and competition for the phosphorus on the primary succession has been studied.

6.3.2. The case of plant communities

In the model developed in this article, only one species of plant has been represented. Therefore, the fixation function φ takes into account the fixation capacities of this single species; in particular, the threshold value was introduced to represent the inhibition of the fixation by the quantity of nitrogen in the soil. However, the plant compartment can also be considered as representative of a community of several species. In this case, the fixation function must be interpreted as the resulting fixation function at the community scale. Then the variability of the fixation function with respect to N is no more due to the inhibition of the process by the quantity of nitrogen in the soil, but to the competition and succession processes inside the community under consideration.

In [30] (Figure 6, appendix A) where the competitive succession process is described, the effective fixation rate has been found to be an increasing function of the soil N limitation, which corresponds well to the sigmoid fixation function proposed in our paper.

Nevertheless, to properly simulate the dynamic of plants succession, it is necessary to explicitly represent the impact of plant biomass on the soil structure in the model. Moreover, it should be mentioned that the livestock grazing can interfere with the succession process. It can maintain the

Model name	Fixation function (with N in g.m^{-3})
SOILN	$\varphi(N) = \begin{cases} 1 - 0.0784 \ln(10^3 N) & \text{if } N \geq 10^{-3} \\ 1 & \text{either} \end{cases}$
Schwimming	$\varphi(N) = \epsilon \times \left(1 - f_{\max} \frac{1}{1 + \frac{K_N}{N}} \right)$
EPIC	$\varphi(N) = \begin{cases} 1 & \text{if } N \leq 10 \\ 1.5 - 0.05N & \text{if } 10 < N < 30 \\ 0 & \text{either} \end{cases}$

Table 5

Different expressions of the the fixation function given in [35].

succession at an "early" stage [45] allowing N -fixers to remain predominant. But livestock can also keep N -fixers at a low level if they graze N -fixers (which may be more apetant in some cases) preferably [55].

6.4. Model limitations

6.4.1. Nitrogen fixation modelling

In the present paper, the biological nitrogen fixation has been modelled. In a review of 2011 [35], the authors give an overview of the different expressions used in the literature to represent the effect of soil mineral N content on N fixation. Three expressions of f are given (see table 5) that are slightly different but all decreasing with N . We chose here to consider a discontinuous fixation function that is also decreasing with the soil nitrogen content but is somewhat simpler than those discussed in [35]. However, it allowed us to perform a mathematical analysis of the model from which we could draw conclusions about the impact of fixation on the optimal livestock management to be implemented to maximize manure transfer. In addition, since there is a wide range of fixing strategies [42, 17], one can expect just as many corresponding functions.

We know from numerous studies that the energetic cost of nitrogen fixation is high [48]. This cost has not been taken into account directly in the model. We just assumed that the fixation rate can not be greater than the mortality rate, which implies that the growth of nitrogen-fixing plants cannot be based on fixation alone. Without nitrogen in the soil, they thus can not grow. In the model, the effect of the fixation is therefore indirect: through the mortality of the plants, it increases the nitrogen compartment N which is then available for the growth of the plants. Obviously, more realistic model of nitrogen fixation can be considered such as the detailed metabolic models and the coarse-grained models presented in [26].

6.4.2. Livestock modelling

In the model studied in this paper, livestock is represented only indirectly through two parameters: the grazing rate and the manure recycling percentage. It is in fact the flow of nutrients transferred by livestock that is represented in the model and that we want to maximize.

Yet, the benefits of livestock in crop-livestock systems with grazing area are not limited to this transfer. Livestock also provide draft power to cultivate the land [24], increase

biodiversity by grazing [43] and even improve the conservation of nutrients in the ecosystem [14]. In addition, in many traditional economies, livestock is also a source of food (meat and milk), and a way to store currency [52, 24]. To represent all that, it is necessary to add a new variable in the model that corresponds to the livestock biomass or population.

This is what is done in [4], based on the same model as the one considered in this article, but without nitrogen fixation. The multi-criteria optimizations that were carried out in this study lead to different strategies that can be applied according to the considered objectives: immediate production (maximizing both crop and meat productions) or risk management (maximizing crop production and the size of the livestock).

Other studies based on modeling approaches explicitly consider livestock in the model variables. In [14, 40], a model of interactions between plants and grazing herbivores is studied in order to assess the impact of grazing on plant production. In [19, 9], the authors use prey-predator ecological models to represent the dynamics of grass (prey) and grazing livestock (predator). They determine the optimal stocking rate, i.e. the number of animals per hectare for which the maximum meat yield (in kg of meat per hectare per year) is achieved. In [23], the question of optimizing the stocking rate is also addressed by an economic modeling approach in which the dynamics of the animal biomass are explicitly represented. The objective this time is to maximize profits. Finally, the impact of some scenarios of decreased availability of feed and synthetic fertiliser imports on the animal and crop production in a farming system is assessed in [50], where a dynamic model is proposed that takes into account the livestock compartment.

7. Conclusion

In this paper we address the issue of the maximization of fertility transfer from grazing land to crop production in a mixed farming system. For this purpose, we used a modeling approach. The pastures are represented by a plant-soil model in which the role of livestock is modeled by nutrient flows between the plant and soil compartments and to the outside. In the model, the plants fix nitrogen only if the nitrogen concentration in the soil is below a given threshold. The objective was to find the optimal livestock management that maximizes the flux of nutrients exported by the livestock. In the model, the livestock management is characterized by both the percentage of recycling of the manure produced by livestock to grazing land, and the grazing rate. We first showed that when grazing rate is high and the capacity of plants to fix nitrogen is important, it is necessary to recycle some of the manure produced by the livestock in the grazing land to maximize the flux of nutrients exported. On the other hand, if we optimize both grazing rate and manure recycling percentage, then it is better to transfer all the produced manure and to adapt the grazing rate accordingly to minimize nitrogen losses from the soil. Finally, to max-

imize the flow of exported nutrients, it is also necessary to bring the system to a state in which the plants fix nitrogen. In this way, we can benefit from the nitrogen fixation which provides an additional input of nitrogen in the system.

The model considered in this article is quite simple, and the results therefore remain theoretical. Nevertheless, it is interesting to see that the study of such a simple model shows that the presence of nitrogen-fixing plants in a mixed farming system can increase crop production, without the addition of chemical fertilizers. This confirms the fact that nitrogen-fixing plants are an interesting alternative to chemical fertilizers, thus allowing a more sustainable agriculture in the future. As for mixed farming systems, their reintegration in Europe in new forms (reconnection of livestock farms with crop fields on a regional scale) also seems relevant, both to increase production and to decrease pollution.

A. Mathematical analysis of model (\mathcal{M}_c)

In this appendix, we give the details about the mathematical analysis of model (\mathcal{M}_c), which consists in the computation of the equilibrium points and the study of their stability.

A.1. Equilibrium points of model (\mathcal{M}_c)

The graphical determination of the equilibrium points of (\mathcal{M}_c) that is presented in section 4.1.1 can be formulated mathematically by the following proposition:

Proposition A.1. *Let denote $s = \frac{e}{f+(\alpha-1)h}$ and:*

$$\Delta = r^2 \left(\frac{i}{e} + \frac{K}{s} \right)^2 - 4r \frac{K}{s} (m+h-f) \quad (17)$$

If $\frac{i}{e} < \frac{m+h-f}{r}$, we also define $\bar{s} = \frac{K(m+h-f)}{r\bar{N}^2} > 0$ with:

$$\bar{N} = \frac{m+h-f}{r} + \frac{1}{r} \sqrt{(m+h-f)(m+h-f-r\frac{i}{e})} \quad (18)$$

The system (\mathcal{M}_c) admits $E_0 = (N_0 = \frac{i}{e}, P_0 = 0)$ as equilibrium point whatever the parameter values are.

In addition to E_0 , we have the following equilibrium points:

- if $\frac{i}{e} > \frac{m+h-f}{r}$, then there exists a unique positive equilibrium point $E_1^f := (N_1^f, P_1^f) \in (\mathbb{R}^+)^2$ given by:

– if $f + (\alpha - 1)h \neq 0$:

$$E_1^f = \left(\frac{1}{2} \left(\frac{i}{e} + \frac{K}{s} + \frac{\sqrt{\Delta}}{r} \right), \frac{1}{2} \left(K - \frac{is}{e} + s \frac{\sqrt{\Delta}}{r} \right) \right) \quad (19)$$

– if $f + (\alpha - 1)h = 0$:

$$E_1^f = \left(\frac{i}{e}, K \frac{e}{ri} (r \frac{i}{e} + f - m - h) \right) \quad (20)$$

We moreover have:

$$\lim_{f+(\alpha-1)h \rightarrow 0^+} E_1^f = \lim_{f+(\alpha-1)h \rightarrow 0^-} E_1^f = \left(\frac{i}{e}, K \frac{e}{ri} (r \frac{i}{e} + f - m - h) \right). \quad (21)$$

- if $\frac{i}{e} < \frac{m+h-f}{r}$ and $0 < s = \bar{s}$, then there exists a unique positive equilibrium point $E_1^f := (N_1^f, P_1^f) \in (\mathbb{R}^+)^2$ which is given by:

$$E_1^f = \left(\frac{1}{2} \left(\frac{i}{e} + \frac{K}{s} \right), \frac{1}{2} \left(K - \frac{is}{e} \right) \right) \quad (22)$$

- if $\frac{i}{e} < \frac{m+h-f}{r}$ and $0 < s < \bar{s}$ then there exists two positive equilibrium points $E_1^f := (N_1^f, P_1^f) \in (\mathbb{R}^+)^2$ and $E_2^f := (N_2^f, P_2^f) \in (\mathbb{R}^+)^2$ which are given by:

$$E_1^f = \left(\frac{1}{2} \left(\frac{i}{e} + \frac{K}{s} + \frac{\sqrt{\Delta}}{r} \right), \frac{1}{2} \left(K - \frac{is}{e} + s \frac{\sqrt{\Delta}}{r} \right) \right) \quad (23)$$

$$E_2^f = \left(\frac{1}{2} \left(\frac{i}{e} + \frac{K}{s} - \frac{\sqrt{\Delta}}{r} \right), \frac{1}{2} \left(K - \frac{is}{e} - s \frac{\sqrt{\Delta}}{r} \right) \right) \quad (24)$$

Proof:

Consider the case where $f + (\alpha - 1)h \neq 0$ and let us solve the equation $F_1(N) = F_2(N)$ where F_1 and F_2 are defined in (10). We have, for all $N \in \mathbb{R}^+ \setminus \{0\}$:

$$F_1(N) = F_2(N) \Leftrightarrow \mathcal{P}(N) = 0 \quad (25)$$

with $\mathcal{P}(N) = rN^2 - rN \left(\frac{i}{e} + \frac{K}{s} \right) + \frac{K}{s} (m+h-f)$. The discriminant of \mathcal{P} is written:

$$\begin{aligned} \Delta &= r^2 \left(\frac{i}{e} + \frac{K}{s} \right)^2 - 4r \frac{K}{s} (m+h-f) \\ &= r^2 \left(\frac{i}{e} - \frac{K}{s} \right)^2 + 4r \frac{K}{s} \left(r \frac{i}{e} - m - h + f \right) \end{aligned} \quad (26)$$

In the case where $\frac{i}{e} > \frac{m+h-f}{r}$, we thus have $\Delta > 0$ whatever the sign of s . In that case, there exists two roots:

$$N^* = \frac{1}{2} \left(\frac{i}{e} + \frac{K}{s} \right) \pm \frac{\sqrt{\Delta}}{2r} \quad (27)$$

the corresponding value of $P^* = s(N^* - \frac{i}{e})$ being:

$$P^* = \frac{K}{2} - \frac{is}{2e} \pm s \frac{\sqrt{\Delta}}{2r}. \quad (28)$$

Among these two points, only one is positive in the sense $(P^*, N^*) \in (\mathbb{R}^+)^2$; it is the one given by (19).

In the case where $\frac{i}{e} < \frac{m+h-f}{r}$, and:

- if $\Delta = 0$, then there exists only one solution to the equation $F_1(N) = F_2(N)$. Moreover, a simple study of the function $\Delta : s \mapsto \Delta(s)$ shows that there exists two values of s such that $\Delta(s) = 0$. Among these two values, only one ensures that the solution of $F_1(N) = F_2(N)$ is positive (i.e. $\in (\mathbb{R}^+)^2$); it is the value $s = \bar{s}$ which leads to the equilibrium point given by (22).
- if $\Delta > 0$, then there exists two real solutions to the equation $F_1(N) = F_2(N)$. A simple study of the function $\Delta : s \mapsto \Delta(s)$ shows that the condition $0 < s < \bar{s}$ is the necessary and sufficient condition for the positivity of Δ and the positivity of at least one of the two solutions of $F_1(N) = F_2(N)$. In fact, the two solutions of $F_1(N) = F_2(N)$ are in this case positive; it is the ones which correspond to the equilibrium points given by (23) and (24).

In the case where $f + (\alpha - 1)h = 0$, system (8) leads to $N = \frac{i}{e}$ and $P \left(rN \left(1 - \frac{P}{K} \right) + f - m - h \right) = 0 \Leftrightarrow P = 0$ or $P = F_1(\frac{i}{e})$.

A.2. Stability of the equilibrium points of (\mathcal{M}_c)

Proposition A.2. • E_0 is stable if and only if $\frac{i}{e} < \frac{m+h-f}{r}$;

- if $\frac{i}{e} > \frac{m+h-f}{r}$, then the unique positive equilibrium point E_1^f is always stable;
- if $\frac{i}{e} < \frac{m+h-f}{r}$ and $0 < s < \bar{s}$ then the equilibrium point E_1^f is always stable and the equilibrium point E_2^f is always unstable.
- if $\frac{i}{e} < \frac{m+h-f}{r}$ and $0 < s = \bar{s}$, then the equilibrium point E_1^f is non hyperbolic.

Proof: The Jacobian matrix of the system (1) at the point E_0 is given by:

$$J(E_0) = J\left(\frac{i}{e}, 0\right) = \begin{pmatrix} r\frac{i}{e} - m - h + f & 0 \\ -r\frac{i}{e} + m + \alpha h & -e \end{pmatrix} \quad (29)$$

This matrix has two eigenvalues that are $r\frac{i}{e} - m - h + f$ and $-e < 0$. As a consequence, E_0 is stable if and only if $r\frac{i}{e} - m - h + f < 0 \Leftrightarrow \frac{m+h-f}{r} > \frac{i}{e}$.

The equilibrium points E_1^f and E_2^f are such that:

$$rP_i^f N_i^f \left(1 - \frac{P_i^f}{K} \right) = i + mP_i^f + \alpha hP_i^f - eN_i^f \quad (30)$$

$$\text{and } rN_i^f \left(1 - \frac{P_i^f}{K} \right) = m + h - f \quad (31)$$

By using these relationships, we get the following expression of the Jacobian matrix of system (1) at the point $E_i^f, i = 1, 2$:

$$J(E_i^f) = \begin{pmatrix} -\frac{rP_i^f N_i^f}{K} & rP_i^f \left(1 - \frac{P_i^f}{K} \right) \\ \frac{rP_i^f N_i^f}{K} + f + (\alpha - 1)h & -rP_i^f \left(1 - \frac{P_i^f}{K} \right) - e \end{pmatrix} \quad (32)$$

The real part of the eigenvalues of a 2×2 matrix are strictly negative if and only if the trace of the matrix is strictly negative and the determinant of the matrix is strictly positive. Here we have:

$$\text{Tr}(J(E_i^f)) = -\frac{rP_i^f N_i^f}{K} - rP_i^f \left(1 - \frac{P_i^f}{K} \right) - e \quad (33)$$

which is always strictly negative, because $N_i^f > 0$ and $0 < P_i^f < K$. Moreover, after simple calculations, we have:

$$\det(J(E_i^f)) = \frac{rP_i^f}{K} \left(i + \frac{e}{s}(2P_i^f - K) \right) \quad (34)$$

The equilibrium point E_i^f is therefore stable if and only if:

$$\det(J(E_i^f)) > 0 \Leftrightarrow \begin{cases} \frac{K}{2} - i\frac{s}{2e} < P_i^f & \text{if } s > 0 \\ \frac{K}{2} - i\frac{s}{2e} > P_i^f & \text{if } s < 0 \end{cases} \quad (35)$$

We have:

- if $\frac{i}{e} > \frac{m+h-f}{r}$, then only E_1^f exists and we have $P_1^f := \frac{1}{2}(K - \frac{is}{e} + s\frac{\sqrt{\Delta}}{r})$. So $P_1^f > \frac{1}{2}(K - \frac{is}{e})$ if $s > 0$ and $P_1^f < \frac{1}{2}(K - \frac{is}{e})$ if $s < 0$. The equilibrium point E_1^f is therefore always stable in that case if it exists.
- if $\frac{i}{e} < \frac{m+h-f}{r}$ and $0 < s = \bar{s}$, then only one equilibrium point E_1^f exists and we have $P_1^f = \frac{1}{2}(K - \frac{is}{e})$. The Jacobian matrix has therefore at least one of its eigenvalue which is equal zero: E_1^f is non hyperbolic.
- if $\frac{i}{e} < \frac{m+h-f}{r}$ and $0 < s < \bar{s}$ then there exists two equilibrium points E_1^f and E_2^f with $P_1^f = \frac{1}{2}(K - \frac{is}{e} + s\frac{\sqrt{\Delta}}{r})$ and $P_2^f = \frac{1}{2}(K - \frac{is}{e} - s\frac{\sqrt{\Delta}}{r})$. We so have $P_1^f > \frac{1}{2}(K - \frac{is}{e})$ and $P_2^f < \frac{1}{2}(K - \frac{is}{e})$, which means (as $s > 0$) that, if they exist, E_1^f is always stable and E_2^f is always unstable.

B. Maximization of T with respect to α

This appendix focuses on the maximization of the flux of nutrient exported by the livestock from grazing land (the quantity T). In section B.1, we give some details about the computation of the value of α for which T is maximal, for a given value of h with the model with constant fixation function. In sections B.2 and B.3, a more detailed analysis of the case with discontinuous fixation function is given.

B.1. Model with constant fixation function

Consider a given value of h . The objective is here to find the value of α for which T is maximal.

The equilibrium point $E_1^f = (N_1^f, P_1^f)$ is solution of the equations 8, which lead, after simple computations to:

$$T = (1 - \alpha)hP_1^f = P_1^f f + i - \frac{eK}{r} \frac{m + h - f}{K - P_1^f} \quad (36)$$

After derivation with respect to α , we get:

$$\frac{\partial T}{\partial \alpha} = \frac{\partial P_1^f}{\partial \alpha} \left(f - \frac{eK}{r} \frac{m + h - f}{(K - P_1^f)^2} \right) \quad (37)$$

It can be easily shown that $\frac{\partial P_1^f}{\partial \alpha} > 0$. Indeed, E_1^f is the intersection point of the curves of F_1 and F_2 (see equations (10)). When α increases from 0 to 1, the curve of F_1 does not move but the curve of F_2 rotates around the point $(\frac{i}{e}, 0)$ clockwise (see figure 8). The intersection point between F_1

and F_2 moves therefore to the right on the curve of F_1 : thus P_1^f and N_1^f increase with α .

The sign of $\frac{\partial T}{\partial \alpha}$ therefore depends on the sign of $f - \frac{eK}{r} \frac{m+h-f}{(K-P_1^f)^2}$. We have:

$$f - \frac{eK}{r} \frac{m+h-f}{(K-P_1^f)^2} > 0 \Leftrightarrow \begin{cases} P_1^f < K - \sqrt{\frac{eK}{rf}(m+h-f)} \\ \text{or} \\ P_1^f > K + \sqrt{\frac{eK}{rf}(m+h-f)}. \end{cases} \quad (38)$$

However, we know (see proposition A.1) that $P_1^f < K$, so we have:

$$\frac{dT}{d\alpha} \begin{cases} > 0 \text{ if } P_1^f < P^m \\ = 0 \text{ if } P_1^f = P^m \\ < 0 \text{ if } P^m < P_1^f < K \end{cases} \quad (39)$$

with $P^m = K - \sqrt{\frac{eK}{rf}(m+h-f)}$. So, if P^m is in the range of reachable values for P_1^f , that is if there exists $\alpha \in [0, 1]$ such that $P_1^f = P^m$ exists, then the maximal value T_{max} of T is reached for $P_1^f = P^m$ and is given by:

$$T_{max} = P^m f + i - \frac{eK}{r} \frac{m+h-f}{K-P^m} \quad (40)$$

This expression can be simplified, because P^m is such that $\frac{eK}{r} \frac{m+h-f}{(K-P^m)^2} = f$. We so have:

$$T_{max} = P^m f + i - f(K - P^m) = (2P^m - K)f + i \quad (41)$$

This value is reached for $\alpha = \alpha_m$ such that:

$$(1 - \alpha_m)hP^m = T_{max} \Leftrightarrow \alpha_m = 1 - \frac{2f}{h} - \frac{i - Kf}{hP^m} \quad (42)$$

B.2. Model with discontinuous fixation function

In section 5.1.2, the maximization of T with respect to α , in the case of the model with discontinuous fixation function has been studied. To further understand the results shown in this section, we introduce here after some quantities which can help for a better understanding of the model behavior.

Indeed, as for the equilibrium points, the determination of the optimal value α_{opt}^d of α can be partly deduced from the study of the model with constant fixation function (\mathcal{M}_c) and the model without fixation (\mathcal{M}_0). Remember that with the model (\mathcal{M}_d), the space $\mathcal{D} := \{(N, P) \in [0, \infty) \times [0, K]\}$ is divided in two parts: \mathcal{D}_f and \mathcal{D}_0 , the first part gathering the states with values of N smaller than N_b and the second one the states with values of N greater than N_b (see section 4.1.2). For a given value of $h > 0$, the idea is first to determine the range of values of α for which (\mathcal{M}_0) (respectively (\mathcal{M}_c)) admits a stable positive equilibrium point in \mathcal{D}_0 (respectively in \mathcal{D}_f). Then we can determine the maximal value of T in both \mathcal{D}_0 and \mathcal{D}_f and keep the largest one. However there is in fact a third candidate for the optimal

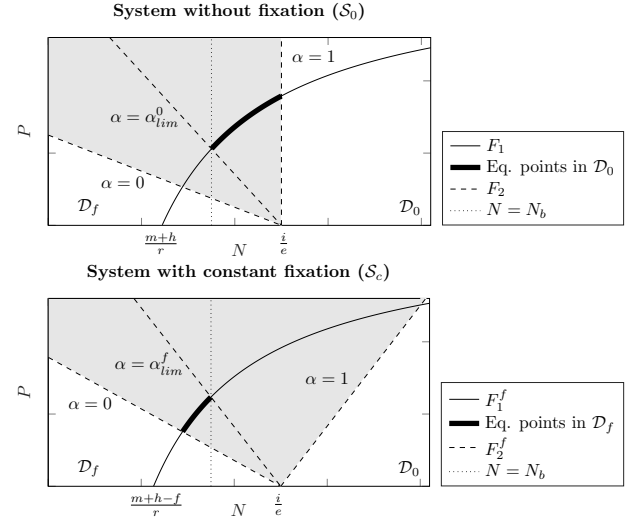


Figure 8: Graphical illustration of the definition of α_{lim}^0 and α_{lim}^f on some concrete configurations of the system without fixation (\mathcal{M}_0) (top) and of the system with constant fixation function (\mathcal{M}_c) (bottom).

value of T as there exist some values of α for which neither (\mathcal{M}_0) nor (\mathcal{M}_c) admit a stable equilibrium point in \mathcal{D}_0 or \mathcal{D}_f (see Fig. 4b). In that cases, recall that the system (\mathcal{M}_d) converge to an equilibrium point E_{N_b} located on the frontier between \mathcal{D}_0 and \mathcal{D}_f , that is on the straight line $N = N_b$. We therefore also have to determine the maximal value of T on this frontier if such cases are possible, and to compare this value with the two other ones to find the maximal value of T .

Provided that $h < \frac{ir}{e} - m$, the system (\mathcal{M}_0) admits a stable positive equilibrium point in \mathcal{D} whatever the value of $\alpha \in [0, 1]$. With the introduction of N_b and the consideration of a discontinuous fixation function, we are now only interested in the cases where this stable positive equilibrium point is located in \mathcal{D}_0 . As highlighted on figure 8, the range of values of α for which it is the case is reduced to a set of the form $[\alpha_{lim}^0, 1]$, with $0 \leq \alpha_{lim}^0 \leq 1$. The analytical expression of α_{lim}^0 is given in appendix B.3.

The system (\mathcal{M}_c) admits a stable positive equilibrium point for all the values of α in the set Ω_α . As highlighted on figure 8, the range of values of α for which this equilibrium point is located in \mathcal{D}_f is of the form $[\min(\Omega_\alpha), \alpha_{lim}^f]$ where $\min(\Omega_\alpha) \leq \alpha_{lim}^f \leq 1$. The analytical expression of α_{lim}^f is given in appendix B.3.

Finally, if $\alpha_{lim}^f < \alpha_{lim}^0$, then the values of α in $[\alpha_{lim}^f, \alpha_{lim}^0]$ correspond to cases where neither (\mathcal{M}_0) nor (\mathcal{M}_c) admit a stable equilibrium point in \mathcal{D}_0 or \mathcal{D}_f , and (\mathcal{M}_d) converges to E_{N_b} .

On this figure, the values of α_{lim}^0 , α_{lim}^f and α_{opt} have also been added.

On Fig. 9, we also introduced a color code to indicate in which part of \mathcal{D} the equilibrium point of (\mathcal{M}_d) is located,

and so if the plant fix the nitrogen at equilibrium (D_f) or not (D_0). In the cases of bi-stability, this is the equilibrium for which the value of T is the greatest that is considered. The white area correspond to cases where P^* (and as a consequence T) is always equal to 0. The light gray, middle gray and dark gray areas respectively correspond to cases where the equilibrium point of (\mathcal{M}_d) is located in D_0 (no fixation), on the straight line $N = N_b$ (limit case) and in D_f (fixation) respectively. These areas are delimited by the curves of α_{lim}^0 and α_{lim}^f and the lines $\alpha = 0$ and $\alpha = 1$.

The smaller the value of N_b , the wider the light gray area. Indeed, in that cases, the plants can fix only for small values of N , which promotes cases where the plants are not fixing at equilibrium. On the contrary, the larger the value of N_b , the wider the dark gray area: as plants fix for a wide range of values of N , this will be also the case at equilibrium. Note finally, that the middle gray area is also increasing with N_b .

The area between the curve of α_{lim}^0 and $\alpha = 1$ (respectively $\alpha = \min(\Omega_\alpha)$ and the curve of α_{lim}^f) corresponds to the cases where (\mathcal{M}_d) admits a stable positive equilibrium point in D_0 (respectively in D_f). These two areas can overlap, the common part corresponding to the cases where (\mathcal{M}_d) admits two stable positive equilibrium points, one in D_0 and one in D_f . We note that this common part is always colored in dark gray, which means that when there is bi-stability, this is always the equilibrium point located in D_f that leads to the greatest value of T . Finally, we notice that, when the optimal value α_{opt}^c leads to an equilibrium point located in D_f (i.e. α_{opt}^c is inside the dark gray area), we have $\alpha_{opt}^d = \alpha_{opt}^c$. It means that, if the optimal equilibrium point of the model with constant fixation function (\mathcal{M}_c) is also an equilibrium point for (\mathcal{M}_d), then it is the optimal configuration for (\mathcal{M}_d) too, in terms of maximisation of T .

B.3. Expression of α_{lim}^0 and α_{lim}^f

We consider here the model with discontinuous fixation function (\mathcal{M}_d). In this section, we give the analytical expression of the variables α_{lim}^0 and α_{lim}^f that were introduced in the previous section.

If $\frac{i}{e} > \frac{m+h}{r}$, the system (\mathcal{M}_0) admits a stable positive equilibrium point E_1 in D whatever the value of $\alpha \in [0, 1]$. The range of values of α for which this equilibrium point $E_1 = (N_1, P_1)$ is in D_0 is of the form $[\alpha_{lim}^0, 1]$ (see figure 8). Let's denote $N_1(\alpha)$ the value of N_1 for a given value of α . The value of α_{lim}^0 depends on the value of N_b as follows:

- if $N_b < N_1(0)$, then $\alpha_{lim}^0 = 0$;
- if $N_b > \frac{i}{e}$, then $\alpha_{lim}^0 = 1$;
- if $N_1(0) < N_b < \frac{i}{e}$, then α_{lim}^0 is equal to the value of α such that $F_1(N_b)|_{f=0} = F_2(N_b)|_{f=0}$ (see (10)) :

$$\alpha_{lim}^0 = 1 + \frac{e}{hF_1(N_b)|_{f=0}} \left(N_b - \frac{i}{e} \right) \quad (43)$$

If $\frac{i}{e} > \frac{m+h-f}{r}$ or if $\frac{i}{e} < \frac{m+h-f}{r}$ and $0 < s < \bar{s}$, then the system (\mathcal{M}_c) admits a stable positive equilibrium point E_1^f

Parameter	range of values	source
r	0.0035 - 0.0065 ha kgN ⁻¹ d ⁻¹	[5]
K	63 - 117 kgN ha ⁻¹	[37]
f	0.0006 - 0.0025 d ⁻¹	[44, 56]
N_b	0 - 12	computed
m	0.000014 - 0.022 d ⁻¹	[38]
e	0.0035 - 0.0065 d ⁻¹	[49]
i	0.014 - 0.026 kgN ha ⁻¹ d ⁻¹	[15, 8]
h	0 - 0.11 d ⁻¹	computed
α	0 - 1 unitless	percentage

Table 6

Ranges of model parameter values and associated references.

in D . Let's consider only the cases where $\Omega_\alpha \neq \emptyset$ (see table 4). The range of values of α for which the equilibrium point $E_1^f = (N_1^f, P_1^f)$ is in D_f is of the form $[\min(\Omega_\alpha), \alpha_{lim}^f]$ (see figure 8). Let's denote $N_1^f(\alpha)$ the value of N_1^f for a given value of α . The value of α_{lim}^f depends on the value of N_b as follows:

- if $N_b < N_1^f(\min(\Omega_\alpha))$, $\alpha_{lim}^f = \min(\Omega_\alpha)$
- if $N_1^f(1) < N_b$, $\alpha_{lim}^f = 1$
- if $N_1^f(\min(\Omega_\alpha)) < N_b < N_1^f(1)$, then α_{lim}^f is equal to the value of α such that $F_1(N_b)|_f = F_2(N_b)|_f$:

$$\alpha_{lim}^f = 1 + \frac{e}{hF_1(N_b)|_f} \left(N_b - \frac{i}{e} \right) - \frac{f}{h} \quad (44)$$

C. Parameter values and sensitivity analysis

The ranges of values for the model parameters found in literature are given in the table 6 with the associated references.

A sensitivity analysis was performed with R [53] using the Morris's Elementary Effects Screening Method that is implemented in the package sensitivity [27]. For each model parameter and for both values of N and P at equilibrium, two sensitivity indices were computed with this method [10]: μ^* and σ , that are respectively the mean and standard deviation of the distribution of the elementary effects of a given parameter on a given output. The values of these indices are given in Table 7.

We note that e and i are the parameters that most influence the value N^* of nitrogen at equilibrium. The value P^* of plant nitrogen compartment at equilibrium is strongly influenced by the fixation threshold N_b and the parameters related to the livestock management (h and α).

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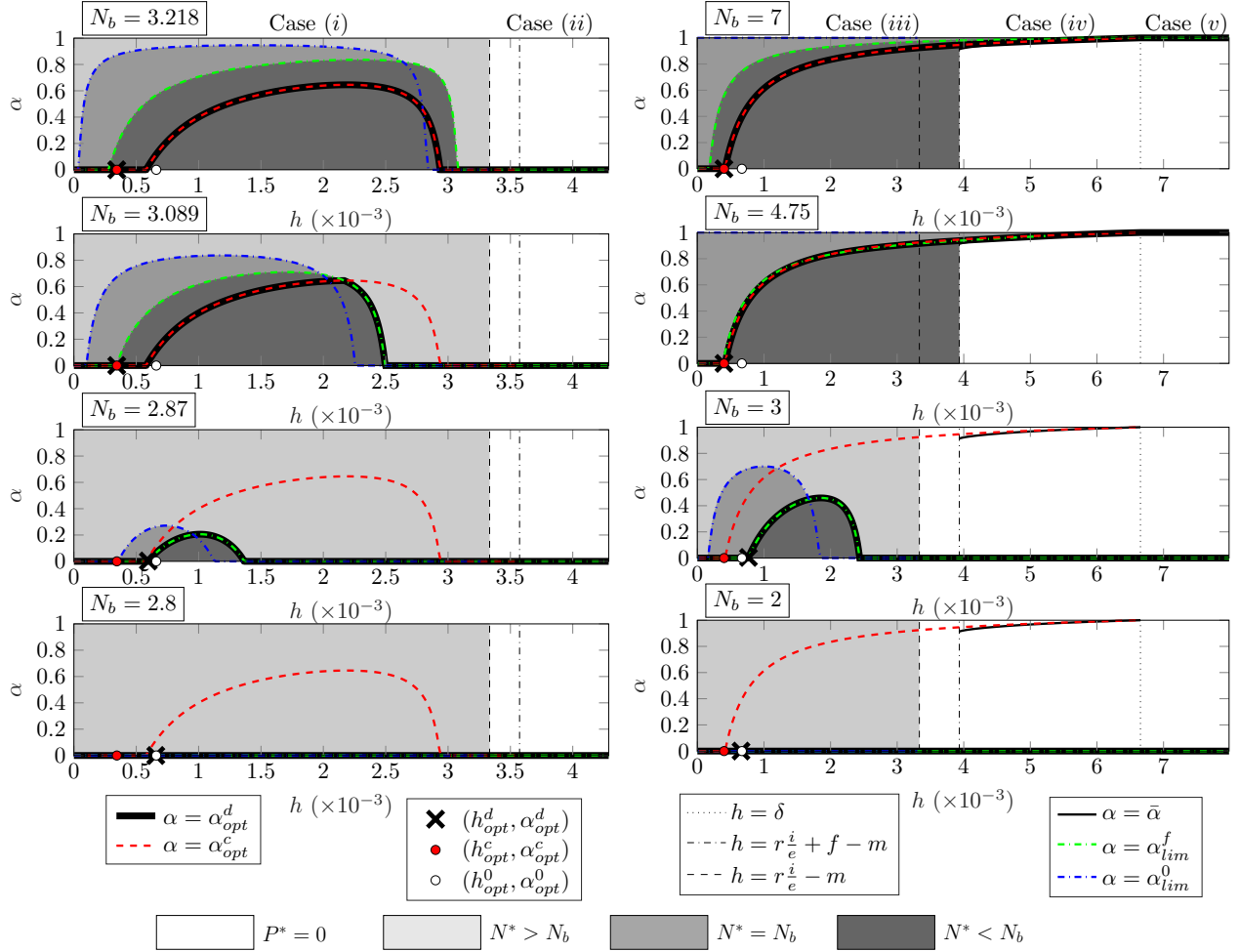


Figure 9: Optimal value α_{opt} of α with respect to h for the model with discontinuous fixation function (\mathcal{M}_d) for different values of f and N_b . The other parameters of the grazing land take the following values: $r = 0.004$, $m = 0.01$, $e = 0.006$, $K = 80$, $i = 0.02$. Left: Cases (i) and (ii): $0 < f = 2.4 \times 10^{-4} < \frac{i}{K} = \frac{0.02}{80} = 2.5 \times 10^{-4}$. Right: Cases (iii) to (v): $\frac{i}{K} = \frac{0.02}{80} = 2.5 \times 10^{-4} < f = 6 \times 10^{-4}$.

parameters	outputs			
	N^*		P^*	
	μ^*	σ	μ^*	σ
r	0.135	0.443	0.655	2.692
K	0.023	0.138	0.671	4.594
f	0.189	1.369	1.217	8.530
N_b	0.468	2.141	2.337	11.451
m	0.205	0.831	1.253	5.339
e	2.269	0.951	0.902	4.805
i	2.212	0.794	1.048	4.385
h	0.994	2.867	4.416	12.867
α	0.392	1.901	2.319	10.079

Table 7

Sensitivity indices (μ^* and σ) obtained with the Morris's Elementary Effects Screening Method.

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