



HAL
open science

Maximization of fertility transfers from rangeland to cropland: the contribution of control theory

Anne Bisson, Céline Casenave, Simon Boudsocq, Tanguy Daufresne

► To cite this version:

Anne Bisson, Céline Casenave, Simon Boudsocq, Tanguy Daufresne. Maximization of fertility transfers from rangeland to cropland: the contribution of control theory. *Journal of Theoretical Biology*, 2019, 469, pp.187-200. 10.1016/j.jtbi.2019.01.039 . hal-02066979

HAL Id: hal-02066979

<https://hal.science/hal-02066979v1>

Submitted on 13 Mar 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Accepted Manuscript

Maximization of fertility transfers from rangeland to cropland: the contribution of control theory.

Anne Bisson, Céline Casenave, Simon Boudsocq, Tanguy Daufresne

PII: S0022-5193(19)30032-3
DOI: <https://doi.org/10.1016/j.jtbi.2019.01.039>
Reference: YJTBI 9830



To appear in: *Journal of Theoretical Biology*

Received date: 17 July 2018
Revised date: 16 November 2018
Accepted date: 21 January 2019

Please cite this article as: Anne Bisson, Céline Casenave, Simon Boudsocq, Tanguy Daufresne, Maximization of fertility transfers from rangeland to cropland: the contribution of control theory., *Journal of Theoretical Biology* (2019), doi: <https://doi.org/10.1016/j.jtbi.2019.01.039>

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

Highlights

- A simple meta-ecosystem model is proposed to represent mixed farming system
- Optimization of livestock-induced nutrient transfer from rangeland to cropland improves crop production
- Control theory provides tools that take into account the variability over time of agricultural practices
- Time-varying livestock management can lead to higher crop production

Maximization of fertility transfers from rangeland to cropland: the contribution of control theory.

Anne Bisson^{a,b,*}, Céline Casenave^a, Simon Boudsocq^b, Tanguy Daufresne^b

^aUMR MISTEA, Univ Montpellier, INRA, Montpellier SupAgro, Montpellier, France

^bUMR Eco&Sols, Univ Montpellier, IRD, INRA, Montpellier Supagro, CIRAD, Montpellier, France

Abstract

In traditional mixed farming systems, soil fertility in cropland relies on the transfer of fertility from rangeland through the transfer of manure produced by livestock that grazes in rangeland. In this work, we introduce a simple meta-ecosystem model in which the mixed farming system is represented by a cropland sub-system connected to a rangeland sub-system by nutrient fluxes. The livestock plays the role of nutrient-pump from the rangeland sub-system to the cropland sub-system. We use this model to study how spatial organization and practices of livestock management such as the control of grazing pressure and night corralling can help optimize both nutrient transfers and crop production.

We argue that addressing the optimization of crop production requires different methods, depending on whether the agricultural practice in focus is constant or variable over time. We first used classical optimization methods at equilibrium to address optimization when the grazing pressure was as-

*Corresponding author

Email address: anne.bisson@supagro.fr (Anne Bisson)

sumed to be constant over time. Second, we address optimization for a more realistic configuration of our model, where grazing pressure was assumed to vary over the course of a year. In this case, we used methods developed in the field of the control theory. Classical methods showed the existence of an optimal level of constant grazing pressure that maximizes the transfers from rangeland to cropland, leading to the maximization of crop production. Control methods showed that by varying the grazing pressure adequately an additional gain of production is possible, with higher crop production and lower nutrient transfer from rangeland to cropland. This additional gain arises from the fact that the requirement of nutrient by crops is variable along the year. Consequently, a constant adjustment of the grazing pressure allows a better match between nutrient transfer and nutrient requirement over time, leading to a substantial gain of crop biomass. Our results provide new insights for a “smarter” management of fertility transfers leading to higher crop production with less rangeland surface.

Keywords: meta-ecosystem, fertility transfer, crop production, control theory

1. Introduction

In the context of demographic growth and economic changes, modern agriculture is facing an increasing demand in crop production. The crop production strongly relies on soil fertility which is usually maintained by addition of nutrient from external sources. In intensive high-yield agriculture, soil fertility relies on addition of synthetic fertilizers (Tilman et al., 2002). In traditional mixed farming systems, exploited by most smallholders in developing

8 countries (Food and Agriculture Organization of the United Nations., 2011),
9 the addition of fertilizers from external sources is usually too costly (Dugué
10 et al., 2011) and soil fertility relies on the addition of organic matter from
11 animal manure (Powell et al., 1996, Manlay et al., 2004). Therefore, increas-
12 ing crop production relies mostly on the optimization of these agricultural
13 practices, which are the driving forces of the agro-ecosystem functioning.

14 Indeed, the current practice is to use livestock as a “nutrient pump”,
15 displacing nutrient from rangeland to cropland. The terminology “biological
16 pump” comes from Longhurst and Glen Harrison (1989) which defines the
17 transfer of carbon and nitrogen from the euphotic zone through the downward
18 flow of various organic matters (see also the terminology “whale pump” of
19 Roman and McCarthy (2010) and “nutrient pump” of Bisson et al., in review).
20 Livestock is herded in rangeland during the day where it feeds and ingests
21 nutrient that it partly transfers to cropland by excreting manure during night
22 corralling. Many agricultural practices affect the transfer of nutrient. We
23 focused on three key practices, namely, the rangeland to cropland surface
24 ratio, the grazing pressure, and the fraction of nutrient consumed by livestock
25 in rangeland that is effectively transferred to cropland. The first one may
26 be referred to as an “organizational” practice since it transforms the spatial
27 organization of the landscape. It has strong implications for the balance
28 of nutrient at landscapes scale. The two later practices may be referred to
29 as “interconnection” practices because they directly determine the fluxes of
30 nutrient between rangeland and cropland.

31 Here we propose to study these key practices through the use of a math-
32 ematical model, a classical approach in theoretical ecology (DeAngelis, 1992,

33 Loreau, 2010). Several dynamical systems have already been proposed to
34 help optimize the grazing in agro-ecosystems (e.g. Noy-Meir (1975), Wood-
35 ward et al. (1993). In the vein of these works, some recent studies suggest
36 that theoretical ecology provides some valuable theoretical tools to address
37 agronomic questions (Dieguez Cameroni and Fort, 2017, Fort et al., 2017).

38 To take into account the patchiness of the landscape with regard to nu-
39 trient, and more specifically the source-sink dynamics between rangeland
40 and cropland, we based our approach on the meta-ecosystem theory (Loreau
41 et al., 2003). We define sources and sinks according to Loreau et al. (2013)
42 where a source (sink) sub-system is an exporter (importer) of nutrient within
43 the whole agro-ecosystem. By construction, our model shows sources-sink
44 properties. Sources-sink dynamics simply result from the nutrient transfer
45 by livestock from rangeland to cropland. This theory provides a convenient
46 framework to address source-sink dynamics and its consequences for primary
47 production in natural landscapes (Loreau et al., 2013). It has been proved
48 recently to be applicable to agro-ecosystems (Bisson et al., in review). We
49 built a simple meta-ecosystem model with two sub-systems (rangeland and
50 cropland) to assess the optimization of crop production through the three
51 agricultural practices introduced earlier.

52 We looked for configurations and management strategies that maximized
53 crop production. Depending on whether the practices are of the “organiza-
54 tional” or “interconnection” types, the optimization of crop production with
55 respect to these practices require different methods. Therefore, for “organi-
56 zational” practices, that do not change over time (at least over one year), the
57 optimization can be addressed through the use of “classical” methods, such

58 as sensitivity analysis, numerical exploration or minimization of an objective
59 function. However, such methods are not well-adapted to study practices of
60 livestock management that may change over a year. For “interconnection”
61 practices, we advocate for the use of methods of control theory. Control the-
62 ory is a mathematical framework dedicated to the control of systems (Astrom
63 and Murray, 2008, Levine, 2010, Corriou, 2004). It has already been used for
64 agronomic and environmental issues such as the reduction of the soil sodicity
65 (Mau and Porporato, 2016), the optimization of cutting frequency of grass-
66 land (Chen, 1986, Chen and Wang, 1988), or robust management of natural
67 resource (Anderies et al., 2007). Its objective is to propose some mathemat-
68 ical expressions for the inputs of a system that makes the controlled system
69 behave as desired. The input values adapt over time according to the system
70 state and to the constraints on the parameters values, creating a feedback
71 loop. In this paper, we first address the optimization of crop production
72 by using a classical method of optimization at equilibrium. Second, we no
73 longer study the values at equilibrium but take advantage of the transient
74 dynamics to lead the system at a given state: we address optimization of
75 crop production when grazing pressure can vary over the course of the year
76 with the use of methods developed in the control theory.

77 **2. Ecological model of the agro-ecosystem**

78 We model the agro-ecosystem as a simple meta-ecosystem composed of
79 a cropland sub-system of surface s_c and a rangeland sub-system of surface
80 s_r (figure C.1). Each sub-system (z), with $z = c$ for cropland and $z = r$
81 for rangeland is composed of two compartments: plants (P_z) and inorganic

82 nutrient (N_z). Both P_z and N_z compartment represent stocks of nutrient. For
 83 the sake of simplicity and genericity, only one limiting nutrient (for instance
 84 nitrogen, phosphorus or potassium) of primary production is represented in
 85 this model. We are aware that considering multiple nutrients instead of
 86 a single, and considering specificities of nutrient biogeochemical cycles (for
 87 instance, the symbiotic fixation for nitrogen) would carry out more outcomes.
 88 However, it would also bring complexity that would prevent the detection of
 89 generic mechanisms.

90 [Figure 1 about here.]

91 We used a classic formalism in ecology (DeAngelis, 1992, Loreau, 2010).
 92 The equations of the meta-ecosystem model are:

$$\begin{cases} \dot{P}_r &= u_r P_r N_r \left(1 - \frac{P_r}{K_r}\right) - m_r P_r - d_r P_r \\ \dot{N}_r &= -u_r P_r N_r \left(1 - \frac{P_r}{K_r}\right) - e_r N_r + i_r + m_r P_r + \alpha d_r P_r \\ \dot{P}_c &= u_c P_c N_c \left(1 - \frac{P_c}{K_c}\right) - m_c P_c \\ \dot{N}_c &= -u_c P_c N_c \left(1 - \frac{P_c}{K_c}\right) - e_c N_c + i_c + m_c P_c + \underbrace{(1 - \alpha) d_r P_r}_{T} \frac{s_r}{s_c} \end{cases} \quad (1)$$

93 The units and definition of the model parameters are summarized in ta-
 94 ble C.1. In each sub-system (z), plants take-up nutrient from the inorganic
 95 nutrient compartment N_z following a modified logistic growth with a max-
 96 imal growth rate u_z and a carrying capacity K_z . Nutrient is recycled back
 97 to the N_z compartment at a constant rate m_z through plant mortality and
 98 mineralization. Nutrient input in each sub-system is a constant flux of inor-
 99 ganic nutrient i_z . Losses of inorganic nutrient N_z are mainly due to erosion,
 100 leaching and are modelled by a linear term with a constant rate e_z .

101 In this model, we only consider livestock as a vector of nutrient from the
 102 rangeland sub-system to the cropland sub-system, therefore livestock is not
 103 explicitly represented. The rate of grazing pressure d_r (in d^{-1}) is proportional
 104 to the amount of plants P_r . We can consider the grazing pressure d_r as an
 105 aggregated parameter of livestock biomass (in kgN ha^{-1}) multiplied by the
 106 consumption coefficient of grass biomass by livestock (in $\text{ha kgN}^{-1} \text{d}^{-1}$).
 107 The flux of nutrient from compartment P_r carried by livestock from the
 108 rangeland sub-system is split in two parts: a fraction α is recycled directly
 109 in the inorganic compartment of the rangeland sub-system (N_r), the other
 110 part ($1 - \alpha$) is transferred to the inorganic compartment of the cropland
 111 sub-system (N_c). The term $T = (1 - \alpha)d_r P_r$ is the one which connects both
 112 sub-systems.

113 In the cropland sub-system, harvest is not modelled as a continuous pro-
 114 cess along the year but as a punctual event; it consists in the removal of a
 115 percentage h of the plant compartment in the cropland sub-system every 365
 116 days.

117 [Table 1 about here.]

118 The meta-ecosystem model has a particular structure hereafter named
 119 “cascade structure” (Seibert and Suarez, 1990). Indeed, the rangeland sub-
 120 system (r), composed of the equations of P_r and N_r , does not depend on the
 121 dynamics of the cropland sub-system (c), that is composed of the equations
 122 of P_c and N_c . This cascade structure enables to study independently the two
 123 sub-systems. Moreover, the two sub-systems have the same organization and

124 both can be written under the following form:

$$\begin{cases} \dot{P} = uPN(1 - P/K) - mP - dP \\ \dot{N} = -uPN(1 - P/K) - eN + i + mP + \beta dP \end{cases} \quad (2)$$

- 125 • with $P = P_r$ and $N = N_r$ for the state variables and $u = u_r$, $K =$
126 K_r , $m = m_r$, $e = e_r$, $i = i_r$, $\beta = \alpha$ and $d = d_r$ for the parameters of
127 the rangeland sub-system,
- 128 • with $P = P_c$ and $N = N_c$ for the state variables and $u = u_c$, $K =$
129 K_c , $m = m_c$, $e = e_c$, $i = i_c + T\frac{s_r}{s_c}$, $\beta = 0$ and $d = 0$ for the parameters
130 of the cropland sub-system.

131 2.1. Equilibrium points of the generic sub-system model and their stability

132 Let us study the generic sub-system (2). For biological relevance, both
133 plant biomass and inorganic nutrient stocks have to be positive ($P, N \geq 0$).
134 Furthermore the model is built such that plant biomass cannot exceed the
135 carrying capacity K . We therefore only look at the equilibrium points that
136 are inside the set $[0, K] \times \mathbb{R}^+$: it represents the set of (P, N) values of the
137 dynamical system (2) that are biologically acceptable.

138 We show that the system (2) always admits one and only one stable
139 equilibrium point whose value depends on the parameters. By definition,
140 the equilibrium points (P^*, N^*) of the system (2) are the solutions of the
141 following equations:

$$\begin{cases} uPN(1 - P/K) - mP - dP = 0 \\ -uPN(1 - P/K) - eN + i + mP + \beta dP = 0 \end{cases} \quad (3)$$

142 The trivial equilibrium point E_0 corresponds to the case where there is
143 no plant in the sub-system. E_0 exists whatever the parameter values and is

144 given by:

$$E_0 := \left(P^* = 0, N^* = \frac{i}{e} \right) \quad (4)$$

145 The equilibrium point E_0 is locally stable if and only if $\frac{i}{e} < \frac{m+d}{u}$ (see Ap-
146 pendix A.1) that is if the inputs of nutrient and the growth rate are not high
147 enough to balance inorganic losses and plant mortality.

148 Let us now consider the case where $P \neq 0$. In this case, if $(\beta - 1)d < 0$,
149 then the system (3) can be written:

$$\begin{cases} P = K \frac{uN - c - d}{uN} =: F_1(N) \\ P = \frac{eN - i}{(\beta - 1)d} =: F_2(N) \end{cases} \quad (5)$$

150 Finding the solution of (5) amounts to find the intersection points of the
151 curves F_1 and F_2 , which is done graphically in the sequel. The two functions
152 F_1 and F_2 are differentiable on $\mathbb{R}^+ \setminus \{0\}$ and we have, $\forall N \in \mathbb{R}^+ \setminus \{0\}$:

$$F_1'(N) = \frac{K(m+d)}{uN^2} > 0 \quad \text{and} \quad F_2'(N) = \frac{e}{(\beta-1)d} < 0 \quad (6)$$

153 We deduce from (6) that F_1 is strictly increasing whereas F_2 is decreasing on
154 $\mathbb{R}^+ \setminus \{0\}$. Moreover we have: $\lim_{N \rightarrow 0^+} F_1(N) = -\infty$, $\lim_{N \rightarrow +\infty} F_1(N) = K$,
155 $F_2(0) = -\frac{i}{(\beta-1)d} > 0$ and $\lim_{N \rightarrow 0^+} F_2(N) = -\infty$.

156 F_1 and F_2 have therefore one and only one intersection point on $\mathbb{R}^+ \setminus \{0\}$.
157 Let us now find the conditions for which this intersection point is biologically
158 acceptable. We have: $F_1(N) = 0 \Leftrightarrow N = \frac{m+d}{u}$ and $F_2(N) = 0 \Leftrightarrow N = \frac{i}{e}$.

159 The relative position of $\frac{m+d}{u}$ and $\frac{i}{e}$ of the N-axis determines if the in-
160 tersection point is above or below the N-axis. Indeed, as we can see on
161 the figure C.2, if $\frac{i}{e} > \frac{m+d}{u}$ then the intersection point of F_1 and F_2 is
162 above the N-axis: it is therefore a biologically acceptable equilibrium point

163 $E_1 := (P_1^*, N_1^*) \in \mathbb{R}^+ \times [0, K]$. On the contrary, if $\frac{i}{e} < \frac{m+d}{u}$ then the inter-
 164 section of F_1 and F_2 is below the N-axis and it does not exist any positive
 165 equilibrium point on $[0, K] \times \mathbb{R}^+$. Note that in this case the trivial equilibrium
 166 point E_0 is stable.

167 [Figure 2 about here.]

168 The analytic expression of the positive equilibrium point E_1 can be ob-
 169 tained by solving the equation $F_1(N) = F_2(N)$ which leads to a second
 170 degree polynomial equation (see Appendix A.1). The positive equilibrium
 171 point $E_1 := (P_1^*, N_1^*)$ is finally given by:

$$E_1 := \left(P^* = \frac{1}{2}(K - a\frac{i}{e} + a\frac{\sqrt{\Delta}}{u}), N^* = \frac{1}{2}\left(\frac{i}{e} + \frac{K}{a} + \frac{\sqrt{\Delta}}{u}\right) \right) \quad (7)$$

172 for $(\beta - 1)d \neq 0$ with $a = \frac{e}{(\beta-1)d}$ and $\Delta = u^2\left(\frac{i}{e} + \frac{K}{a}\right)^2 - 4u\frac{K}{a}(m+d)$ and only
 173 exists if $\frac{i}{e} > \frac{m+d}{u}$. The analysis of its stability shows that when it exists, E_1
 174 is always locally stable (see Appendix A.1).

175 In the particular case where $(\beta - 1)d = 0$, $F_2(N)$ is a vertical line with a
 176 x coordinate $N = \frac{i}{e}$. The equilibrium point E_1 becomes:

$$E_1 := \left(P^* = K \left(1 - \frac{e(m+d)}{ui}\right), N^* = \frac{i}{e} \right) \quad (8)$$

177 Finally, there are two cases: the case where $\frac{i}{e} > \frac{m+d}{u}$, for which only E_1
 178 is stable and for which living conditions are met for plants to settle and the
 179 case where $\frac{i}{e} < \frac{m+d}{u}$, for which only E_0 is stable and for which plants cannot
 180 survive.

181 **3. Methods: optimization of the system at equilibrium and contri-**
 182 **bution of control theory**

183 In this section, we detail the optimization methods used to maximize the
 184 flux of crop production. This flux is represented by the term:

$$C = s_c P_{c,t_h}, \quad (9)$$

185 where s_c is the surface of the cropland sub-system and P_{c,t_h} the crop biomass
 186 in the cropland sub-system at the end of the year, at harvest time t_h .

187 In this paper, we will first apply a classical approach used in ecology,
 188 which consists in finding the constant values of parameters that optimize
 189 one or several quantities at equilibrium. We hereafter refer to the classical
 190 method of optimization at equilibrium with constant parameters simply as
 191 the optimization at equilibrium. The values of the optimal parameters will
 192 be obtained analytically if possible or numerically in other cases. To use
 193 this approach we have to assume that the biomass of plant has reached an
 194 equilibrium when the harvest occurs.

195 The optimization at equilibrium is well adapted to “organizational” prac-
 196 tices which are constant over time or at least fixed for a whole year, as it
 197 is the case for the rangeland to cropland surface ratio. These practices can
 198 be mathematically represented by setting constant values to parameters. On
 199 the other hand, this optimization at equilibrium is not adapted to study “in-
 200 terconnection” practices that may change over a year as it is the case for
 201 herbivory pressure. It is the very purpose of the control theory to take into
 202 account the fact that some input variables can vary over time. Secondly,
 203 we will thus study how performances of the agro-ecosystem may change if

204 grazing pressure change over the year by applying some methods developed
 205 in control theory.

206 *3.1. Optimization at equilibrium method (constant parameters)*

207 The cropland sub-system dynamics directly (and so the value of P_c and N_c
 208 at equilibrium) depends on the rangeland sub-system management through
 209 the inputs term $i = i_c + T \frac{s_r}{s_c}$ where $T = (1 - \alpha)d_r P_r$. Regarding the “in-
 210 terconnection” practices, we will focus on livestock management, which is a
 211 driver of the amount of nutrient per unit of surface that is transferred each
 212 day by livestock from the rangeland to the cropland sub-system:

$$T = (1 - \alpha)d_r P_r \quad (10)$$

213 Two parameters of the rangeland sub-system, the grazing pressure d_r and the
 214 recycled fraction α are under farmer influence and may be used as driving
 215 forces to optimize the transfer T (and maximize the crop production). Both
 216 d_r and α influence crop production C through the term T . Thanks to the
 217 cascade structure of the meta-ecosystem model, we can study this indirect
 218 impact in three steps. First we will study the variation of crop production
 219 C with T . Second, we will focus on the variation of T with α and d_r .
 220 Finally we will also study the variation of crop production C with respect to
 221 the “organizational” practice in focus: the ratio between the surfaces of the
 222 cropland sub-system and the rangeland sub-system s_r and s_c . This ratio has
 223 an impact on both the crop biomass in cropland sub-system (in kgN ha^{-1})
 224 and the crop production at the scale of the agro-ecosystem (in kgN).

225 *3.2. Control method (varying herbivory pressure)*

226 The aim is to propose a mathematical expression of the grazing pressure
 227 d_r that makes the controlled system behave as desired. We want the crop
 228 production C to reach a given value \tilde{C} , which corresponds to a value $\tilde{P}_c = \frac{\tilde{C}}{s_c}$
 229 of the crop biomass at harvest time. The mathematical expression of d_r
 230 will depend on the current state of the system and will take into account
 231 the constraints on the parameters values: in our case, d_r is positive and
 232 $\alpha \in [0, 1]$. Contrary to the previous optimization at equilibrium (section
 233 3.1), we do not assume that crop biomass has reached equilibrium when
 234 the harvest occurs. Following the cascade structure of the system, we use a
 235 control strategy composed of two feedback control loops (see figure C.3): a
 236 first loop controlling P_c with T , the amount of nutrient transferred from the
 237 rangeland to the cropland sub-system, and a second one controlling T with
 238 the grazing pressure d_r . We use feedback linearizing control laws (Isidori,
 239 1995) for the two loops and we choose some control parameters values that
 240 fulfill the constraints on the inputs.

241 [Figure 3 about here.]

242 *3.2.1. First loop: controlling P_c with T*

243 Let first design the feedback control law of the first loop. Remind that
 244 \tilde{P}_c is the value of P_c that we expect P_c to reach at the end of the year: it
 245 is the set-point. Assume that T can be modified by the farmer all over the
 246 year: T is the control input.

247 Consider the functions G_1 and G_2 defined by:

$$G_1(P_c, N_c) = u_c P_c N_c (1 - P_c/K_c) - m_c P_c, \quad (11)$$

$$G_2(P_c, N_c) = -u_c P_c N_c (1 - P_c/K_c) - e_c N_c + i_c + m_c P_c, \quad (12)$$

248 that are such that system (23) can be written:

$$\begin{cases} \dot{P}_c = G_1(P_c, N_c) \\ \dot{N}_c = G_2(P_c, N_c) + T \frac{s_r}{s_c} \end{cases} \quad (13)$$

249 The equation of P_c has a relative degree equal to 2 with respect to the
250 control input T : it means that we need to derivate two times P_c to make
251 appear explicitly the control input T in the equation of P_c . We thus get:

$$\ddot{P}_c = G_1 \partial_1 G_1 + \left(G_2 + T \frac{s_r}{s_c} \right) \partial_2 G_1. \quad (14)$$

252 To obtain a second order dynamics for P_c , that is, an equation of the form
253 $\ddot{P}_c + 2\xi\omega\dot{P}_c + \omega^2 P_c = \omega^2 \tilde{P}_c$ where ω is the cutoff frequency and ξ the damping
254 factor, we have to consider the following expression of T :

$$T = \frac{u - G_1 \delta_1 G_1 - G_2 \delta_2 F}{\frac{s_r}{s_c} \delta_2 G_1} \quad (15)$$

255 with $u = -2\xi\omega\dot{P}_c + \omega^2(\tilde{P}_c - P_c)$. The expression (15) of T is called a “lin-
256 earizing control law” as it enables to get a linear dynamics of the closed loop
257 system. To be biologically acceptable, the value of T has to be positive; we
258 so define the quantity \tilde{T} by:

$$\tilde{T} = \max \left(0, \frac{-2\xi\omega G_1 + \omega^2(\tilde{P}_c - P_c) - G_1 \delta_1 G_1 - G_2 \delta_2 F}{\frac{s_r}{s_c} \delta_2 G_1} \right) \quad (16)$$

259 *3.2.2. Second loop: controlling T with the grazing pressure d_r*

260 Contrary to what was assumed in the previous paragraph, T can not be
 261 directly modified by the farmer. \tilde{T} has to be viewed as a set-point for T ,
 262 that is a value that we expect T to be close of at any time. Note that, unlike
 263 the first loop, the value of the set-point \tilde{T} varies over the time.
 264 There are 2 driving forces in the agro-ecosystem which may control the value
 265 of T : d_r and α . In the sequel, we assume that α is fixed and we consider
 266 d_r as the control input. The objective of the second control loop is therefore
 267 to control T with d_r . The quantity T is given by $T = (1 - \alpha)d_r P_r^*$. After
 268 derivation, we get:

$$\dot{T} = (1 - \alpha)\dot{d}_r P_r + (1 - \alpha)d_r \dot{P}_r \quad (17)$$

269 The equation of T is therefore of relative degree equal to 1 with respect to
 270 the control input d_r . To obtain a first order dynamics for T in closed loop,
 271 that is, an equation of the form $\dot{T} = k(\tilde{T} - T) = k(\tilde{T} - (1 - \alpha)d_r P_r)$ with k
 272 a control parameter, we have to use the following control law for d_r :

$$\dot{d}_r = \frac{k(\tilde{T} - (1 - \alpha)d_r P_r) - (1 - \alpha)d_r \dot{P}_r}{(1 - \alpha)P_r}. \quad (18)$$

273 In practice, we add a saturation to this control law in order to ensure
 274 that the applied value of d_r is realistic, that is non negative. The applied
 275 control law is so:

$$d_r = \max(0, d) \text{ with } \dot{d} = \frac{k(\tilde{T} - (1 - \alpha)d P_r) - (1 - \alpha)d \dot{P}_r}{(1 - \alpha)P_r}. \quad (19)$$

276 *3.2.3. Choice of the control parameters values*

277 The values of the control parameters (ω , ξ and k) are chosen to make the
 278 system stabilize after about 365 days. To ensure that, we consider the two
 279 loops independently.

280 The first loop is the slowest one: it will impose its stabilization time to
 281 the whole system. The closed loop equation of P_c is a second order one,
 282 with parameters ξ and ω . For such systems, an approximation of the 1%
 283 settling time, that is the time necessary for the response to reach and remain
 284 in the interval $[0.99\tilde{P}_c, 1.01\tilde{P}_c]$ (with \tilde{P}_c the set-point), is given by Goodwin
 285 and Sin (1984) $\frac{4.6}{\xi\omega}$. The value of ξ will also determine whether the output
 286 will oscillate before stabilizing or not. For values of ξ greater than 0.7, the
 287 response is very damped, there is almost no oscillations. For this reason, we
 288 chose to take a value of ξ equal to 0.9. To get a 1% settling time smaller
 289 than 365 days, we have to consider a value of ω that is such that:

$$\frac{4.6}{\xi\omega} < 365 \Leftrightarrow \omega > \frac{4.6}{365\xi} \simeq 0.014 \text{ (with } \xi = 0.9) \quad (20)$$

290 We chose to take a value of ω equal to 0.015 that is a little bit greater
 291 than 0.014: it ensures that the system will have reached the set-point at the
 292 harvest time. For $\omega = 0.015$ and for $\xi = 0.9$, we indeed have $\frac{4.6}{\xi\omega} \simeq 341$ days.

293 The second loop, which is the internal loop, has to be faster than the first
 294 one in order to ensure the stability of the first loop. In general, we try to
 295 have a settling time at least 1000 times faster in the internal loop, which in
 296 our case corresponds to a maximum value of 0.34 days. The equation of T is
 297 a first order system with time constant $\frac{1}{k}$. For such systems, the 1% settling
 298 time is about $\frac{5}{k}$ (Corriou, 2004). We therefore have:

$$\frac{5}{k} < 0.34 \Leftrightarrow k > \frac{5}{0.34} \simeq 14.7 \quad (21)$$

299 We chose to take a value of k equal to 20 that is a little bit greater than 14.7.

300 So finally, the values of the control parameters used for the control strat-

301 egy are the following ones:

$$\omega = 0.015, \xi = 0.9 \text{ and } k = 20. \quad (22)$$

302 4. Results

303 *4.1. Cropland sub-system as a sink: the greater the transfers, the greater the*
304 *crop production*

305 We first focus on the sub-system (*c*) that corresponds to cropland and
306 look at the variation of the crop production with respect to the nutrient
307 transfer T .

308 Remind that the equations of the cropland sub-system are of the form
309 (2) with $P = P_c$ and $N = N_c$ for the state variables and $u = u_c$, $K =$
310 K_c , $m = m_c$, $e = e_c$, $i = i_c + T \frac{s_r}{s_c}$, $\beta = 0$ and $d = 0$ for the parameters (with
311 $T = (1 - \alpha)d_r P_r$):

$$\begin{cases} \dot{P}_c &= u_c P_c N_c (1 - P_c / K_c) - m_c P_c \\ \dot{N}_c &= -u_c P_c N_c (1 - P_c / K_c) - e_c N_c + i_c + m_c P_c + T \frac{s_r}{s_c} \end{cases} \quad (23)$$

312 From section 2.1, the cropland sub-system always admits one stable equi-
313 librium point which depends on the parameter values and on the value P_r^*
314 reached by \bar{P}_r at equilibrium. If $\frac{i_c + T^* \frac{s_r}{s_c}}{e_c} \leq \frac{m_c}{u_c}$, this equilibrium point is given
315 by:

$$E_{0,c} := \left(P_c^* = 0, N_c^* = \frac{i_c + T^* \frac{s_r}{s_c}}{e} \right) \quad (24)$$

316 and if $\frac{i_c + T^* \frac{s_r}{s_c}}{e_c} > \frac{m_c}{u_c}$, it is given by:

$$E_{1,c} := \left(P_c^* = K_c \left(1 - \frac{m_c}{u_c} \frac{e_c}{i_c + (1 - \alpha)d_r P_r^* \frac{s_r}{s_c}} \right), N_c^* = \frac{i_c + T^* \frac{s_r}{s_c}}{e_c} \right) \quad (25)$$

317 As explained in section 3, the parameters d_r and α impact on the crop
 318 production C through the quantity $T^* = (1 - \alpha)d_r P_r^*$. We therefore study
 319 the variation of C with respect to T^* in order to determine the value of T^*
 320 that maximizes C .

321 [Figure 4 about here.]

322 From section 2.1, we know that, when $\frac{i_c + T^* \frac{s_r}{s_c}}{e_c} > \frac{m_c}{u_c}$, P_c^* is given by the
 323 intersection point between the curve of $F_1 : N_c \mapsto K_c \frac{u_c N_c - m_c}{u_c N_c}$ and the vertical
 324 line of equation $N_c = \frac{i_c + T^* \frac{s_r}{s_c}}{e_c}$. When T^* increases, the curve of F_1 stays at
 325 the same place whereas the vertical line is shifted to the right (figure C.4).
 326 Consequently the equilibrium point moves to the right on the curve of F_1 .
 327 As F_1 increases, P_c^* increases.

328 This can also be shown analytically because we have:

$$\frac{dP_{1,c}^*}{dT^*} = \frac{d}{dT^*} \left(K_c \left(1 - \frac{m_c}{u_c} \frac{e_c}{i_c + T^* \frac{s_r}{s_c}} \right) \right) = \frac{K_c m_c s_r}{u_c s_c} \frac{e_c}{(i_c + T^* \frac{s_r}{s_c})^2} > 0. \quad (26)$$

329 Finally, as $\frac{dC}{dT^*} = s_c \frac{dP_{1,c}^*}{dT^*}$, we show that the crop production C is increasing
 330 with T^* and therefore reaches its maximal value for the maximal value T_{max}^*
 331 that T^* can take in $\left[\max(0, \frac{s_r}{s_c} (\frac{e_c u_c}{u_c} - i_c)), +\infty \right)$. However, it is important
 332 to notice that the relationship between $C := s_c P_{1,c}^*$ and T^* is nonlinear. The
 333 closer $P_{1,c}^*$ is to K_c , the less profitable is the increase of T^* . For example, as
 334 we can see on the figure C.4, for a same increase of T^* between T_2^* and T_3^*
 335 and between T_1^* and T_2^* (i.e $T_3^* - T_2^* = T_2^* - T_1^*$), the increase of crop biomass
 336 $P_c^{*,3} - P_c^{*,2}$ is inferior to $P_c^{*,2} - P_c^{*,1}$. This non-linearity in the efficiency of
 337 the inputs impacts the optimization of the cropland sub-system to rangeland
 338 sub-system surfaces ratio (see 4.3).

339 4.2. Rangeland sub-system as a source: maximizing the transfers without
 340 jeopardizing plant biomass

341 After studying the variation of crop production with T^* , we now look at
 342 the variation of T^* with the two driving forces α and d_r ; we search for the
 343 values of α and d_r that maximize the amount $T^* = (1 - \alpha)d_r P_r^*$ of transferred
 344 nutrient.

345 For that, we now focus on the rangeland sub-system (r) only. Remind
 346 that the equations of this sub-system are written under the form (2) with
 347 $P = P_r$ and $N = N_r$ for the state variables and $u = u_r$, $K = K_r$, $m =$
 348 m_r , $e = e_r$, $i = i_r$, $\beta = \alpha$ and $d = d_r$ for the parameters:

$$\begin{cases} \dot{P}_r &= u_r P_r N_r (1 - P_r / K_r) - m_r P_r - d_r P_r \\ \dot{N}_r &= -u_r P_r N_r (1 - P_r / K_r) - e_r N_r + i_r + m_r P_r + \alpha d_r P_r \end{cases} \quad (27)$$

349 From the section 2.1 and similarly to the cropland sub-system, the range-
 350 land sub-system always admits one stable equilibrium, which depends on the
 351 parameter values. If $\frac{i_r}{e_r} \leq \frac{m_r + d_r}{u_r}$, this equilibrium point without plant is given
 352 by

$$E_{0,r} = \left(P_r^* = 0, N_r^* = \frac{i_r}{e_r} \right) \quad (28)$$

353 and if $\frac{i_r}{e_r} > \frac{m_r + d_r}{u_r}$, it is given by:

$$E_{1,r} = \left\{ \left(P_r^* = \frac{1}{2} \left(K_r - \frac{i_r}{e_r} a + \frac{\sqrt{\Delta}}{u_r} a \right), N_r^* = \frac{1}{2} \left(\frac{i_r}{e_r} + \frac{K_r}{a} + \frac{\sqrt{\Delta}}{u_r} \right) \right) \right\} \quad (29)$$

354 with $\Delta = u_r^2 \left(\frac{i_r}{e_r} + \frac{K_r}{a} \right)^2 - 4u_r \frac{K_r}{a} (m_r + d_r)$ and $a = \frac{e_r}{(\alpha - 1)d_r} < 0$ if $(\alpha - 1)d_r \neq 0$.

355 The case $(\alpha - 1)d_r = 0$ corresponds to an absence of grazing pressure or a
 356 case where all the uptake by livestock is recycled in the rangeland sub-system.

357 In this case, the equilibrium point $E_{1,r}$ becomes:

$$E_{1,r} = \left\{ \left(P_r^* = K_r \left(1 - \frac{e_r(m_r+d_r)}{u_r i_r} \right), N_r^* = \frac{i_r}{e_r} \right) \right. \quad (30)$$

358 Let's now look at how the nutrient transfer $T^* = (1 - \alpha)d_r P_r^*$ varies with
359 α and d_r .

360 *4.2.1. Minimizing the recycled fraction (α) to increase the transferred amount*
361 *(T^*)*

362 The first driving force that we consider is the parameter α , which repre-
363 sents the percentage of the grazed part of P_r which, after transformation by
364 livestock, is recycled to the inorganic nutrient compartment N_r . The other
365 fraction $(1 - \alpha)$ is exported to the cropland sub-system. α can vary from 0
366 (all nutrient is transferred to the cropland sub-system) to 1 (all nutrient is
367 recycled within the rangeland sub-system). We are looking for the value of
368 α that maximizes the amount T^* of nutrient transferred.

369 When $\frac{i_r}{e_r} \leq \frac{m_r+d_r}{u_r}$, there is no positive equilibrium point whatever the
370 value of α : $P_r^* = 0$ for all $\alpha \in [0, 1]$. If we consider the case where $\frac{i_r}{e_r} > \frac{m_r+d_r}{u_r}$,
371 as depicted in figure C.5, $P_{1,r}^*$ and $N_{1,r}^*$ increase with α . Indeed when α
372 increases from 0 to 1, the curve of F_1 does not move but the slope of F_2 goes
373 from $-\frac{e_r}{d_r}$ to $-\infty$ by rotating around the point $(\frac{i_r}{e_r}, 0)$ clockwise (see figure
374 C.5a). The intersection point between F_1 and F_2 moves therefore to the right
375 on the curve of F_1 : thus $P_{1,r}^*$ and $N_{1,r}^*$ increase with α . The mathematical
376 proof is given in Appendix B.1

377 [Figure 5 about here.]

378 Let us consider the function $\alpha \in [0, 1] \mapsto T^* = (1 - \alpha)d_r P_r^*$ and let us
379 denote T_{max}^* the maximal value taken by T^* on $[0, 1]$.

380 If $\frac{i_r}{e_r} \leq \frac{m_r+d_r}{u_r}$, then $P_r^* = 0$ for all $\alpha \in [0, 1]$. The function $\alpha \in [0, 1] \mapsto$
 381 $T^* = (1 - \alpha)d_r P_r^*$ is therefore null on $[0, 1]$ and $T_{max}^* = 0$.

382 Let us now consider the case where $\frac{i_r}{e_r} > \frac{m_r+d_r}{u_r}$. We showed earlier
 383 that the quantity of biomass produced in the rangeland sub-system ($P_{1,r}^*$)
 384 increases with α . The less we transfer, the higher this biomass is. However,
 385 we can wonder how the quantity $T^* = (1 - \alpha)d_r P_{1,r}^*$ varies with α . Indeed,
 386 whereas $P_{1,r}^*$ increases with α , the quantity $1 - \alpha$ decreases. This could lead
 387 to a trade-off between the biomass produced $P_{1,r}^*$ and the fraction $(1 - \alpha)$ of
 388 nutrient transferred to the cropland sub-system.

389 From (27), we can show that the amount of transferred nutrient T is
 390 written:

$$T^* = (1 - \alpha)d_r P_{1,r}^* = i_r - e_r N_{1,r}^* \quad (31)$$

391 From this equation (31), we deduce that T^* is maximal for the minimal
 392 value of $N_{1,r}^*$. Yet, we saw that both $N_{1,r}^*$ and $P_{1,r}^*$ increase with α . As a
 393 consequence, the quantity T^* is maximal for $\alpha = 0$: it corresponds to the
 394 case where all nutrient is transferred to the cropland sub-system. So there is
 395 no trade-off and we have

$$T_{max}^* = T(\alpha = 0) = d_r P_{1,r}^* \quad (32)$$

396 Finally, we showed that it is necessary to minimize the recycled fraction α
 397 of livestock uptake into rangeland sub-system to maximize the total amount
 398 of nutrient transferred to the cropland sub-system.

399 *4.2.2. Maximizing the transferred amount T^* with an intermediate grazing*
 400 *pressure d_r*

401 The second driving force that we can consider in this system is the graz-
 402 ing pressure d_r , a parameter which takes into account the size of the herd
 403 multiplied by the time spent by the herd on the rangeland sub-system. The-
 404 oretically d_r can vary from 0 (no livestock) to ∞ . In practice, there exists a
 405 bound for d_r which corresponds to the maximal herd size that can graze on
 406 the rangeland sub-system multiplied by the maximum of time that the herd
 407 can spend in the rangeland sub-system. The grazing pressure is also bounded
 408 by the capacity of rangeland to produce enough biomass to feed the livestock,
 409 and by the resistance of rangeland to overgrazing. In the model, the con-
 410 ditions of existence of the positive equilibrium $E_{1,r}$ that lead to a non-zero
 411 value of the transfer T^* require that d_r must be smaller than $\frac{u_r i_r}{e_r} - m_r$. If
 412 $d_r \geq \frac{u_r i_r}{e_r} - m_r$, there is not enough nutrient left in the rangeland sub-system
 413 to maintain the plant biomass: in that case of overgrazing, the rangeland
 414 sub-system goes to the equilibrium point $E_{0,r}$.

415 [Figure 6 about here.]

416 We are looking for the value of d_r in $(0, \frac{u_r i_r}{e_r} - m_r)$ that maximizes the
 417 transferred amount T^* . We set α to 0, since it is the value of α for which
 418 T^* is maximal whatever the value of d_r . However, we obtain similar results
 419 for a non-zero value of α . As in section 4.2.1, we deduce from the expression
 420 (31) of T that T^* is maximal for the minimal value of N_r^* . Moreover, we
 421 know that $T^* = 0$ for $d_r = 0$ and for $d_r = \frac{u_r i_r}{e_r} - m_r$ (case of overgrazing
 422 that implies $P_r^* = 0$). As T^* is a continuous and positive function of d_r on

423 $(0, \frac{u_r i_r}{e_r} - m_r)$, we deduce that the amount of nutrient transferred depends
 424 on a trade-off between the grazing pressure and the plant biomass in the
 425 rangeland sub-system .

426 Therefore, there exists a value $d_r^{opt} \in (0, \frac{u_r i_r}{e_r} - m_r)$ of d_r for which T^* is
 427 maximal on $(0, \frac{u_r i_r}{e_r} - m_r)$. It also means that T^* and N_r^* are not strictly
 428 monotonic on $(0, \frac{u_r i_r}{e_r} - m_r)$. Figure C.6 shows the variation of P_r^* , N_r^* and T^*
 429 with $d_r \in (0, \frac{u_r i_r}{e_r} - m_r)$ for $\alpha = 0$. We see that on the interval $(0, \frac{u_r i_r}{e_r} - m_r)$, P_r^*
 430 decreases with d_r . Indeed, when d_r increases from 0 to $\frac{u_r i_r}{e_r} - m_r$, the curve of
 431 F_1 moves to the right and the slope of F_2 goes from $-\infty$ to $\frac{e_r^2}{(\alpha-1)(u_r i_r - m_r e_r)} < 0$
 432 by rotating anticlockwise around the point $(\frac{i_r}{e_r}, 0)$ (see figure C.5b). The
 433 intersection point between F_1 and F_2 moves therefore to the left on the curve
 434 of F_1 : so $P_{1,r}^*$ decreases with d_r . However, as the curve of F_1 is shifted to the
 435 right when d_r increases, the variation of $N_{1,r}^*$ is not easily noticeable. We see
 436 on Figure C.6 and C.5 that N_r^* first decreases and then increases with d_r : it
 437 therefore admits a global minimum on $d_r^{opt} \in (0, \frac{u_r i_r}{e_r} - m_r)$.

438 As we deduced earlier from equation (31), we also observe that the value
 439 $d_r^{opt} \in (0, \frac{u_r i_r}{e_r} - m_r)$ of d_r which minimizes N_r^* is the same as the one which
 440 maximizes the transfer $T^* = (1 - \alpha)d_r P_r^*$ from the rangeland sub-system to
 441 the cropland sub-system.

442 Among the set of grazing pressure values that do not compromise the
 443 plant production in the rangeland sub-system, there is a value that optimizes
 444 the amount of nutrient transferred to the cropland sub-system. Moreover,
 445 we observe that this value d_r^{opt} is a low value among the set of possible values
 446 of grazing pressure $(0, d_r^{max})$.

447 4.3. Surface ratio of cropland:rangeland sub-systems affects the trade-off be-
 448 tween plan biomass in cropland sub-system and production at the scale
 449 of the agro-ecosystem

450 We now look at the variation of the crop production with respect to the
 451 respective surfaces of cropland and rangeland sub-systems (s_c for cropland
 452 sub-system and s_r for rangeland subsystem). At the agro-ecosystem scale,
 453 the maximization of crop production C does not depend on the absolute value
 454 of the surface of the subsystems but depends on the relative surface area of
 455 each subsystem in relation to the total surface area of the agro-ecosystem.
 456 When the surface of cropland sub-system s_c increases (at the expense of
 457 the rangeland sub-system), a positive effect comes from the increase of the
 458 surface devoted to crop production (equation 9) whereas a negative effect
 459 comes from the dilution effect on the amount of transferred nutrient ($T^* \frac{s_r}{s_c}$).

460 Let $\gamma = \frac{s_c}{s_r+s_c}$ be the fraction of the agro-ecosystem surface $S := s_r + s_c$
 461 occupied by the cropland sub-system and $1 - \gamma = \frac{s_r}{s_r+s_c}$ the fraction occupied
 462 by the rangeland sub-system. The fraction occupied by cropland/rangeland
 463 impacts the crop production directly as $C := s_c P_c^* = \gamma S P_c^*$ and indirectly
 464 through the quantity $T^* \frac{s_r}{s_c} = T^* \frac{1-\gamma}{\gamma}$ on which depends the value P_c^* .

465 We are looking for the value of γ in $(0, 1]$ that maximizes the crop pro-
 466 duction C . We can show (see Appendix B.2 for mathematical proofs) that
 467 there exist two different situations depending on if the inputs i_c are greater
 468 or smaller than a threshold value i^+ defined as:

$$i^+ = \frac{e_c m_c + \sqrt{e_c m_c (e_c m_c + 4u_c T)}}{2u_c} > 0. \quad (33)$$

469 If $i_c > i^+$, then the inputs i_c are high enough to ensure a good production
 470 in the cropland sub-system without any transfer. In that case, the transfer

471 is no more interesting for crop production, and it becomes more profitable to
 472 cultivate the maximum available surface ($\gamma = 1$). The maximal value C_{max}
 473 of C is then given by:

$$C_{max} = SP_{1,c}^*(\gamma = 1) = SK_c \left(1 - \frac{m_c e_c}{u_c i_c} \right). \quad (34)$$

474 If $i_c < i^+$, then the inputs i_c are not high enough and there exists an
 475 optimal value γ^{opt} of γ for which the crop production C is maximal. In
 476 that case, the optimal value γ^{opt} depends on the trade-off between the crop
 477 biomass and the surface of the cropland sub-system (see figure C.7).

478 [Figure 7 about here.]

479 γ^{opt} is given by:

$$\gamma^{opt} = \frac{T}{P^{opt} + e_c N^{opt} + T - i_c} \text{ with } N^{opt} = \frac{K_c m_c}{u_c (K_c - P^{opt})} \quad (35)$$

480 where P^{opt} , the value of P_c^* for which the crop production C is maximal, is
 481 expressed:

$$P^{opt} = K_c \left[1 - \frac{-e_c m_c + \sqrt{e_c m_c [e_c m_c + u_c (T - i_c)]}}{u_c (T - i_c)} \right] \in [0, K_c]. \quad (36)$$

482 The maximal value C_{max} of C is then given by:

$$C_{max} = \gamma^{opt} S P^{opt}. \quad (37)$$

483 When atmospheric depositions and other inputs independent of livestock
 484 are not sufficiently high in the cropland sub-system compared to the capacity
 485 of transfer of the rangeland sub-system, it is adequate to keep both rangeland
 486 and cropland surfaces in the agro-ecosystem to optimize crop production.

487 *4.4. Changing functioning of the agro-ecosystem by changing grazing pressure*
 488 *over the year*

489 In this section, we give the results obtained with the control strategy de-
 490 scribed in section 3.2, that corresponds to the case where the grazing pressure
 491 can vary over the year.

492 *4.4.1. A same production with less transfer, a higher production with as*
 493 *much?*

494 [Figure 8 about here.]

495 We first look at the maximal crop production value that the system can
 496 reach with the control strategy. Figures C.8a, C.8b and C.8c represent the
 497 average stock of plant in rangeland over a year ($\frac{1}{t_h} \int_0^{t_h} P_r(t) dt$), the stock of
 498 plant in cropland at harvest time (P_{c,t_h}) and the total amount of nutrient
 499 transferred over a year ($\int_0^{t_h} T(t) dt$) with respect of the value of the set-point
 500 \tilde{P}_c . The values obtained with the optimization at equilibrium (that is with
 501 a constant value $d_r = d_r^{opt}$) are represented by the horizontal straight lines.
 502 The black and gray vertical straight lines mark the values of P_c^{opt} and of the
 503 maximal crop production value reached with the control strategy respectively.
 504 The set-point \tilde{P}_c is reached in all the cases until $\tilde{P}_c = 1.085 \times P^{opt}$. Above this
 505 point the feedback control fails to make P_c reach the set-point: the cropland
 506 sub-system “collapses” and we get $P_c = 0$. As the value of the set-point
 507 \tilde{P}_c increases from 0 to $1.085 \times P^{opt}$, the average stock of plant in rangeland
 508 ($\frac{1}{t_h} \int_0^{t_h} P_r(t) dt$) decreases and the total amount of nutrient transferred over a
 509 year ($\int_0^{t_h} T(t) dt$) increases. By simulations, we observe that the total amount
 510 of nutrient transferred over a year obtained for the highest crop production

511 value ($\tilde{P}_c = 1.085 \times P^{opt}$) with the control strategy is equal to the total
 512 amount of nutrient transferred over a year ($t_h \times T_{max}^*$) obtained with the
 513 optimization at equilibrium (that is for a constant value of $d_r = d_r^{opt}$).

514 4.4.2. Comparison of scenarios

515 Let us now compare the different optimization strategies, through the
 516 simulated trajectories of 3 different scenarios.

517 The first scenario (1) consists in the application of the optimal values
 518 of d_r , α and γ that have been calculated with the classical approach of
 519 optimization at equilibrium as constant values. We set $\alpha = 0$ (see section
 520 4.2.1) and get the optimal value of d_r^{opt} by simulation (see section 4.2.2). From
 521 the so-obtained value of T^* , we compute the optimal value γ^{opt} (see equation
 522 35) of γ that determines the surfaces s_r and s_c for which C is maximal (see
 523 equation 34). This scenario is our “control sample” to be compared with
 524 two other scenarios (2) and (3) obtained with the control theory for different
 525 values of the set point \tilde{P}_c . For scenario (2), \tilde{P}_c is defined as the optimal value
 526 of crop biomass obtained with the optimization at equilibrium ($\tilde{P}_c = P^{opt}$)
 527 and for scenario (3), \tilde{P}_c is defined as the maximal value reached numerically
 528 with the feedback control (see C.8). \tilde{P}_c is equal to 1.085 times the optimal
 529 value obtained with the optimization at equilibrium ($\tilde{P}_c = 1.085 P^{opt}$). There
 530 is no difference in the parametrization of the scenarios (1), (2) and (3) except
 531 for the expression of the grazing pressure d_r .

532 Figures C.9a, C.9b, C.9c and C.9d represent the dynamics of plant and
 533 inorganic nutrient in the cropland sub-system and the rangeland sub-system
 534 over five years for the 3 scenarios. Scenarios (1), (2) and (3) are plotted in
 535 black lines, dotted black lines and grey lines respectively.

536 In the scenario (1), only the stocks of the cropland sub-system change
 537 over the year and the equilibrium point is reached each year. These changes
 538 are due to the harvest event that occurs at the end of each year. In this
 539 scenario, both scenarios 2 and 3 reach their set-point \tilde{P}_c . We observe that
 540 the growth of plants is slower with feedback than without feedback (figure
 541 C.9b). Note that in scenario (2) and (3), we are no longer looking for the
 542 solution at equilibrium but instead we used the transient dynamics to reach
 543 the set-point at the time of the harvest.

544 With the feedback control, the dynamics of nutrient in the rangeland sub-
 545 system becomes dependent of the state of the cropland sub-system and varies
 546 over time following the dynamics of d_r . In both scenarios, levels of plant and
 547 inorganic nutrient in the rangeland sub-system are always higher than for
 548 scenario 1. Considering that the end of the year matches with the harvest
 549 event, we observe in scenarios (2) and (3) that the value of d_r is minimal in the
 550 middle of the year (figure C.9e). The low value of d_r promotes the increase
 551 of plant biomass in the rangeland sub-system P_r and as a consequence, the
 552 increase of the inorganic nutrient level N_r (figure C.9b,d). Note that in the
 553 scenario (3), the value of d_r is a bit higher than d_r^{opt} but much lower than the
 554 value above which there is overgrazing ($\frac{u_r i_r}{e_r} - m_r$)

555 These higher values of P_r and N_r allow a higher transfer of nutrient for
 556 the growth of cropland plants during the second part of the year. Indeed, as
 557 depicted in figure C.9f the amount of nutrient transferred over time decreases
 558 slightly at the beginning of the year and then increases to be maximal at the
 559 end of the year. The calculation of the total amount of nutrient transferred
 560 during a year gives 237.3 kgN y⁻¹ for scenario (1), and respectively 216.1 and

561 234.7 kgN y⁻¹ for scenarios (2) and (3).

562 In scenario (2) and (3), losses are lower in the rangeland sub-system and
563 higher in the cropland sub-system compared to scenario (1). At the scale
564 of the agro-ecosystem the lowest losses are obtained for scenario (2) (249.1
565 kgN y⁻¹). Losses are a bit higher in scenario (3) (254.1 kgN y⁻¹) than in
566 scenario (1) (253.7 kgN y⁻¹). In scenario (3), higher losses associated with a
567 larger biomass at the end of the year are due to the fact that loss rates are
568 much lower in the rangeland sub-system than in the cropland sub-system,
569 and that the average biomass (over a year) in the cropland sub-system is
570 lower in scenario (3) than in scenario (1).

571 [Figure 9 about here.]

572 Hence, by constantly adjusting the grazing pressure over a year, one can
573 promote a higher crop production, thanks to the transient dynamics. Indeed,
574 as we showed, bringing nutrient to crops at the right time when they require
575 it for growth maximizes the overall crop production over a year.

576 5. Discussion

577 We addressed the optimization of crop production in a mixed farming
578 system, using a simple meta-ecosystem model. Our purpose was to find the
579 optimal values of three quantities of interest to maximize crop production,
580 namely, the fraction of the agro-ecosystem occupied by the cropland sub-
581 system γ , the grazing pressure in rangeland d_r , and the fraction of nutrient
582 transferred to cropland by livestock $(1 - \alpha)$. We first used the classical
583 method of optimization at equilibrium to maximize the production when

584 these quantities are constant over time. Second, we used methods from the
585 control theory to optimize crop production when the grazing pressure d_r can
586 be constantly adjusted, α and γ being kept constant.

587 With the optimization at equilibrium, our results suggest that maximizing
588 crop production is obtained by maximizing the flux of nutrient transferred by
589 livestock from rangeland to cropland. To maximize this flux, the following
590 conditions must be met:

- 591 1. the fraction α of nutrient ingested by livestock and recycled within the
592 rangeland must be minimal, the best strategy being to transfer all the
593 nutrient ingested by livestock to cropland.
- 594 2. the grazing pressure d_r cannot be higher than a threshold value that
595 leads to the overgrazing of the rangeland, with the extirpation of plants
596 at steady-state. Hence, there is a trade-off between exporting as much
597 nutrient as possible from cropland and avoiding overgrazing.
- 598 3. Once the driving forces d_r and α related to livestock are optimized, it
599 is possible to determine the optimal value of the rangeland to cropland
600 surface ratio $\gamma/(1-\gamma)$. This ratio strongly depends on the quantity of
601 inputs independent from livestock in the cropland sub-system i_c com-
602 pared to the capacity of transfer of the rangeland sub-system T .

603 The control theory allows a further gain of optimization, based on a better fit
604 of the driving forces to the transient dynamics of the system. By constantly
605 adjusting the grazing pressure over time, we showed that it is possible to ob-
606 tain the same yearly crop production with a lower yearly amount of nutrient
607 transferred by livestock. We even show that it is possible to reach higher
608 values of crop biomass.

609 Our model allows a better understanding of the mechanisms that lead
610 to optimization. First, we note that the maximal flux of nutrient trans-
611 ferred corresponds to the case where the stock of inorganic nutrient in the
612 rangeland is minimal, a result similar to what has been shown in previous
613 models (Boudsocq et al., 2009, Loreau, 1998). Indeed, these studies showed
614 that primary productivity was maximized when the inorganic resource was
615 minimized. Since T^* is proportional to the primary productivity obtained
616 in rangeland, our result is consistent with these other nutrient cycling mod-
617 els. This arises from the fact that the inputs of nutrient in the rangeland
618 sub-system are independent on plant biomass. Second, note that there are
619 two output fluxes of nutrient from the rangeland sub-system: one in organic
620 form, through the grazing of plant biomass followed by an exportation to
621 cropland, and one in inorganic form through erosion and leaching of the
622 inorganic stock. Therefore, maximizing the flux of nutrient transferred by
623 livestock consists in minimizing the inorganic losses in favors of the organic
624 output.

625 With our model, when the grazing pressure is adjusted over time, we ob-
626 serve that to maximize the crop biomass at the moment of harvest, one must
627 boost the growth of crops during the second part of the year. This unex-
628 pected result comes from the fact that both the plant growth function and
629 the mortality rate stay constant all along the year. In reality, the deposition
630 of manure on the one hand, and the growth of plants, on the other hand,
631 are decoupled over the year. For instance, in West Africa, manure deposi-
632 tion occurs during the dry season, when the livestock is corralled at night in
633 the cropland, whereas growth occurs during the wet season. During the dry

634 season, the livestock is kept in rangeland to protect the crops (Manlay et al.,
635 2004, Guerin and Roose, 2015).

636 With the control method, we obtain a grazing pressure curve (figure C.9e)
637 and a plant biomass curve in the rangeland sub-system (figure C.9b) whose
638 shapes are similar to the ones obtained by Chen and Wang (1988). In their
639 work, these authors used optimal control theory to determine the maximal
640 potential productivity of grassland under grazing over a year. In our study,
641 we showed that maximizing the integral of the transfers over a year does
642 not guarantee to get the maximal crop production at harvest time. Indeed,
643 for the same yearly average, a time-varying transfer can lead to greater crop
644 production than a constant one. Note that using time-varying inputs to
645 improve the performance of a system is a well-known practice (see for example
646 (Ruan and Chen, 1996) in the case of a fermentation process).

647 Thanks to the control method which allows to implement a time-varying
648 grazing pressure and with the set of parameters used in our simulation, we
649 succeeded to reach a crop production (set-point \tilde{P}_c) 1.085 times higher (8.5%
650 increase) than the optimal crop production obtained with optimization at
651 equilibrium. Above this value, the grazing pressure calculated by the feed-
652 back linearizing control law (equation 19) does not allow plants to subsist in
653 the rangeland sub-system (overgrazing) and the dynamical system does not
654 reach the desired crop production. In both the “classical” scenario (1) and
655 the scenario where time-varying grazing pressure is applied and the optimal
656 crop production value is reached (3), the total annual amount of transferred
657 nutrient was almost the same. It suggests that the control on d_r has almost
658 no effect on the transfer capacity of the rangeland sub-system.

659 In this study, we only applied the control theory to the grazing pressure d_r .
660 Yet, we could have applied it as well to the fraction of nutrient recycled in the
661 rangeland sub-system over a year α . In this case, as suggested by simulations
662 (not shown), we would observe similar dynamics but with a lower maximal
663 value of crop production. This result is partly due to the constraints on the
664 value of the fraction of recycled nutrient that is bounded between 0 and 1,
665 but it also arises from the fact that to maximize nutrient transfer, it is more
666 profitable to minimize α than to maximize d_r .

667 We could as well apply the control theory on both d_r and α . In this
668 case, possibilities of control are numerous, and some of them might allow a
669 higher crop production \tilde{P}_c than the one obtained with only one parameter
670 as control input. However, in the simulations we performed, the recycled
671 fraction always went to 0 after a few years (simulations not shown), which
672 finally amounts to control the system with the grazing pressure as the only
673 control input.

674 In the paper, we assume that farmers have the full control on the three
675 driving forces in focus. We know however that depending on the context,
676 some constraints may restrict this control. Initially, our model was built to
677 represent traditional mixed farming systems. In these systems, α is not really
678 a driving-force: it depends on the time passed (day/night) in the rangeland
679 by livestock and on its metabolism. However the model is generic enough to
680 be used for other systems or at different scales. For instance in areas where
681 the crop production and the livestock production are decoupled at the scale
682 of the farms (cattle fattening), our model can be used to couple them at
683 the scale of the landscape. In that case, the rangeland sub-system is in fact

684 a field in which fodder is cultivated and used to feed the livestock: α can
685 therefore be considered as a full leverage.

686 The model presented in this paper is rather simple, which serves our capa-
687 bility to extract the basic mechanisms underlying the optimization process,
688 but which bears some limitations. For instance, we assumed that the input
689 of nutrient to the rangeland is independent on plant biomass. This may be
690 relevant for phosphorus but not for nitrogen, which is often subject to sym-
691 biotic fixation by legumes, plants that are present in most rangeland. The
692 quantity of nitrogen fixed depends on the biomass of legumes, which relieves
693 the assumption of independence between nitrogen inputs and plant biomass.
694 Without this assumption, some of the results presented earlier may not hold.

695 Overall, we are fully aware of the theoretical nature of our results. The
696 results obtained by the study of our model are qualitative more than quanti-
697 tative. These results are not meant to be straightforward recommendations
698 to farmers but rather, to allow a better understanding of the different possi-
699 bilities that exist to optimize crop production. These results also show the
700 relevance of both the meta-ecosystem and the control theory to address opti-
701 mization in agricultural systems. Indeed, agricultural systems are by essence
702 highly dynamics, and are usually very patchy in terms of biogeochemistry,
703 with source-sink dynamics. Our results suggest that both the patchiness and
704 the dynamics provide a set of unexplored ways to optimize the production
705 of crops, meat, or other goods.

706 **Acknowledgments**

707 This research was supported by the LABEX AGRO – Agropolis Fondation
 708 (Project 1605-039 ECOW) and the French National Research Agency (ANR)
 709 through the CERAO project (ANR 13AGRO0002)

710 **Appendix A. Model**

711 *Appendix A.1. Equilibrium points of generic model (2) and their stability*

712 • Equilibrium points

713 Consider the case where $(\beta - 1)d \neq 0$ and let us solve the equation
 714 $F_1(N) = F_2(N)$ with $F_1(N) = K \frac{uN - m - d}{uN}$, $F_2(N) = a(N - \frac{i}{e})$ and $a = \frac{e}{(\beta - 1)d}$.
 715 We have, for all $N \in \mathbb{R}^+ \setminus \{0\}$:

$$F_1(N) = F_2(N) \Leftrightarrow \mathcal{P}(N) = 0 \quad (\text{A.1})$$

716 with $\mathcal{P}(N) = uN^2 - uN(\frac{i}{e} + \frac{K}{a}) + \frac{K}{a}(m + d)$. The discriminant of \mathcal{P} is written:

$$\Delta = u^2 \left(\frac{i}{e} + \frac{K}{a} \right)^2 - 4u \frac{K}{a} (m + d); \quad (\text{A.2})$$

717 in the case where $\frac{i}{e} > \frac{m+d}{u}$ and as $a < 0$ we have $\Delta > 0$. Therefore, there
 718 exists two roots that are given by:

$$N^* = \frac{1}{2} \left(\frac{i}{e} + \frac{K}{a} \right) \pm \frac{\sqrt{\Delta}}{2u} \quad (\text{A.3})$$

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

$$P^* = \frac{K}{2} - \frac{ia}{2e} \pm a \frac{\sqrt{\Delta}}{2u}. \quad (\text{A.4})$$

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

$$E_1 = \left(\frac{1}{2} \left(K - \frac{ia}{e} + a \frac{\sqrt{\Delta}}{u} \right), \frac{1}{2} \left(\frac{i}{e} + \frac{K}{a} + \frac{\sqrt{\Delta}}{u} \right) \right) \quad (\text{A.5})$$

722 In the case where $(\beta - 1)d = 0$, system (3) leads to $N = \frac{i}{e}$ and $uP \frac{i}{e} \left(1 - \frac{P}{K}\right) -$
 723 $mP - dP = 0 \Leftrightarrow P = 0$ or $P = K \left(1 - \frac{e(m+d)}{ui}\right)$.

724 • Stability of the equilibrium points:

725 The Jacobian matrix of the system (2) at the point E_0 is given by:

$$J(E_0) = J \left(0, \frac{i}{e} \right) = \begin{pmatrix} u \frac{i}{e} - m - d & 0 \\ -u \frac{i}{e} + m + \beta d & -e \end{pmatrix} \quad (\text{A.6})$$

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

728 The equilibrium point E_1 exists when $\frac{i}{e} > \frac{m+d}{u}$; it is such that:

$$uN_1^* \left(1 - \frac{P_1^*}{K}\right) = m + d \text{ and } uP_1^* N_1^* \left(1 - \frac{P_1^*}{K}\right) = i + mP_1^* + \beta dP_1^* - eN_1^*. \quad (\text{A.7})$$

729 By using these relationships, we get the following expression of the Jacobian
 730 matrix of system (2) at the point E_1 :

$$J(E_1) = \begin{pmatrix} -\frac{uP_1^* N_1^*}{K} & uP_1^* \left(1 - \frac{P_1^*}{K}\right) \\ \frac{uP_1^* N_1^*}{K} + (\beta - 1)d & -uP_1^* \left(1 - \frac{P_1^*}{K}\right) - e \end{pmatrix} \quad (\text{A.8})$$

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

$$\text{Tr}(J(E_1)) = -\frac{uP_1^* N_1^*}{K} - uP_1^* \left(1 - \frac{P_1^*}{K}\right) - e \quad (\text{A.9})$$

734 which is always strictly negative, because $N_1^* > 0$ and $0 < P_1^* < K$. More-
 735 over, after simple calculations, we have:

$$\det(J(E_1)) = \frac{uP_1^*}{K} \left(i + \frac{e}{a}(2P_1^* - K) \right) \quad (\text{A.10})$$

736 The equilibrium point E_1 is therefore stable if and only if:

$$\det(J(E_1)) > 0 \Leftrightarrow i + \frac{e}{a}(2P_1^* - K) > 0 \Leftrightarrow P_1^* < \frac{1}{2} \left(K - i\frac{a}{e} \right) \quad (\text{as } a < 0), \quad (\text{A.11})$$

737 which is always true as $P_1^* := \frac{1}{2}(K - \frac{ia}{e} + a\frac{\sqrt{\Delta}}{u})$ and $a < 0$. When it exists,
 738 the equilibrium point E_1 is therefore always stable.

739 Appendix B. Results

740 Appendix B.1. Impact of α on $P_{1,r}^*$ and $N_{1,r}^*$

741 $N_{1,r}^*$ is solution of the equation $F_1(N) = F_2(N, \alpha)$ where $F_1 : N \mapsto$
 742 $K_r \frac{u_r N - m_r - d_r}{u_r N}$ is a strictly increasing concave function defined on $\mathbb{R}^+ \setminus \{0\}$,
 743 and $F_2(N, \alpha) = a(\alpha)(N - \frac{i_r}{e_r})$ with $a(\alpha) = \frac{e_r}{(\alpha-1)d_r} < 0$. It only exists if
 744 $\frac{i_r}{e_r} > \frac{m_r + d_r}{u_r}$, so we only consider this case. We then have:

$$\frac{d}{d\alpha} (F_1(N_{1,r}^*)) = \frac{d}{d\alpha} (F_2(N_{1,r}^*, \alpha)) \Leftrightarrow \frac{dN_{1,r}^*}{d\alpha} F_1'(N_{1,r}^*) = \frac{dN_{1,r}^*}{d\alpha} \frac{\partial F_2}{\partial N}(N_{1,r}^*, \alpha) + \frac{\partial F_2}{\partial \alpha}(N_{1,r}^*, \alpha). \quad (\text{B.1})$$

745 As $\frac{\partial F_2}{\partial N} = a(\alpha)$ and $\frac{\partial F_2}{\partial \alpha} = a'(\alpha)(N - \frac{i_r}{e_r})$ with $a'(\alpha) = \frac{-e_r}{(\alpha-1)^2 d_r} < 0$, we get:

$$\frac{dN_{1,r}^*}{d\alpha} = \frac{a'(\alpha)(N_{1,r}^* - \frac{i_r}{e_r})}{F_1'(N_{1,r}^*) - a(\alpha)} \quad (\text{B.2})$$

746 As $a(\alpha) < 0$ and $a'(\alpha) < 0$, we know that $N_{1,r}^* < \frac{i_r}{e_r}$, so $a'(\alpha)(N_{1,r}^* - \frac{i_r}{e_r}) > 0$.

747 Moreover, $F_1'(N_{1,r}^*) = \frac{K_r(m_r + d_r)}{u_r(N_{1,r}^*)^2} > 0$ and $a(\alpha) < 0$, so $F_1'(N_{1,r}^*) - a(\alpha) > 0$.

748 We so have $\frac{dN_{1,r}^*}{d\alpha} > 0$.

749 The derivative of $P_{1,r}^*$ with respect to α can then be deduced; we indeed
 750 have $P_{1,r}^* = F_1(N_{1,r}^*)$ which leads to:

$$\frac{dP_{1,r}^*}{d\alpha} = \frac{dN_{1,r}^*}{d\alpha} \underbrace{F_1'(N_{1,r}^*)}_{>0} > 0. \quad (\text{B.3})$$

751 *Appendix B.2. Impact of γ on C*

752 Impact of γ on $P_{1,c}^*$

753 The equilibrium point $E_{1,c} = (P_{1,c}^*, N_{1,c}^*)$ exists if and only if $\frac{i_c + T \frac{1-\gamma}{\gamma}}{e_c} > \frac{m_c}{u_c}$
 754 and for $\gamma \in (0, 1]$. We have:

$$\frac{i_c + T \frac{1-\gamma}{\gamma}}{e_c} > \frac{m_c}{u_c} \Leftrightarrow \begin{cases} \gamma < \frac{T}{\frac{m_c e_c}{u_c} - i_c + T} & \text{if } \frac{m_c e_c}{u_c} - i_c + T > 0 \\ \gamma > \frac{T}{\frac{m_c e_c}{u_c} - i_c + T} & \text{if } \frac{m_c e_c}{u_c} - i_c + T < 0 \end{cases} \quad (\text{B.4})$$

755 If $\frac{m_c e_c}{u_c} - i_c + T > 0$, then $\frac{T}{\frac{m_c e_c}{u_c} - i_c + T} > 0$ and $\frac{T}{\frac{m_c e_c}{u_c} - i_c + T} \leq 1 \Leftrightarrow \frac{m_c e_c}{u_c} - i_c \geq 0$.

756 If $\frac{m_c e_c}{u_c} - i_c + T < 0 \Rightarrow \frac{m_c e_c}{u_c} - i_c < -T < 0$, then $\frac{T}{\frac{m_c e_c}{u_c} - i_c + T} < 0$.

757 So $P_{1,c}^*$ only exists for values of γ included in a domain Ω_γ given by:

- 758 • $\Omega_\gamma = \left(0, \frac{T}{\frac{e_c}{u_c} m_c - i_c + T}\right] \subset [0, 1]$ if $\frac{i_c}{e_c} \leq \frac{m_c}{u_c}$;
- 759 • $\Omega_\gamma = (0, 1]$ if $\frac{i_c}{e_c} > \frac{m_c}{u_c}$.

760 It is given by $P_{1,c}^* = K_c \left(1 - \frac{m_c}{u_c} \frac{e_c}{i_c + T \frac{1-\gamma}{\gamma}}\right)$. We so have, for all $\gamma \in \Omega_\gamma$:

$$\frac{dP_{1,c}^*}{d\gamma} = -K_c \frac{m_c e_c T}{u_c \gamma^2} \frac{1}{(i_c + T \frac{1-\gamma}{\gamma})^2} < 0. \quad (\text{B.5})$$

761 The function $\gamma \mapsto P_{1,c}^*$ is therefore strictly decreasing on Ω_γ .

762 Impact of γ on C

763 The crop production defined by $C = \gamma S P_c^*$ is positive only when $P_c^* = P_{1,c}^*$,

764 that is when $P_{1,c}^*$ exists, i.e $\forall \gamma \in \Omega_\gamma$. After simple computations, we can
 765 show from (3) that C is given on Ω_γ by:

$$C := \gamma S P_{1,c}^* = \frac{T}{e_c N_{1,c}^* + T - i_c} S P_{1,c}^* \quad (\text{B.6})$$

766 with

$$N_{1,c}^* = \frac{m_c}{u_c} \frac{K_c}{K_c - P_{1,c}^*}. \quad (\text{B.7})$$

767 We then get:

$$\forall \gamma \in \Omega_\gamma, \frac{dC}{d\gamma} = S \frac{dP_{1,c}^*}{d\gamma} \frac{T}{(e_c N_{1,c}^* + T - i_c)^2} \frac{\rho(K_c - P_{1,c}^*)}{u_c (K_c - P_{1,c}^*)^2} \quad (\text{B.8})$$

768 where $\rho(x) = a_2 x^2 + a_1 x + a_0$ with $a_2 = u_c (T - i_c)$, $a_1 = 2e_c K_c m_c > 0$
 769 and $a_0 = -e_c K_c^2 m_c < 0$. The discriminant of polynomial ρ is given by
 770 $a_1^2 - 4a_2 a_0 = 4e_c K_c^2 m_c [e_c m_c + u_c (T - i_c)]$ which leads to the following cases:

771 • if $\frac{e_c m_c}{u_c} + T < i_c$, then $\rho(x) < 0, \forall x \in \mathbb{R}$ and $\frac{dP_{1,c}^*}{d\gamma} < 0$ for $\gamma \in [0, 1]$ so
 772 $\frac{dC}{d\gamma} > 0$ for all $\gamma \in [0, 1]$ and C is therefore maximal for $\gamma = 1$.

773 • if $\frac{e_c m_c}{u_c} + T > i_c$, then the polynomial ρ has two roots. After sim-
 774 ple computations (not detailed here for simplicity), we can show that,
 775 whatever the value of a_2 is, among these two roots only the root given
 776 by $x^+ = \frac{-a_1 + \sqrt{a_1^2 - 4a_2 a_0}}{2a_2}$ corresponds to a value $P^{opt} = K_c - x^+$ of
 777 $P_{1,c}^*$ that belongs to $[0, K_c]$. We also easily show that for all $P_{1,c}^*(\gamma) \in$
 778 $(0, P^{opt})$, $\frac{dC}{d\gamma} < 0$ and for all $P_{1,c}^*(\gamma) \in (P^{opt}, K_c)$, $\frac{dC}{d\gamma} > 0$. By denot-
 779 ing $\gamma_0 = \frac{T}{\frac{e_c m_c}{u_c} - i_c + T}$ the value of γ such that $P_{1,c}(\gamma_0) = 0$, and because
 780 $\frac{dP_{1,c}^*}{d\gamma} < 0$ for $\gamma \in \left[0, \min\left(\frac{T}{\frac{e_c m_c}{u_c} - i_c + T}, 1\right)\right]$, we can finally deduce the
 781 variations table of the function $\gamma \in (0, \gamma_0] \mapsto C$ that is given in figure
 782 C.10.

783

784

[Figure 10 about here.]

785

786

787

788

789

We then have to consider two cases. If $\gamma_0 > 1$ and $P_{1,c}^*(\gamma = 1) > P^{opt}$, then the maximal value of C on $(0, 1]$ is reached for $\gamma = 1$. If $\gamma_0 < 1$ or if $\gamma_0 > 1$ and $P_{1,c}^*(\gamma = 1) < P^{opt}$, then the maximal value of C on $(0, 1]$ is reached for the value γ^{opt} of γ such that $P_{1,c}^*(\gamma = \gamma^{opt}) = P^{opt}$. From (B.6) and (B.7), γ^{opt} is given by:

$$\gamma^{opt} = \frac{T}{e_c \frac{K_c m_c}{u_c(K_c - P^{opt})} + T - i_c} \quad (\text{B.9})$$

790

with:

$$P^{opt} = K_c - \frac{-a_1 + \sqrt{a_1^2 - 4a_2a_0}}{2a_2} = K_c \left[1 - \frac{e_c m_c}{e_c m_c + \sqrt{e_c m_c [e_c m_c + u_c(T - i_c)]}} \right] \quad (\text{B.10})$$

791

We finally get two cases: C is maximal either for $\gamma = 1$, or for $\gamma = \gamma^{opt}$.

792

793

Let us now express the different conditions that lead to these cases in terms of values of i_c .

794

795

796

797

Case 1: C is maximal for $\gamma = 1$ if $\frac{e_c m_c}{u_c} + T < i_c$ OR if $\frac{e_c m_c}{u_c} + T > i_c$, $\gamma_0 > 1$ and $P_{1,c}^*(\gamma = 1) > P^{opt}$. We first have $\gamma_0 > 1 \Leftrightarrow \frac{T}{\frac{e_c m_c}{u_c} - i_c + T} > 1 \Leftrightarrow T > \frac{e_c m_c}{u_c} - i_c + T \Leftrightarrow \frac{e_c m_c}{u_c} < i_c$. For the condition $P_{1,c}^*(\gamma = 1) > P^{opt}$, we can show that:

$$P_{1,c}^*(\gamma = 1) > P^{opt} \Leftrightarrow 0 < \underbrace{u_c i_c^2 - e_c m_c i_c - e_c m_c T}_{\mathcal{P}(i_c)}. \quad (\text{B.11})$$

798

The polynomial \mathcal{P} has two roots, one negative and one positive:

$$i^- = \frac{e_c m_c - \sqrt{e_c m_c (e_c m_c + 4u_c T)}}{2u_c} < 0 \text{ and } i^+ = \frac{e_c m_c + \sqrt{e_c m_c (e_c m_c + 4u_c T)}}{2u_c} > 0, \quad (\text{B.12})$$

799 which leads to $\mathcal{P}(i_c) > 0 \Leftrightarrow i_c > i^+$ or $i_c < i^-$. As we only consider positive
 800 values of i_c , the condition $P_{1,c}^*(\gamma = 1) > P^{opt}$ is simply rewritten $i_c > i^+$.
 801 After computations, we can show that:

$$\frac{e_c m_c}{u_c} < i^+ < \frac{e_c m_c}{u_c} + T. \quad (\text{B.13})$$

802 The conditions for which C is maximal at $\gamma = 1$ can be therefore reduced to
 803 $i_c > i^+$.

804 Case 2: C is maximal for $\gamma = \gamma^{opt}$ if $e_c m_c + u_c(T - i_c) > 0$ and $\gamma_0 < 1$ OR
 805 if $e_c m_c + u_c(T - i_c) > 0$, $\gamma_0 > 1$ and $P_{1,c}^*(\gamma = 1) < P^{opt}$. In the same way as
 806 for case 1, we can show that these conditions reduced to $i_c < i^+$.

807 References

808 References

809 J. M. Anderies, A. A. Rodriguez, M. A. Janssen, and O. Cifdaloz. Panaceas,
 810 uncertainty, and the robust control framework in sustainability sci-
 811 ence. *Proceedings of the National Academy of Sciences*, 104(39):15194–
 812 15199, 2007. ISSN 0027-8424. doi: 10.1073/pnas.0702655104. URL
 813 <http://www.pnas.org/cgi/doi/10.1073/pnas.0702655104>.

814 K. J. K. J. Astrom and R. M. Murray. Feedback systems: an intro-
 815 duction for scientists and engineers. *Choice Reviews Online*, 46(04):
 816 46-2107-46-2107, 2008. ISSN 0009-4978. doi: 10.5860/CHOICE.46-
 817 2107. URL <https://authors.library.caltech.edu/25062/>
 818 <http://choicereviews.org/review/10.5860/CHOICE.46-2107>.

- 819 A. Bisson, S. Boudsocq, C. Casenave, S. Barot, R. J. Manlay, J. Vayssières,
820 D. Masse, and T. Daufresne. West-African farming systems as meta-
821 ecosystems: an ecological source-sink modelling approach of the nitrogen
822 cycle and crop production. *Ecosystems (in review)*.
- 823 S. Boudsocq, J. C. Lata, J. Mathieu, L. Abbadie, and S. Barot. Modelling
824 approach to analyse the effects of nitrification inhibition on primary pro-
825 duction. *Functional Ecology*, 23(1):220–230, 2009. ISSN 1365-2435. doi:
826 10.1111/j.1365-2435.2008.01476.x.
- 827 J.-l. Chen. Optimal cutting frequency and intervals derived from Johnson
828 and Thornley’s model of grass growth. *Agricultural Systems*, 22(4):305–
829 314, jan 1986. doi: 10.1016/0308-521X(86)90097-1.
- 830 J.-L. Chen and Q. Wang. A theoretical analysis of the potential productivity
831 of ryegrass under grazing. *Journal of Theoretical Biology*, 133(3):371–383,
832 aug 1988. doi: 10.1016/S0022-5193(88)80328-X.
- 833 J.-P. Corriou. *Process Control: Theory and Applications*. Springer London,
834 London, 2004. ISBN 978-1-4471-3848-8.
- 835 D. L. DeAngelis. *Dynamics of nutrient cycling and food web*. Springer, 1992.
- 836 F. Dieguez Cameroni and H. Fort. Towards scientifically based man-
837 agement of extensive livestock farming in terms of ecological predator-
838 prey modeling. *Agricultural Systems*, 153:127–137, may 2017. doi:
839 10.1016/J.AGSY.2017.01.021.
- 840 P. Dugué, J. Vayssieres, E. Chia, S. Ouedraogo, M. Havard, D. Coulibaly,
841 H. B. Nacro, F. Sissoko, M. Sangare, and E. Vall. L’intensification

842 écologique : réflexions pour la mise en pratique de ce concept dans les
843 zones de savane d'Afrique de l'Ouest. *Actes du séminaire ASAP*, 2011.

844 Food and Agriculture Organization of the United Nations. *Save and grow*
845 *: a policymaker's guide to sustainable intensification of smallholder crop*
846 *production*. Food and Agriculture Organization of the United Nations,
847 2011. ISBN 9789251068717.

848 H. Fort, F. Dieguez, V. Halty, and J. M. S. Lima. Two examples of applica-
849 tion of ecological modeling to agricultural production: Extensive livestock
850 farming and overyielding in grassland mixtures. *Ecological Modelling*, 357:
851 23–34, aug 2017. doi: 10.1016/J.ECOLMODEL.2017.03.023.

852 G. Goodwin and K. Sin. *Adaptive Filtering Prediction and Control*. Prentice-
853 Hall, 1984. ISBN 0486137724.

854 H. Guerin and E. Roose. Ingestion, restitution et transfert d'éléments fer-
855 tilisants aux agro systèmes par les ruminants domestiques en régions semi
856 arides d'Afrique occidentale : point de vue d'un zootechnicien et d'un
857 agro-pédologue, 2015.

858 A. Isidori. *Nonlinear control systems*. Springer Verlag, London, 1995. ISBN
859 1846286158.

860 W. S. Levine. *The Control Handbook*. CRC Press, 2nd editio edi-
861 tion, 2010. ISBN 978-1-4200-7366-9. doi: 10.1201/b10383. URL
862 <https://www.taylorfrancis.com/books/9781420073614>.

863 A. R. Longhurst and W. Glen Harrison. The biological pump: Profiles of
864 plankton production and consumption in the upper ocean. *Progress in*

865 *Oceanography*, 22(1):47–123, jan 1989. ISSN 00796611. doi: 10.1016/0079-
866 6611(89)90010-4.

867 M. Loreau. Ecosystem development explained by competition within
868 and between material cycles. *Proceedings of the Royal Society B: Bi-*
869 *ological Sciences*, 265(1390):33–38, jan 1998. ISSN 14712970. doi:
870 10.1098/rspb.1998.0260.

871 M. Loreau. *From Populations to Ecosystems : Theoreti-*
872 *cal Foundations for a New Ecological Synthesis*. Prince-
873 ton University Press, 2010. ISBN 9780691122700. URL
874 <https://press.princeton.edu/titles/9238.html>.

875 M. Loreau, N. Mouquet, and R. D. Holt. Meta-ecosystem: a theoretical
876 framework for a spatial ecosystem ecology. *Ecology Letters*, 6:673–679,
877 2003. doi: 10.1046/j.1461-0248.2003.00483.x.

878 M. Loreau, T. Daufresne, A. Gonzalez, D. Gravel, F. Guichard, S. J. J.
879 Leroux, N. Loeuille, F. Massol, and N. Mouquet. Unifying sources and
880 sinks in ecology and Earth sciences. *Biological Reviews of the Cambridge*
881 *Philosophical Society*, 88(2):365–379, 2013. doi: 10.1111/brv.12003.

882 R. J. Manlay, A. Ickowicz, D. Masse, C. Feller, D. Richard, C. Floret,
883 D. Richard, and C. Feller. Spatial carbon, nitrogen and phosphorus budget
884 in a village of the West African savanna - II. Element flows and functioning
885 of a mixed-farming system. *Agricultural Systems*, 79(1):83–107, jan 2004.
886 ISSN 0308521X. doi: 10.1016/S0308-521X(03)00054-4.

- 887 Y. Mau and A. Porporato. Optimal control solutions to sodic soil reclama-
888 tion. *Advances in Water Resources*, 91:37–45, may 2016. ISSN 03091708.
889 doi: 10.1016/j.advwatres.2016.02.014.
- 890 I. Noy-Meir. Stability of grazing systems. An application of the predator-prey
891 graphs. *Journal of Ecology*, 63:459–481, 1975.
- 892 J. M. Powell, S. Fernandez-Rivera, P. Hiernaux, and M. D. Turner. Nutrient
893 Cycling in Integrated Rangeland/Cropland System of the Sahel. *Agricultural
894 Systems*, 52(2/3):143–170, 1996.
- 895 J. Roman and J. J. McCarthy. The Whale Pump: Marine Mammals Enhance
896 Primary Productivity in a Coastal Basin. *PLOS ONE*, 5(10):e13255, oct
897 2010. ISSN 1932-6203. doi: 10.1371/journal.pone.0013255.
- 898 L. Ruan and X. D. D. Chen. Comparison of Several Periodic Operations of a
899 Continuous Fermentation Process. *Biotechnology Progress*, 12(2):286–288,
900 apr 1996. doi: 10.1021/bp960006l.
- 901 P. Seibert and R. Suarez. Global stabilization of nonlinear cascade systems.
902 *Systems & Control Letters*, 14(4):347–352, apr 1990. doi: 10.1016/0167-
903 6911(90)90056-Z.
- 904 D. Tilman, K. G. Cassman, P. A. Matson, R. Naylor, S. Po-
905 lasky, N. Rosamuond, S. Polasky, R. Naylor, S. Polasky,
906 N. Rosamuond, and S. Polasky. Agricultural sustainability
907 and intensive production practices. *Nature*, 418(6898):671–677,
908 aug 2002. ISSN 00280836. doi: 10.1038/nature01014. URL
909 <http://www.nature.com/doifinder/10.1038/nature01014>.

910 S. J. R. R. Woodward, G. C. Wake, A. B. Pleasants, and D. G. McCall. A
911 simple model for optimizing rotational grazing. *Agricultural Systems*, 41
912 (2):123–155, jan 1993. doi: 10.1016/0308-521X(93)90037-3.

913 **Appendix C. Figures**

ACCEPTED MANUSCRIPT

914 **List of Figures**

- 915 C.1 Model of the main limiting nutrient cycle in a simplify agro-
 916 ecosystem. Representation of all stocks and fluxes presents in
 917 the model. See the table C.1 for the parameters description
 918 and units. 49
- 919 C.2 Graphical determination of the equilibrium points for the generic
 920 sub-system model. 50
- 921 C.3 Scheme of the two loops control strategy. 51
- 922 C.4 Graphical determination of the equilibrium points in the crop-
 923 land sub-system for 4 different values of T . The quantity T_0
 924 is not high enough to compensate losses, the positive equilib-
 925 rium $E_{c,1}$ does not exist. P_c increase with T until the carrying
 926 capacity K is reached, in a non-linear way. 52
- 927 C.5 (left) Evolution of $F_2(N) = \frac{eN-i}{(\alpha-1)d_r}$ when α goes from 0 to
 928 1. (right) Evolution of $F_2(N) = \frac{eN-i}{(\alpha-1)d_r}$ when d_r goes from
 929 0 to $+\infty$. Graphical method of determination of equilibrium
 930 points for 3 values of d_r with $d_r^1 \leq d_r^2 \leq d_r^3$. $P_{1,r}^*$ decreases
 931 with d_r but the variation of $N_{1,r}^*$ is not monotonous. 53
- 932 C.6 Variation of P^* and N^* (left) and T (right) with d_r (and for
 933 $\alpha_{max} = 0$) 54
- 934 C.7 Variation of crop biomass P_c^* and the production C^* of the
 935 cropland sub-system with the fraction of the agro-ecosystem
 936 surface occupied by the cropland sub-system (γ) 55
- 937 C.8 Yearly averaged stock of plants in rangeland (in kgN h^{-1}),
 938 stock of plants in cropland at harvest time (value of P_{c,t_h} ,
 939 in kgN ha^{-1}) and total amount of nutrient transferred from
 940 rangeland to cropland over a year ($\int_0^{t_h} T(t)dt$) with respect
 941 of the value of the set-point \tilde{P}_c . The set of parameters used
 942 is $u_r = 0.08$, $u_c = 0.01$, $K_r = 80$, $K_c = 40$, $e_r = 0.08$, $e_c =$
 943 0.4 , $i_r = 0.8$, $i_c = 0.05$, $m_r = 0.08$, $m_c = 0.05$, $h = 90\%$.
 944 We moreover define $\alpha = 0$ and $\gamma = \gamma^{opt} = 0.131$ from the
 945 optimization at equilibrium with $d_r^{opt} = 0.036$. The black hor-
 946 izontal straight lines represent the values obtained with the
 947 optimization at equilibrium such as $P_c^{opt} = 21.7$ (black ver-
 948 tical straight line). The gray vertical straight line represents
 949 the maximal value of \tilde{P}_c reached with the control strategies. . . 56

950	C.9	Dynamic over time of stocks of plants (a) and (b) and inorganic nutrient (c) and (d) in the cropland sub-system and the rangeland sub-system respectively. Dynamic of grazing pressure d_r (e) and transfer of inorganic nutrient T (f). The optimal scenario obtained with the optimization at equilibrium (scenarios 1), and the scenario obtained with the control theory (scenario (2), $\tilde{P}_c = P^{opt}$ and scenario (3), $\tilde{P}_c > P^{opt}$) are plotted in black lines, dotted black lines and grey lines respectively. In the subfigure (a), black and gray dashed lines respectively represent the value of the set point $\tilde{P}_c = P^{opt}$ and $\tilde{P}_c > P^{opt}$	
951		The set of parameters used is $u_r = 0.08$, $u_c = 0.01$, $K_r = 80$, $K_c = 40$, $e_r = 0.08$, $e_c = 0.4$, $i_r = 0.8$, $i_c = 0.05$, $m_r = 0.08$, $m_c = 0.05$, $h = 90\%$. We moreover define $\alpha = 0$, $\gamma^{opt} = 0.131$, $d_r^{opt} = 0.036$ (value of d_r for scenario (1) only) and get $d_r^{max} = 0.72$, $T_{max} = 0.65$	57
952			
953			
954			
955			
956			
957			
958			
959			
960			
961			
962			
963			
964			
965	C.10	Variations table of the function $\gamma \mapsto C$ in the case when $\frac{e_c m_c}{u_c} + T - i_c > 0$	58
966			

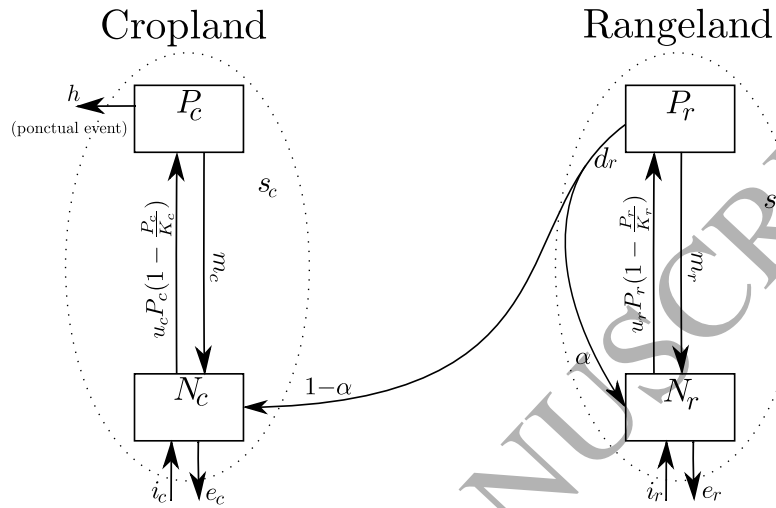
967 **Figures**

Figure C.1: Model of the main limiting nutrient cycle in a simplify agro-ecosystem. Representation of all stocks and fluxes presents in the model. See the table C.1 for the parameters description and units.

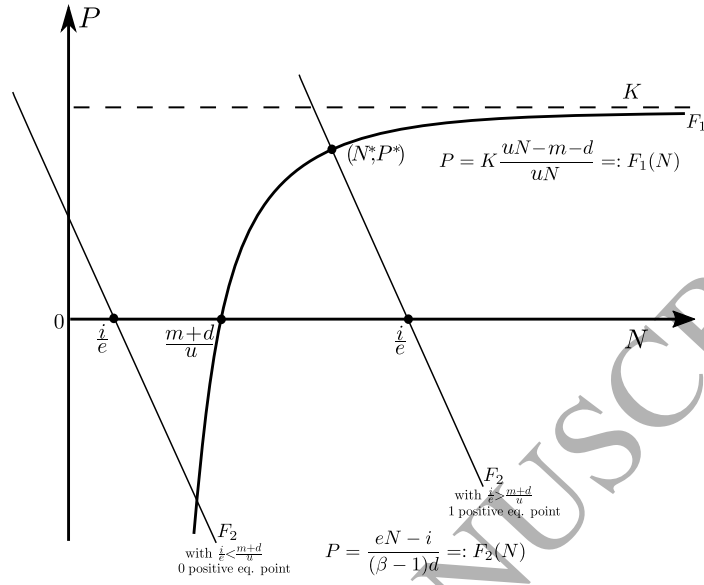


Figure C.2: Graphical determination of the equilibrium points for the generic sub-system model.

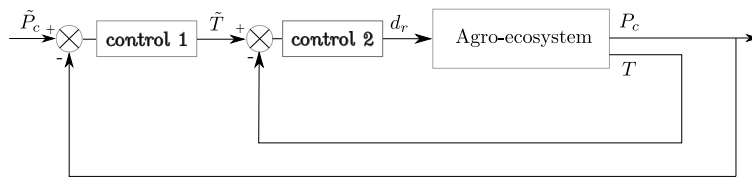


Figure C.3: Scheme of the two loops control strategy.

ACCEPTED MANUSCRIPT

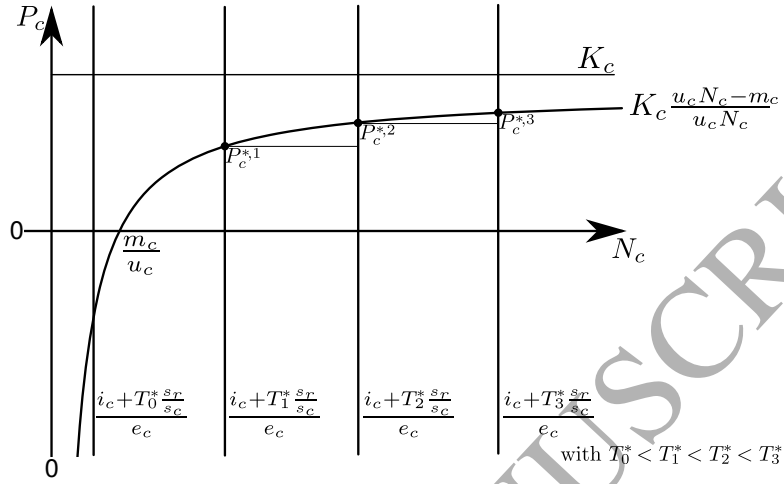


Figure C.4: Graphical determination of the equilibrium points in the cropland sub-system for 4 different values of T . The quantity T_0 is not high enough to compensate losses, the positive equilibrium $E_{c,1}$ does not exist. P_c increase with T until the carrying capacity K is reached, in a non-linear way.

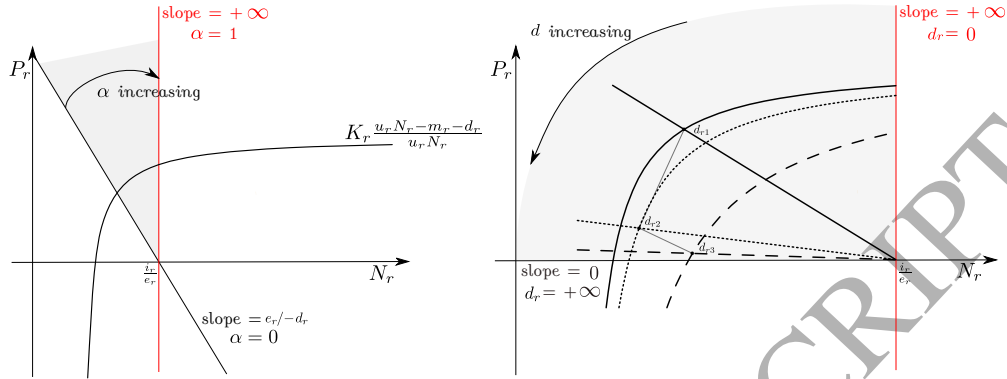


Figure C.5: (left) Evolution of $F_2(N) = \frac{eN-i}{(\alpha-1)d_r}$ when α goes from 0 to 1. (right) Evolution of $F_2(N) = \frac{eN-i}{(\alpha-1)d_r}$ when d_r goes from 0 to $+\infty$. Graphical method of determination of equilibrium points for 3 values of d_r with $d_r^1 \leq d_r^2 \leq d_r^3$. $P_{1,r}^*$ decreases with d_r but the variation of $N_{1,r}^*$ is not monotonous.

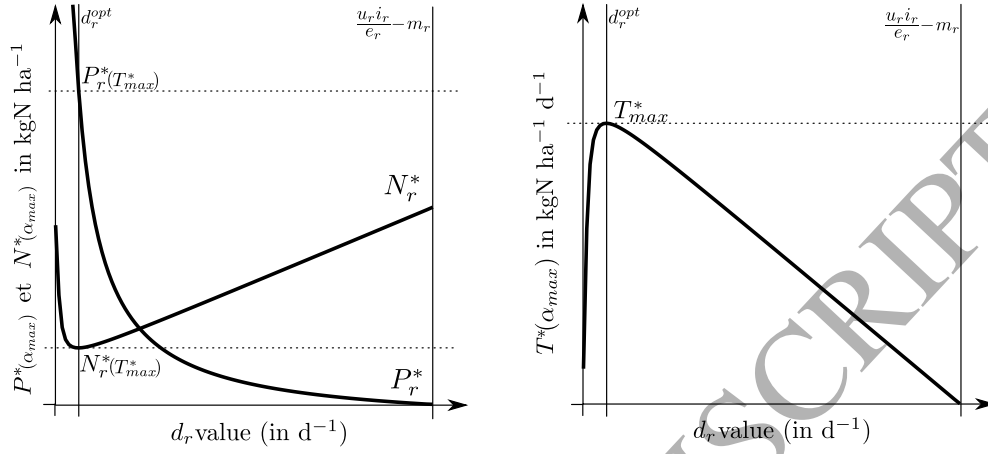


Figure C.6: Variation of P^* and N^* (left) and T (right) with d_r (and for $\alpha_{max} = 0$)

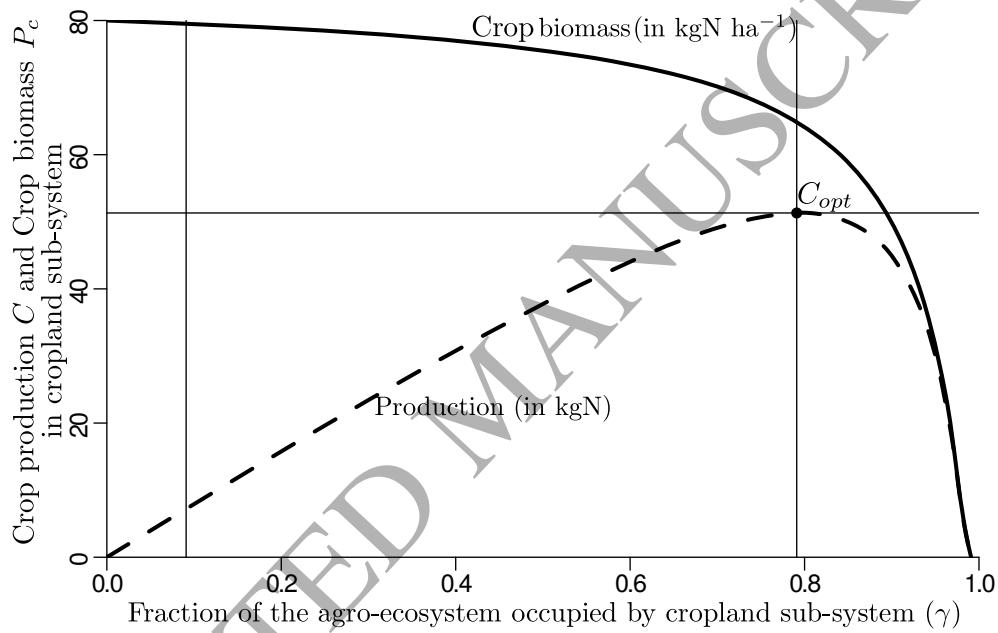


Figure C.7: Variation of crop biomass P_c^* and the production C^* of the cropland sub-system with the fraction of the agro-ecosystem surface occupied by the cropland sub-system (γ)

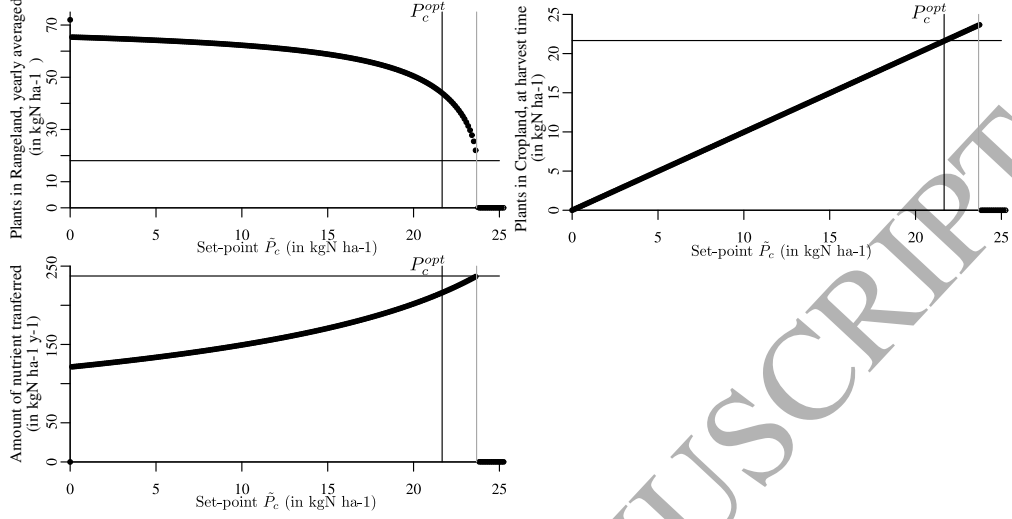


Figure C.8: Yearly averaged stock of plants in rangeland (in kgN h^{-1}), stock of plants in cropland at harvest time (value of P_{c,t_h} , in kgN ha^{-1}) and total amount of nutrient transferred from rangeland to cropland over a year ($\int_0^{t_h} T(t)dt$) with respect of the value of the set-point \tilde{P}_c . The set of parameters used is $u_r = 0.08$, $u_c = 0.01$, $K_r = 80$, $K_c = 40$, $e_r = 0.08$, $e_c = 0.4$, $i_r = 0.8$, $i_c = 0.05$, $m_r = 0.08$, $m_c = 0.05$, $h = 90\%$. We moreover define $\alpha = 0$ and $\gamma = \gamma^{opt} = 0.131$ from the optimization at equilibrium with $d_r^{opt} = 0.036$. The black horizontal straight lines represent the values obtained with the optimization at equilibrium such as $P_c^{opt} = 21.7$ (black vertical straight line). The gray vertical straight line represents the maximal value of \tilde{P}_c reached with the control strategies.

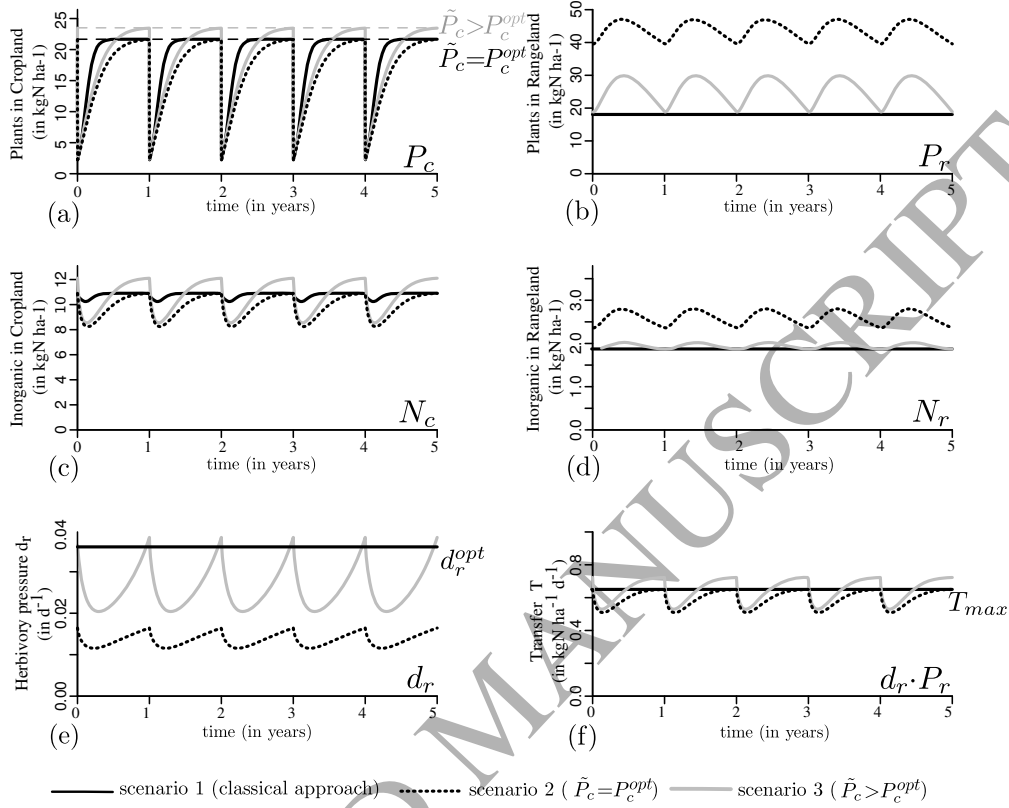


Figure C.9: Dynamic over time of stocks of plants (a) and (b) and inorganic nutrient (c) and (d) in the cropland sub-system and the rangeland sub-system respectively. Dynamic of grazing pressure d_r (e) and transfer of inorganic nutrient T (f). The optimal scenario obtained with the optimization at equilibrium (scenarios 1), and the scenario obtained with the control theory (scenario 2), $\tilde{P}_c = P_c^{opt}$ and scenario 3), $\tilde{P}_c > P_c^{opt}$ are plotted in black lines, dotted black lines and grey lines respectively. In the subfigure (a), black and gray dashed lines respectively represent the value of the set point $P_c = P_c^{opt}$ and $\tilde{P}_c > P_c^{opt}$. The set of parameters used is $u_r = 0.08$, $u_c = 0.01$, $K_r = 80$, $K_c = 40$, $e_r = 0.08$, $e_c = 0.4$, $i_r = 0.8$, $i_c = 0.05$, $m_r = 0.08$, $m_c = 0.05$, $h = 90\%$. We moreover define $\alpha = 0$, $\gamma^{opt} = 0.131$, $d_r^{opt} = 0.036$ (value of d_r for scenario (1) only) and get $d_r^{max} = 0.72$, $T_{max} = 0.65$.

γ	0	γ^+	γ_0
$dP/d\gamma$	-	-	-
P	K	p^+	0
$dC/d\gamma$	+	0	-
C	0	C^+	0

Figure C.10: Variations table of the function $\gamma \mapsto C$ in the case when $\frac{e_c m_e}{u_c} + T - i_c > 0$.

968 **List of Tables**

969	C.1	Nomenclature of model parameters. The subscript z stands for	
970		either r or c depending on the sub-system considered (range-	
971		land or cropland).	60

ACCEPTED MANUSCRIPT

972 **Tables**

variable	dimensions	description
P_z	kgN ha ⁻¹	Stock of nutrient in the plant compartment
N_z	kgN ha ⁻¹	Stock of nutrient in the inorganic nutrient compartment
parameter	dimensions	description
u_z	ha kgN ⁻¹ d ⁻¹	nutrient uptake rate of plants
K_z	kgN ha ⁻¹	carrying capacity of plant
m_z	d ⁻¹	mortality rate of plants
e_z	d ⁻¹	losses (ex: leaching) of inorganic nutrient
i_z	kgN ha ⁻¹ d ⁻¹	inputs of inorganic nutrient (ex: atmospheric deposition)
s_z	ha	surface of the sub-system
γ		fraction of agro-ecosystem occupied by cropland
d_r	d ⁻¹	grazing pressure in rangeland
α		fraction of uptake by livestock recycled into rangeland
$1 - \alpha$		fraction of uptake by livestock transferred to cropland
h	%	harvest in cropland in the end of each year
T	kgN ha ⁻¹ d ⁻¹	nutrient transferred from rangeland to cropland $T = (1 - \alpha)d_r P_r$, (see equation 10)

Table C.1: Nomenclature of model parameters. The subscript z stands for either r or c depending on the sub-system considered (rangeland or cropland).