https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

How Can Grazing Increase Grassland Carbon Storage: A Mechanistic Modelling Approach

Emma Escoffier[1,3], Céline Casenave[1], Tanguy Daufresne[2,3]

[1] MISTEA, Univ. Montpellier, INRAE, Institut Agro, 34060 Montpellier, France

[2] Eco&Sols, Univ. Montpellier, INRAE, 34060 Montpellier, France

[3] CEFE, Univ. Montpellier, CNRS, EPHE, IRD, Montpellier Cedex 5, France

Emma ESCOFFIER (Corresponding author)

emma.escoffier@inrae.fr

https://orcid.org/0009-0009-3970-3946

Céline CASENAVE

celine.casenave@inrae.fr

https://orcid.org/0000-0003-0489-4665

Tanguy DAUFRESNE

tanguy.daufresne@inrae.fr

https://orcid.org/0000-0002-3510-0701

Highlights :

- The increase of carbon storage with grazing intensity in grassland ecosystems is more an exception than the rule.
- Net primary production alone is not a reliable indicator of carbon sequestration.

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

- High herbivore-induced root exudation can contribute to increasing carbon storage at low to moderate grazing intensity.

Abstract: Permanent grassland soils have high carbon sequestration potential, but this potential is highly dependent on environmental conditions and grazing practices. In this paper, we study the impact of herbivore grazing intensity on grassland carbon storage. We present and study a parsimonious stocks and fluxes model coupling carbon and nitrogen cycles and including microbial decomposers, root exudates, rhizosphere priming effect and the impact of grazing by domestic herbivores. Our main objective is to understand the mechanisms through which herbivore grazing can contribute to increasing carbon stocks in grasslands. Analysis of model outcomes shows that the bell-shaped response of carbon storage to grazing intensity, as reported in the literature, is the exception rather than the rule. The study also demonstrates that net primary production alone is not a reliable indicator of carbon sequestration. While increasing grazing intensity can lead to an increase in grassland carbon stocks at steady state, this only occurs if the increase in NPP is sufficient to compensate for the increase in carbon output by herbivores. Finally, the study identifies herbivore-induced root exudation as a potential yet underexplored mechanism that could be optimised to increase carbon storage. In this regard, it would be interesting to identify the management practices (timing, duration, intensity, and frequency of grazing) that optimize this mechanism.

1. INTRODUCTION

Grasslands, including sown pasture and rangeland, are among the largest ecosystems in the world, representing up to 40% of the earth's land area (O'Mara, 2012; Panunzi, 2008; White et al., 2000) and storing between 10% and 30% of global soil organic carbon (Scurlock & Hall, 1998; Follett & Reed, 2010). Yet, the magnitude and direction (augmentation or reduction) of this storage are highly contingent upon environmental conditions and

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

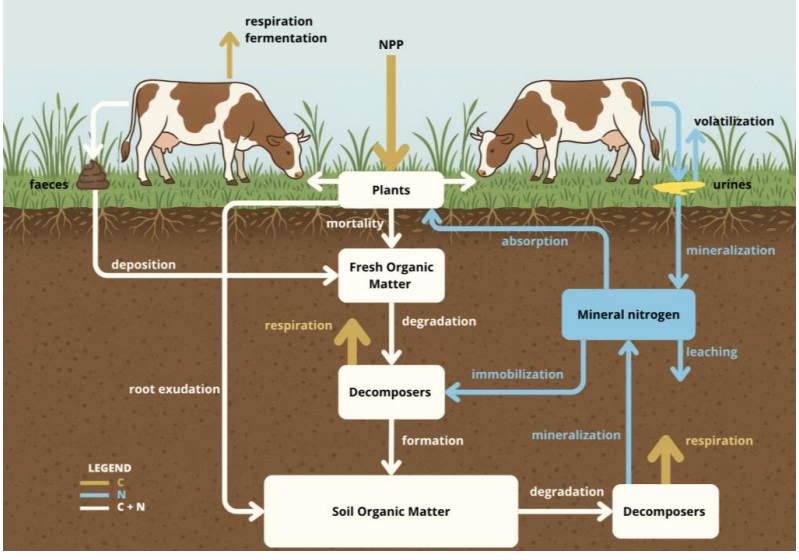
management practices (IPCC, 2006; Soussana et al., 2010; Klumpp et al., 2011), with grazing intensity emerging as a key driver (Hao et al., 2024; Zhou et al., 2017).

Meta-analyses report divergent responses of soil carbon stocks to grazing intensity. Several studies document a consistent decline in carbon storage with increasing grazing intensity (Li et al., 2024; Xu et al., 2023; Zhang et al., 2023; Niu et al., 2025; Abdalla et al., 2018), whereas others document a nonlinear pattern characterized by carbon gains under low to moderate grazing followed by losses at high intensity (Zhou et al., 2017; Lai & Kumar, 2020). Collectively, these syntheses indicate that the effects of grazing intensity on soil carbon storage are strongly context-dependent (McSherry & Ritchie, 2013; Maestre et al., 2022; Niu et al., 2025; Abdalla et al., 2018). Specifically, the response of soil carbon to grazing intensity is modulated by climatic regime (Niu et al., 2025; Maestre et al., 2022; Abdalla et al., 2018), soil properties (Maestre et al., 2022; Niu et al., 2025), grassland functional composition (C3, C4, or mixed C3–C4; Abdalla et al., 2018; McSherry & Ritchie, 2013), broader ecological context (Marks et al., 2024), grassland type and management system (Deng et al., 2023; Niu et al., 2025), and herbivore type (Su et al., 2023; Niu et al., 2025). Given the strong context dependency reported in the literature, the mechanisms leading to increases in soil carbon storage under low to moderate grazing remain insufficiently understood. Approaches to assess the impact of grazing intensity on carbon storage have failed to converge into a cohesive mechanistic understanding (Stanley et al., 2024).

At the ecosystem scale, changes in soil organic matter (SOM) stocks primarily reflect the balance between two dominant fluxes: (i) the fraction of net primary production (NPP) entering the soil via plant mortality and rhizodeposition, and (ii) heterotrophic respiration losses from the soil (Bondeau et al., 2007; Don et al., 2024). The magnitude of these fluxes is biologically regulated. In particular plants and microorganisms adjust their metabolism and uptake fluxes to maintain near-homeostatic stoichiometric ratios under varying nutrient availability (Bernard, 1865; Cannon, 1939; Sterner & Elser, 2003). Herbivores influence both sides of this balance (figure 1; McNaughton, 1979; Hilbert et al., 1981; Dyer et al., 1986;

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

81 Stanley et al., 2024; Risch et al., 2023, Roy et al., 2023) directly by increasing plant mortality
82 and indirectly by modifying the whole ecosystem stoichiometry (Daufresne, 2021).
83



84

85 **Figure 1 : Herbivores impact on grassland carbon and nitrogen cycles**

86 *Carbon fluxes are depicted in brown, nitrogen fluxes in blue, and in white are material fluxes*
87 *that combine carbon and nitrogen (in biomass).*
88

89 Through respiration and enteric fermentation, herbivores release digestible carbon
90 (CO_2 , CH_4), while returning highly labile nitrogen to soils via urine (Soussana & Lemaire,
91 2014). Increased nitrogen availability can stimulate NPP, consistent with the grazing
92 optimization hypothesis (GOH), which predicts peak productivity under low to moderate
93 grazing intensity (McNaughton, 1979; Hilbert et al., 1981; Dyer et al., 1986; Chen et al., 2025).
94 In addition, low to moderate grazing can enhance plant belowground biomass (Zhou et al.,
95 2017; Zhan et al., 2020) and the release of root exudates (Yang et al., 2026; Zhan et al., 2020;
96 Sun et al., 2017, Hamilton et al., 2008). These low-molecular-weight, high-quality compounds
97 such as simple sugars and organic acids (Gunina & Kuzyakov, 2015; Wang & Kuzyakov, 2023)
98 can stimulate soil organic matter mineralization via the rhizosphere priming effect (RPE;

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

Kuzyakov, 2002; Pausch et al., 2024). This process simultaneously increases nitrogen availability for plant uptake (Pausch et al., 2024) and carbon losses to the atmosphere. Consequently, herbivore-induced changes in belowground biomass and rhizodeposition have the potential to jointly regulate both NPP inputs and soil respiration outputs. However, the net effect of these coupled processes on soil carbon balance under grazing remains poorly quantified. In particular, it is unclear whether grazing-induced increases in root exudation can offset priming-driven carbon losses and thereby promote soil carbon accumulation. Addressing this gap requires a mechanistic framework explicitly linking grazing intensity, root exudates, and soil carbon and nitrogen dynamics.

Mechanistic models help moving beyond correlative studies and explicitly identify the processes governing grassland carbon storage under low to moderate grazing intensity. Several large predictive models already exist (DayCent, Parton et al., 1998; PaSim, Riedo et al., 1998; RothC, Coleman and Jenkinson, 1996), but their complexity makes the mechanisms difficult to understand and disentangle. By contrast, minimal models allow examining different factors in isolation by targeting the processes of interest. Furthermore, their relative simplicity facilitates their mathematical analysis, giving the results a more generic scope (Levins 1966). There are many minimal models attempting to characterize organic carbon dynamics in soil (Perveen et al., 2014; Chertov et al., 2022; Abramoff., 2017; Chandel et al., 2023; Rocci et al., 2024). These models mainly differ through the organic matter compartments that are considered, the presence or absence of soil microbial decomposers (Chandel et al., 2023, Zhang et al., 2021), as well as the choice of the mechanisms that link together the soil compartments. Given that the main mechanisms governing carbon storage in soils are still poorly understood (Sokol et al., 2022), it is difficult to integrate herbivores into these models and understand their impact. Some studies have attempted to transpose aquatic models to terrestrial models with herbivores (Daufresne, 2021); however these simplified models do not take into account some important mechanisms that are specific to the soil, such as the rhizosphere priming effect or the occurrence of root exudates (Sulman et al., 2014; Chertov et al., 2022).

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

In the present paper, we present and study a stocks and fluxes model combining carbon and nitrogen cycles which provides a simplified representation of a grassland ecosystem, including microbial decomposers, root exudates, rhizosphere priming effect and the impact of grazing by domestic herbivores. Our main objective is to understand through which mechanisms and conditions low to moderate grazing intensity can cause an increase in grassland carbon stocks (Bork et al., 2023; Zhang et al., 2018; Abdalla and al., 2018; Zhou et al., 2017).

2. MATERIAL AND METHODS

2.1. Model stocks and fluxes

Our model is based on a previous consumer-driven recycling model in a terrestrial ecosystem originally developed by Daufresne (2021) and focusing on the nitrogen and phosphorus cycles. In our model, we do not consider the phosphorus cycle, but we explicitly add up the carbon cycle. The model is a stocks and fluxes model, whose state variables, parameters and functions are summarized in Table 1. A diagram of the model is depicted in Figure 2.

In this section, we present all the stocks and fluxes represented in the model, focusing first on the grassland without herbivores, and then including the carbon and nitrogen fluxes associated with the impact of herbivores.

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

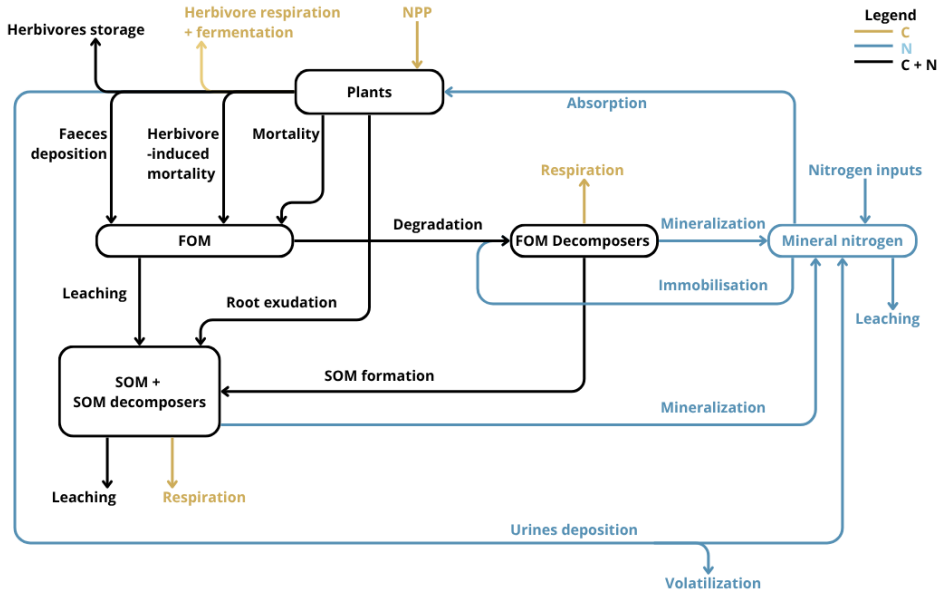


Figure 2: Diagram of the grassland ecosystem model representing the carbon and nitrogen fluxes between plants, herbivores, FOM, FOM decomposers, SOM and its decomposers and soil mineral nitrogen *Carbon fluxes are depicted in brown, nitrogen fluxes in blue, and in black are material fluxes that combine carbon and nitrogen (in biomass).*

2.1.1. Model of the grassland without herbivores

Grassland compartments. The model has five compartments : the Mineral Nitrogen (variable MN in the model), the Plants (P), the Fresh Organic Matter (FOM), the Decomposers of the FOM (D), and the Soil Organic Matter with its decomposers (SOM). In the following, SOM refers to the soil organic matter with its decomposers.

The mineral nitrogen compartment is a stock of nitrogen only, whereas all the other compartments represent organic matter that contains both carbon and nitrogen. In the model, the subscript “c” (respectively "n") is used to denote the carbon (respectively the nitrogen) stock of a compartment, except for the mineral nitrogen compartment. The carbon stocks in the model are therefore the plant carbon stock (variable P_c), the FOM decomposer carbon stock (D_c), the fresh organic matter carbon stock (FOM_c) and the soil organic matter carbon

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

stock (SOM_c). The nitrogen stocks are the mineral nitrogen (MN), the plant nitrogen stock (P_n), the FOM decomposer nitrogen stock (D_n), the fresh organic matter nitrogen stock (FOM_n) and the soil organic matter nitrogen stock (SOM_n).

The carbon-to-nitrogen (C:N) ratios of plants and decomposers (FOM and SOM) are considered constant in this model and are denoted ρ_P and ρ_D respectively. As a consequence, we can deduce the nitrogen stock of plants and FOM decomposers directly from their carbon stock by: $P_n = \frac{P_c}{\rho_P}$ and $D_n = \frac{D_c}{\rho_P}$ and their dynamics is deducted from the dynamical equations of P_c and D_c, respectively.

Plant compartment fluxes :

The flux of nitrogen absorption by the plants from the mineral nitrogen stock (variable MN in the model) is expressed by a Monod equation (Monod, 1949), also known as "Holling Type 2". This equation is classically used for vascular plants (Tilman, 1982) :

$$g_P(MN) \times \frac{P_c}{\rho_P} = \mu_P \frac{MN}{MN+K_P} \times \frac{P_c}{\rho_P}$$

where μ_P is the maximal absorption rate when roots transporters are saturated and K_P is the half-saturation constant, that is, the nitrogen concentration at which the absorption rate is equal to half the maximal absorption rate (Monod, 1949).

In most temperate terrestrial ecosystems, plant growth is limited by nitrogen (Elser et al. 2007, Shi et al. 2024, Fang et al. 2024). In the model, the flux of carbon assimilated by plants during plant production, i.e. the flux of photosynthesis minus respiration (net primary production NPP) is calculated so that the C:N ratio of plants remains constant and equal to ρ_P. Thus, it is equal to the nitrogen absorption flux by the roots multiplied by the ratio ρ_P, that is $\mu_P \frac{MN}{MN+K_P} \times P_c$.

The flux of plant dead tissues (aerial and root), expressed by $m_P \times P_c$ with m_P the mortality rate of plants, feeds the carbon stock of fresh organic matter FOM_c. The carbon flux exuded by plant roots is expressed by $a_e \times P_c$ where a_e is the rate of carbon exuded by roots; this flux feeds the carbon stock of soil organic matter SOM_c (Pausch et al., 2024). The additional flux

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

of carbon exuded by roots enhanced by the presence of herbivores (Sun et al., 2017) is described below in the section: Nutrient uptake and recycling by herbivores.

FOM compartment fluxes:

The term $l_{FOM} \times FOM_c$ represents the flux of carbon leached out from the surface soil, which feeds the SOM_c stock. The corresponding nitrogen flux $l_{FOM} \times FOM_n$ feeds the SOM_n stock.

FOM decomposers compartment fluxes:

The fluxes of carbon and nitrogen uptaken by the FOM decomposers from the FOM_c are represented respectively by $d_D(FOM_c, FOM_n, MN)\, D_c$ and $d_D(FOM_c, FOM_n, MN) \times \frac{FOM_n}{FOM_c} \times D_c$, where $d_D(FOM_c, FOM_n, MN)$ denotes the FOM_c degradation rate, whose expression is given in the sequel. As $\frac{FOM_n}{FOM_c} > r_D$ (see Supplementary material) there is not enough nitrogen in the FOM compared to carbon to allow the FOM decomposers to maintain their C:N ratio constant. Thus, FOM decomposers take up additional nitrogen from the mineral stock of the soil, a process referred to as “immobilization” (Daufresne and Loreau, 2001). This flux is represented by $i_D\,(FOM_c, FOM_n, MN) \times D_c$ with i_D the immobilisation rate of mineral nitrogen whose expression is given in the sequel. $r_D \times D_c$ is the carbon flux released into the atmosphere through decomposer respiration, where r_D characterizes the rate of carbon respired by FOM decomposers. A flux of nitrogen $r_D \times \frac{D_c}{\rho_D}$ proportional to the carbon respired (in order to maintain the ratio ρ_D constant) is mineralized by FOM decomposers and feeds the mineral nitrogen stock. The flux $l_D \times D_c$ is the flux of carbon that feeds the SOM_c stock through biotic processes operated by the FOM decomposers (e.g. decomposers necromass production, exudation, excretion, and carbon transfer through bioturbation), where l_D is the rate of SOM formation by the FOM decomposers. The corresponding nitrogen flux : $l_D \times \frac{D_c}{\rho_D}$ feeds the SOM_n stock.

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

When the flux of carbon absorption by FOM decomposers (during the degradation of the FOM) is limited by the quantity of carbon available in the FOM, the FOM_c degradation rate is expressed as follows : $d_D(FOM_c, FOM_n, MN) = a_d \times FOM_c$. Conversely, when nitrogen is limiting, the immobilisation rate of mineral nitrogen is expressed as follows: $i_D\,(FOM_c, FOM_n, MN) = a_i \times MN$. Since the C:N ratio of decomposers is considered constant in this model, it should be equal to the ratio of carbon fluxes over nitrogen fluxes in the decomposer compartment, that is :

$$\rho_D = \frac{(d_D(FOM_c,FOM_n,MN) - r_D - l_D) \times D_c}{(i_D\,(FOM_c,FOM_n,MN) + d_D(FOM_c,FOM_n,MN) \times \frac{FOM_n}{FOM_c} - \frac{r_D}{\rho_D} - \frac{l_D}{\rho_D}) \times D_c} \quad (1)$$

$$\Leftrightarrow$$

$$i_D\,(FOM_c, FOM_n, MN) = d_D(FOM_c, FOM_n, MN) \times (\frac{1}{\rho_D} - \frac{FOM_n}{FOM_c}) \quad (2)$$

The term $\frac{1}{\rho_D} - \frac{FOM_n}{FOM_c}$ (which is always positive as $\frac{FOM_n}{FOM_c} > \rho_D$) represents the proportion of nitrogen required by the FOM decomposers to maintain the ratio ρ_D constant, minus the proportion of nitrogen already uptaken from the FOM. Thanks to eq (2), when FOM decomposers are limited by the nitrogen immobilization flux, the corresponding carbon flux can be expressed as follows :

$$d_D(FOM_c\,, FOM_n\,, MN) = \frac{a_i \times MN}{\frac{1}{\rho_D} - \frac{FOM_n}{FOM_c}} \quad (3)$$

With the Liebig's law of the minimum, we get :

$$d_D(FOM_c\,, FOM_n\,, MN) = min\,(a_d \times FOMc\,, \frac{a_i \times MN}{\frac{1}{\rho_D} - \frac{FOM_n}{FOM_c}}) \quad (4)$$

$$i_D(FOM_c\,, FOM_n\,, MN) = min\,(a_d \times FOMc \times (\frac{1}{\rho_D} - \frac{FOM_n}{FOM_c}), a_i \times MN\,) \quad (5)$$

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

Mineral nitrogen compartment fluxes:

The mineral nitrogen stock is fed by a flux of nitrogen inputs denoted f_{MN}^{in}, by both atmospheric deposition and fertilisation. Since the grassland is fertilised, biological fixation is considered negligible (see Zheng et al., 2019). The leaching flux of nitrogen from the mineral nitrogen stock is expressed by $l_{MN} \times MN$ where l_{MN}represents the leaching rate.

SOM compartment fluxes:

The soil organic matter (SOM) compartment contains all the carbon molecules in the soil that are not contained in the fresh organic matter or in the FOM decomposers biomass; it includes the biomass of decomposers that specifically degrade this SOM, and which are not explicitly represented by a variable in the model. We assume that the biomass of the SOM decomposers is simply a fraction δ of the SOM that remains constant over time. The SOM compartment is fed by the total carbon flux from root exudation $e_P(h) \times P_c$ with $e_P(h)$ being the root exudation rate. This flux contains molecules (including organic acids, sugars and amino acids) which represent a source of high-quality nutrients for microbes, stimulating their growth (Bardgett et al. 2005) and enhancing SOM decomposition (respiration and mineralization) (Pausch et al., 2024) by the so-called rhizosphere priming effect (RPE). For that reason, the flux of carbon respired by SOM decomposers is assumed to be proportional to the carbon flux from root exudation and expressed by $r_{SOM}(h, P_c) \times \delta \times SOM_c$, where $r_{SOM}(h, P_c) = w \times e_P(h) \times P_c$ is the respiration rate by the SOM decomposers and w is the factor representing the carbon respired by SOM decomposers thanks to the energy received from root exudates. A flux of nitrogen $\frac{1}{\rho_D} \times r_{SOM}(h, P_c) \times \delta \times SOM_c$ proportional to the flux of carbon respired is mineralized by the SOM decomposers and feeds the mineral nitrogen stock. We consider that the SOM decomposers have the same C:N ratio ρ_D than the FOM decomposers. We also assume that the SOM decomposers select molecules that have a C:N ratio equal to ρ_D in order to maintain their own ratio constant. The fluxes of carbon and nitrogen leached from the SOM

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

compartment are expressed by $l_{SOM} \times SOM_c$ and $l_{SOM} \times SOM_n$, with l_{SOM} being the leaching rate.

2.1.2. Herbivores-induced fluxes:

In the model, we assume that the grazing intensity is controlled by human management, and that the herbivores compartment H is fixed and constant over time. The C:N ratio of herbivores is therefore also considered constant and is denoted ρ_H. The impact of herbivores on the plant compartment is represented by a carbon flux leaving the plant compartment. This flux is of the form $h \times P_c$ where h is the grazing intensity, i.e. the rate at which plants are impacted by defoliation, trampling, saliva or faeces (Lefebvre & Gallet, 2017).

The part of this flux that is ingested by herbivores is $\alpha \times h \times P_c$ where α corresponds to the percentage of impacted plants ingested by the herbivores. By denoting γ the percentage of carbon ingested by herbivores that is egested in the form of faeces, the carbon flux egested by the herbivores and feeding the FOM compartment is expressed by $\gamma \times \alpha \times h \times P_c$. The flux $\frac{\gamma \times \alpha \times h}{\rho_f} \times P_c$ represents the nitrogen flux egested by the herbivores, where ρ_f is the C:N ratio of herbivores faeces, assumed to be constant over time. The herbivores enrich the non-digestible carbon fraction with nitrogen, which means that $\rho_f < \rho_P$ (Lecomte and al., 2002, Bloor and al., 2012). The carbon released into the atmosphere by respiration and after fermentation in the herbivores rumen is represented by a carbon flux of the form $\beta \times \alpha \times h \times P_c$, where β is the percentage of carbon respired and fermented by the herbivores. The flux of carbon stored in the herbivores biomass is $(1 - \beta - \gamma) \times \alpha \times h \times P_c$, and the flux of nitrogen stored in the herbivores biomass to maintain ρ_H constant is $\frac{(1-\beta-\gamma) \times \alpha \times h}{\rho_h} \times P_c$. Finally, the flux of nitrogen excreted by the herbivores through urines $u(h)$ can be deduced from the following balance equation:

$$\frac{(1-\beta-\gamma) \times \alpha \times h}{\rho_h} \times P_c = \frac{\alpha \times h}{\rho_P} \times P_c - \frac{\gamma \times \alpha \times h}{\rho_f} \times P_c - u\,(h) \times P_c \quad (6)$$

$$\Leftrightarrow$$

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

$$u(h) \times P_c = (\gamma \times (\frac{1}{\rho_h} - \frac{1}{\rho_f}) + \frac{1}{\rho_P} - \frac{(1-\beta)}{\rho_H}) \times \alpha \times h \times P_c \quad (7)$$

A percentage η of the urine flux is volatilized and therefore lost from the system. We assume that the mineralization rate of urine is almost instantaneous. For this reason, the urine flux that has not been volatilized $u \times (1-\eta)$ directly feeds the mineral nitrogen stock in this model. Finally, the herbivores induce root exudation (Hamilton and Frank, 2001 ; Sun et al., 2017 ; Wilson et al., 2018 ; Yang et al., 2026) propositional to the grazing intensity. This additional root exudation rate induced by the herbivores is expressed by $e_P(h) = a_e + b_e \times h$, where a_e is the nominal exudation rate and b_e is the herbivore-induced root exudation factor of plant impacted at a grazing intensity h.

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

Symbol	Description	Unit
VARIABLES		
P_c	Plant carbon stock	$g\ C\ .m^{-2}$
FOM_c	FOM carbon stock	$g\ C\ .m^{-2}$
FOM_n	FOM nitrogen stock	$g\ N\ .m^{-2}$
D_c	FOM Decomposers carbon stock	$g\ C\ .m^{-2}$
MN	Mineral nitrogen stock	$g\ N\ .m^{-2}$
SOM_c	SOM carbon stock	$g\ C\ .m^{-2}$
SOM_n	SOM nitrogen stock	$g\ N\ .m^{-2}$
PARAMETERS		
ρ_P	C:N ratio of Plants	$g\ C.g\ N^{-1}$
μ_P	Maximal rate of carbon uptake by plants	day^{-1}
K_P	Mineral nitrogen stock in the soil for which absorption reaches half of maximum absorption	$g\ N\ .m^{-2}$
m	Plant mortality rate	day^{-1}
a_e	Root exudation rate	day^{-1}
l_{FOM}	Leaching rate of FOM	day^{-1}
a_d	FOM decomposition rate per FOM decomposer unit when FOM_c is limiting	$m^2.g\ C^{-1}.day^{-1}$
a_i	Mineral nitrogen immobilization rate per FOM decomposer unit when nitrogen is limiting	$m^2.g\ C^{-1}.day^{-1}$
ρ_D	C:N ratio of Decomposers	$g\ C.g\ N^{-1}$
r_D	Respiration rate of FOM Decomposers	day^{-1}
l_D	Rate of SOM formation by FOM decomposers	day^{-1}
f_{MN}^{in}	Incoming nitrogen flux	$g\ N.m^{-2}.day^{-1}$
l_{MN}	Leaching rate of mineral nitrogen	day^{-1}
l_{SOM}	Leaching rate of SOM	day^{-1}
b_e	Herbivore-induced root exudation factor	dimensionless
δ	Fraction of decomposers into the SOM	dimensionless
w	Factor of respiration and mineralization by SOM decomposers per decomposer unit	$m^2.g\ C^{-1}$
h	Grazing intensity	day^{-1}
ρ_h	Herbivores C:N ratio	$g\ C.g\ N^{-1}$
α	Fraction of plant ingested by herbivores	dimensionless
β	Fraction of plant respired and fermented by herbivores from ingested plants	dimensionless
γ	Fraction of plant excreted by herbivores from ingested plants	dimensionless
ρ_f	Herbivores faeces C:N ratio	$g\ C.g\ N^{-1}$
v	Fraction of herbivores urine volatilized	dimensionless
FUNCTIONS		
$g_P(MN)$	Net primary production rate	day^{-1}
$d_D(FOM_c, FOM_n, MN)$	FOM_c degradation rate	day^{-1}
$i_D(FOM_c, FOM_n, MN)$	Immobilisation rate of mineral nitrogen	day^{-1}
$e_P(h)$	Root exudation rate	day^{-1}
$r_{SOM}(h, P_c)$	Respiration rate of SOM decomposers	day^{-1}
$u(h)$	Herbivores urine deposition rate	day^{-1}

Table 1 : Definition and unit of state variables, parameters and functions of the model.

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

2.2. Model equations

The dynamical equations characterizing the evolution of each stock over time are mass balance equations; the derivative over time of each variable is the sum of the incoming fluxes minus the sum of the outgoing fluxes. Since the C:N ratios of plants and decomposers are assumed to be constant, the dynamics of nitrogen associated to these compartments is deducted from the dynamics of carbon. Therefore, only the dynamical equations of the carbon stock of these compartments are presented here. The model's dynamical equations are:

Plant carbon stock :

$$\frac{dP_c}{dt} = (g_P(MN) - m_P - h - e_P(h)) \times P_c \quad (8)$$

with: $g_P(MN) = \mu_P \frac{MN}{MN+K_P}$ and $e_P(h) = a_e + b_e \times h$

FOM carbon stock:

$$\frac{dFOM_c}{dt} = (m_p + (1-\alpha)\, h + \gamma\, \alpha\, h) \times P_c - d_D(FOM_c, FOM_n, MN)\, D_c - l_{FOM}\, FOM_c \quad (9)$$

with: $d_D(FOM_c, FOM_n, MN)$ given by equation (4)

FOM nitrogen stock:

$$\frac{dFOM_n}{dt} = \frac{1}{\rho_P}(m_p + (1-\alpha)\, h)\, P_c + \frac{1}{\rho_f}\gamma\, \alpha\, h\, P_c - \frac{FOM_n}{FOM_c}\; d_D(FOM_c, FOM_n, MN)\, D_c - l_{FOM}\, FOM_n \quad (10)$$

FOM Decomposers carbon stock:

$$\frac{dD_c}{dt} = (d_D(FOM_c, FOM_n, MN) - r_D - l_D) \times D_c \quad (11)$$

Mineral nitrogen stock:

$$\frac{dMN}{dt} = f_{MN}^{in} + (1-v)\, u(h) + \frac{1}{\rho_D}\, r_D\, D_c + \frac{1}{\rho_D}\, r_{SOM}(h, P_c)\, \delta\, SOM_c - \frac{1}{\rho_P} g_P(MN) P_c - i_D(FOM_c, FOM_n, MN)\, D_c - l_{MN}\, MN \quad (12)$$

with: $r_{SOM}(h, P_c) = w \times e_P(h) \times P_c$ and $i_D(FOM_c, FOM_n, MN)$ given by (5)

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

SOM carbon stock :

$$\frac{dSOM_c}{dt} = l_D\, D_c + l_{FOM}\, FOM_c + e_P(h) P_c - r_{SOM}(h, P_c)\, \delta\, SOM_c - l_{SOM}\, SOM_c \quad (13)$$

SOM nitrogen stock:

$$\frac{dSOM_n}{dt} = \frac{1}{\rho_D}\, l_D\, D_c + l_{FOM}\, FOM_n + \frac{1}{\rho_P} e_P(h)\, P_c - \frac{1}{\rho_D} r_{SOM}(h, P_c)\, \delta\, SOM_c - l_{SOM}\, SOM_n \quad (14)$$

These equations are valid only under the following conditions :

- All the parameters are positive
- $\rho_P > \rho_f > \rho_h$ and $\rho_f > \rho_D$
- $\frac{1}{\rho_P} > \frac{FOM_n}{FOM_c} > \frac{1}{\rho_D}$ (Supplementary material)
- $\alpha, \beta, \gamma, \delta, \upsilon \in [0; 1]$

2.3. The model at steady state

The model has four equilibrium points (Eq1 to Eq4) whose expressions are given in the supplementary material (Table S1). At Eq1, plants and FOM decomposers have null biomass; at Eq2 plants have positive biomass and FOM decomposers have null biomass; at Eq3 FOM decomposers and plants have positive biomass and are nitrogen limited, and at Eq4 FOM decomposers and plants have positive biomass and FOM decomposers are carbon limited while plants are nitrogen limited. Since Eq2 is not representative of the functioning of a grassland ecosystem and Eq3 only exists for a specific set of parameters because of the principle of competitive exclusion (Supplementary material), only Eq4, which is stable, will be studied in this paper.

At equilibrium 4, we have :

$$D_c^* = \frac{(m_p + (1-\alpha)\, h + \gamma\, \alpha\, h)\, P_c^* - l_{FOM} \times FOM_c*}{r_D + l_D} \quad (15)$$

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

that is : $\frac{FOM_c\ input\ fluxes - FOM_c\ output\ fluxes}{D_c\ output\ rates}$

$$FOM_c^* = \frac{r_D + l_D}{a_d} \quad (16)$$

that is : $\frac{D_c\ output\ rates}{D_c\ input\ rates}$

$$FOM_n^* = FOM_c^* \times \frac{\frac{m_P}{\rho_P} + \frac{(1-\alpha)\times h}{\rho_P} + \frac{\gamma \times \alpha \times h}{\rho_f}}{m_P + (1-\alpha)\,h + \gamma\,\alpha\,h} \quad (17)$$

$$MN^* = \frac{(m_P + h + e_P(h)) \times K_P}{\mu_P - (m_P + h + e_P(h))} \quad (18)$$

$$SOM_c^* = \frac{l_{FOM} \times FOM_c^* + l_D \times D_c^* + e_P(h) \times P_c^*}{l_{SOM} + r_{SOM}(h, P_c^*) \times \delta} \quad (19)$$

that is : $\frac{SOM_c\ input\ fluxes}{SOM_c\ output\ rates}$

$$SOM_n^* = \frac{l_{FOM} \times FOM_n^* + l_D \times \frac{D_c^*}{\rho_D} + e_P(h) \times \frac{P_c^*}{\rho_P} - r_{SOM}(h, P_c) \times \delta \times \frac{SOM_c^*}{\rho_D}}{l_{SOM}} \quad (20)$$

where P_c^* is the smallest strictly positive solution of a polynomial of degree 2 (supplementary material) which depends on all the parameters, including h. Since P_c^* depends on h, the equation of P_c^* gives an upper limit for h.

3. RESULTS

To examine whether herbivore-induced increases in root exudation followed by rhizosphere priming effect can enhance carbon storage, we explored two key parameters: grazing intensity (h) and the herbivore-induced root exudation factor (b_e). For a given grazing intensity, different grazing regimes—varying in timing, duration, frequency— (Stanley et al., 2024) may differentially affect the root exudation rates. For instance, Sun et al. (2017) showed that introducing rest periods following herbivores defoliation increases root exudation. Consequently, it is essential to consider a range of exudation responses associated with the same nominal grazing intensity. We therefore varied both h and b_e independently to assess their respective influence on grassland carbon stocks at steady state (equilibrium 4), while keeping all the other model parameters constant.

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

Carbon storage responses were evaluated at the ecosystem level with the total carbon stock, defined as the sum of all carbon stocks at steady state ($P_c^* + D_c^* + FOM_c^* + SOM_c^*$). We also examined the nitrogen storage responses at the ecosystem level with the total nitrogen stock, defined as the sum of all nitrogen stocks at steady state ($P_n^* + D_n^* + FOM_n^* + SOM_n^* + MN^*$).

Note that with this model our objective is not to generate quantitative predictions but rather to provide a mechanistic framework for understanding the underlying processes that can lead to increased carbon storage. Accordingly, we chose parameter values to produce qualitative outcomes—i.e., values that reproduce realistic orders of magnitude rather than site-specific predictions (see Tables S2 and S3 in supplementary materials for the parameter values).

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

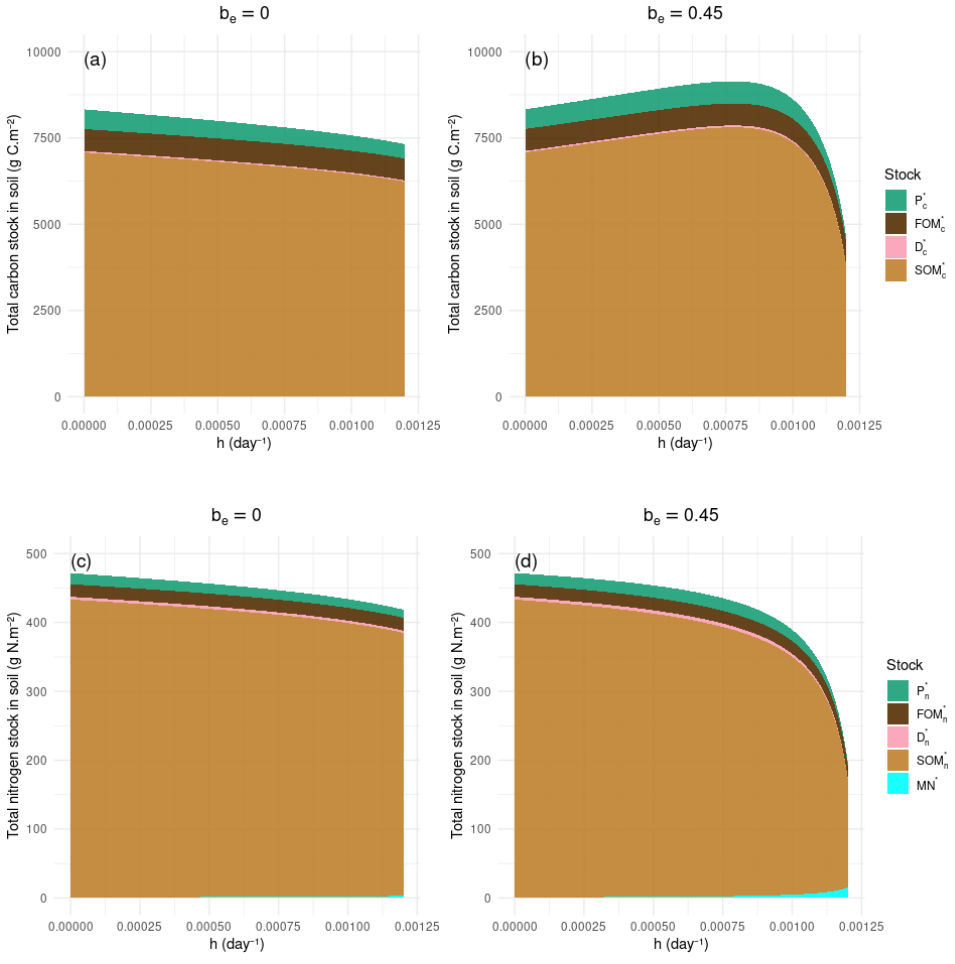


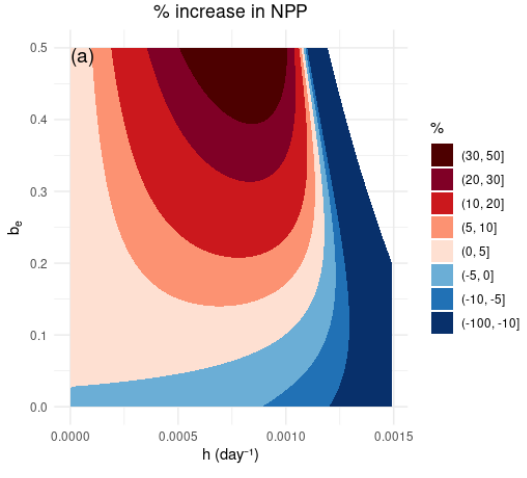
Figure 3 : Grassland carbon and nitrogen stocks at steady state as a function of grazing intensity (h) at two levels of herbivore-induced root exudation rate (b_e).

3.1. Evolution of the carbon and nitrogen stocks as a function of the grazing intensity (h) and the herbivore-induced root exudation rate (b_e)

The values of carbon and nitrogen stocks at steady state for different values of grazing intensity (h) and herbivore-induced root exudation rate (b_e) are shown in figures 3 and 4. In figure 3,

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

two contrasting responses of total carbon and nitrogen stocks (at steady state) to increasing grazing intensity (h) are presented. In the absence of herbivore-induced root exudation (b_e = 0), the total carbon and nitrogen stocks decline monotonically with increasing h (Figs. 3a and 3c). These declines are primarily driven by a decrease in SOM_c^* and SOM_n^*,which represent the dominant ecosystem carbon and nitrogen stocks respectively. In contrast, when the herbivore-induced root exudation is strong (b_e = 0.45), the total carbon stock peaks at moderate grazing intensity (Fig. 3b), a pattern largely driven by a corresponding bell-shaped response of SOM_c^* . This result indicates that herbivore-induced root exudation can promote carbon storage at moderate grazing intensity. Concerning the total nitrogen stock, it decreases more with b_e = 0.45 than with b_e = 0 due to a strong decrease of SOM_n^* (Fig. 3d). In this case, the mineral nitrogen stock MN^* increases with grazing intensity, indicating that herbivores promote the transfer of nitrogen from soil organic matter (SOM) to the mineral nitrogen stock.



https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

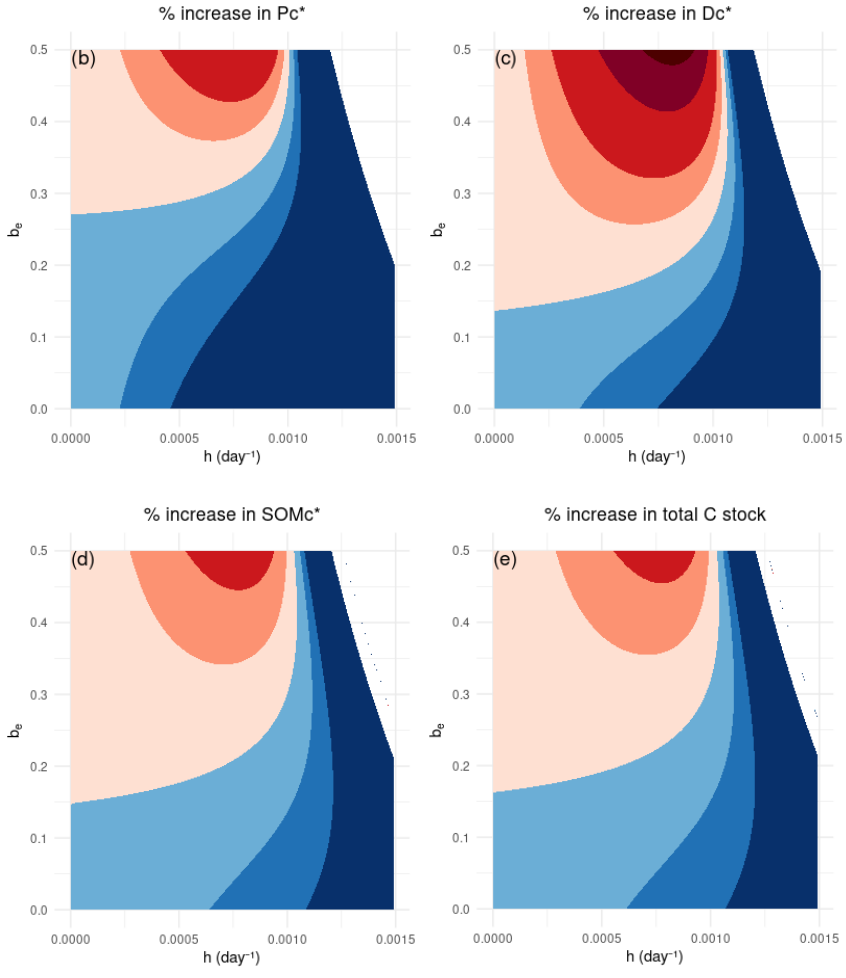


Figure 4 : Evolution of NPP, plants carbon stock (P_c^*), FOM decomposers carbon stock (D_c^*), SOM carbon stock (SOM_c^*) and total carbon stock at steady state as a function of grazing intensity (h) and the herbivore-induced root exudation rate (b_e). *Blue shades denote decreases (%) and red shades denote increases (%) relative to the h = 0 baseline.*

The percentage of increase or decrease in NPP and carbon stocks at steady state compared with the scenario without herbivores (h=0) are presented in figure 4. At very low values of herbivore-induced root exudation rate (b_e < 0.03), all carbon stocks and NPP decline with increasing grazing intensity. For intermediate values of herbivore-induced root exudation rate

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

(0.03 < b_e < 0.135), NPP increases at low to moderate grazing intensity, but this stimulation does not propagate to the carbon stocks. D_c^* starts to increase (still at low to moderate grazing intensity) when b_e > 0.135, SOM_c^* when b_e > 0.145, the total carbon stock when b_e > 0.16 and P_c^* when b_e > 0.275. These results indicate that herbivore-induced root exudation must be sufficiently strong to increase total carbon stock under low to moderate grazing intensity, a response consistently associated with increases in NPP, D_c^*, and SOM_c^*, but not in P_c^* .

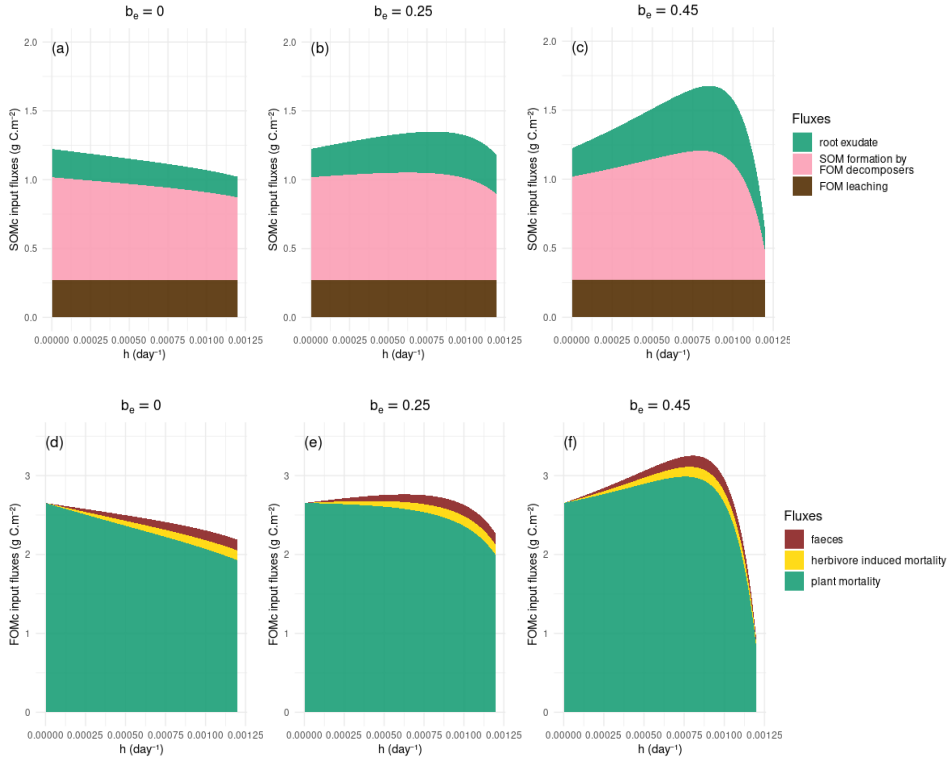


Figure 5 : SOM_c^* and FOM_c^* input fluxes at steady state as a function of grazing intensity (h) at three levels of herbivore-induced root exudation rate (b_e).

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

3.2. Mechanisms responsible for the increase in SOM_c^*, D_c^* and NPP.

The input fluxes of SOM and FOM carbon stock at steady state as a function of grazing intensity and for three different herbivore-induced root exudation rate (b_e) are shown in figure 5. In the former paragraph we have seen that changes in total carbon stocks are primarily driven by changes in SOM_c^*. An increase in SOM_c^* can be achieved by increasing its carbon input fluxes, namely (1) FOM_c leaching, (2) root exudation and (3) SOM_c formation by FOM decomposers (Eq. 19), which is what is observed for b_e = 0.25 and for b_e = 0.45 for example (Figs. 5b, 5c). In the model, FOM leaching remains constant across grazing intensity whatever the value of b_e (Figs. 5a, 5b, 5c): indeed it is proportional to the stock of fresh organic matter at steady state FOM_c^* which is independent of grazing intensity (h) (Eq. 16), as it is primarily regulated by decomposer dynamics.

The flux of root exudation accounts for less than 35% of the SOM_c^* input fluxes (Figs. 5 and S2), and increase with grazing intensity when b_e > 0.06 (Fig. 6). However this increase alone is not sufficient to increase SOM_c^* , since SOM_c^* decrease at low to medium grazing intensity when b_e < 0.145.

The flux of SOM_c formation by FOM decomposer accounts for more than half of the SOM_c^* input fluxes (Figs. 5 and S2). It is proportional to D_c^* which increases with FOM_c^* input fluxes (Eq. 15, Fig. 5) as FOM_c^* output fluxes and D_c^* output rates are constant. We can thus distinguish two configurations which leads to an increase of FOM_c^* input fluxes. In the first configuration, plant carbon stock increase with grazing intensity (see case where b_e = 0.45, figs. 5c and 5f), leading to an increase of all FOM_c^* input fluxes: plant mortality, inputs from faeces and herbivores induced mortality (Eq. 15; Fig. 5f). In the second configuration, plant carbon stock decreases with grazing intensity (see case where b_e = 0.25, figs. 5b and 5e) reducing plant mortality. To obtain an increase of FOM_c^* input fluxes in that case, the increased inputs from faeces and herbivores induced mortality must offset the reduction in inputs associated with

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

lower basal plant mortality (Eq. 15; Fig. 5e). Then the decline in plant biomass cannot be too pronounced, otherwise, the increase in herbivore-derived inputs would be insufficient to compensate for the reduced contribution from plant mortality. For plant biomass not to decrease too strongly, the NPP has to increase more than 5% with increasing grazing intensity. One mechanism that supports such an increase in NPP in this model is the enhancement of herbivore-induced root exudation, which plays a pivotal role by amplifying belowground nitrogen mineralization by the rhizosphere priming effect (Eq. 12), allowing the increase of the mineral nitrogen stock and of the NPP with grazing intensity. This process increases carbon inputs to the fresh organic matter (FOM) stock, thereby stimulating decomposer growth and SOM formation.

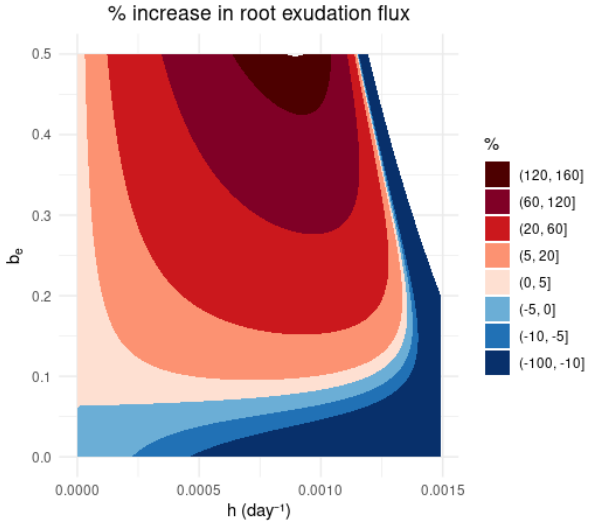


Figure 6 : Evolution of the root exudation flux as a function of grazing intensity (h) and the herbivore-induced root exudation rate (b_e). *Blue shades denote decreases (%) and orange shades denote increases (%) relative to the h = 0 baseline.*

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

3.3. Focus on the case with strong herbivore-induced root exudation (b_e)

We now only consider the case where root exudation is strongly stimulated by the herbivores: b_e = 0.45. We focus here on the percentage of increase or decrease in root exudate flux and carbon stocks at steady state compared with the scenario without herbivores (h=0). Under low grazing intensity ($h = 0.000375\ day^{-1} \approx 0.5\ LU.ha^{-1}.year^{-1}$), the total flux of root exudate increases by 56.64% (Fig. 5), the total carbon stock by 5.42%, SOM_c^* by 5.77%, D_c^* by 12.45% and P_c^* by 6.64% (Fig. 4). At medium grazing intensity ($h = 0.00075\ day^{-1} \approx 1\ LU.ha^{-1}.year^{-1}$), the total flux of root exudate increases markedly (+118.16%; Fig. 6), resulting in substantially larger carbon stocks. Total soil carbon increases by 9.7%, with concomitant increases in SOM_c^* (+10.24%), D_c^* (+24.7%), and P_c^* (+12.6%) (Fig. 4). In contrast, under high grazing intensity ($h = 0.0001125\ day^{-1} \approx 1.5\ LU.ha^{-1}.year^{-1}$), the increase in root exudate flux (+66.32%; Fig. 6) is associated with pronounced carbon losses. Total soil carbon decreases by 14.68%, alongside declines in SOM_c^* (− 14.62%), D_c^* (− 33.45%), and P_c^* (− 30.88%) (Fig. 4).

4. DISCUSSION

The main objective of the model was to understand the mechanisms through which increasing grazing intensity could contribute to increasing carbon stocks at steady state in grasslands. Our results shows that a key mechanism appears to be the increase in herbivore-induced root exudation following defoliation by the herbivores. Indeed, the increase in root exudation enhances SOM decomposition by the rhizosphere priming effect which can then increase net primary production (NPP) that can compensate for the carbon losses caused by increased grazing intensity. In the following parts we will then discuss the impact of herbivore-induced root exudation on soil carbon stock with increasing grazing intensity, the necessity of

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

increasing NPP to increase carbon stocks with grazing intensity and the impact of grazing intensity on nitrogen cycle.

4.1. Evolution of soil carbon stock and root exudates with grazing intensity

In a few metanalysis studies, increasing grazing intensity leads to a bell-shaped curve of the variation of the ecosystem carbon stock (Lai & Kumar, 2020; Abdalla and al., 2018; Zhou et al., 2017). The exploration of our model's outcomes with different realistic parameter sets suggests that such a bell curve can indeed occur (Fig. 3b), but that is more the exception than the rule. The most frequent trend is a monotonous decrease of carbon stocks at steady state with the increase in grazing intensity (Fig. 3a). Our model suggests that the bell-shaped response of carbon storage to grazing intensity may strongly depend on the impact of herbivory on root-exudation. Previous approaches suggest that herbivore-induced root exudate can increase carbon stocks of the ecosystem (Wilson et al., 2018) by modifying belowground microbial transformations of organic matter (Gavrichkova et al., 2008; Hamilton et al., 2008; Stanley et al., 2024). Our model suggests that, if herbivores substantially increase root exudates, the resulting exudation flux enhances SOM mineralization by rhizosphere priming effect and plant nutrient uptake, allowing NPP to increase sufficiently to offset the carbon losses associated with higher grazing intensity. This process increases carbon inputs to the fresh organic matter (FOM) stock, thereby stimulating decomposer growth. As a consequence, SOM formation by FOM decomposers and root exudation both increase, ultimately promoting the accumulation of persistent soil carbon (Fig. 7).

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

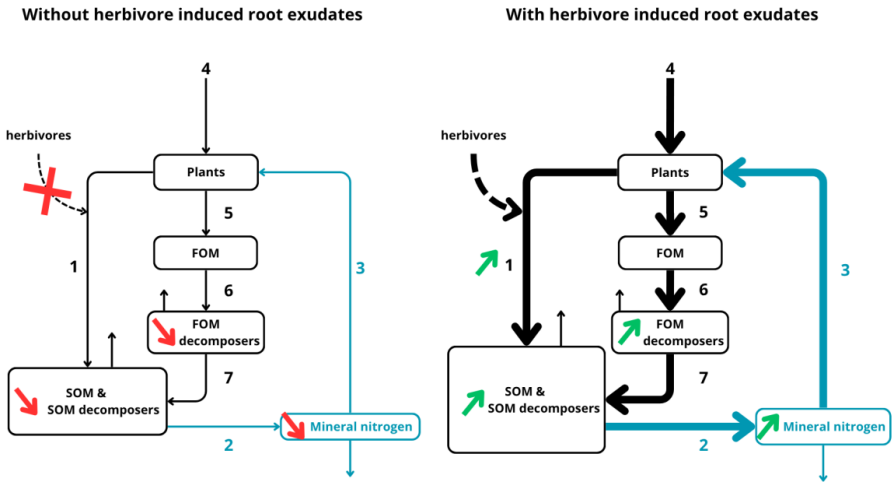


Figure 7 : Chain of mechanisms that can lead to an increase in carbon storage with increasing grazing intensity. ***On the left :*** *grazing inducing low root exudates (either directly by low plant stimulation, or indirectly by reducing plant biomass) lead to a decrease of total carbon stock.* ***On the right :*** *grazing enhancing root exudates (1), allow the increase in the mineralization flux from the SOM through rhizosphere priming effect (2) and the absorption flux by plants (3), allowing the NPP to increase (4) sufficiently for the FOM inputs (5), FOM degradation (6), and SOM formation by FOM decomposers to increase (7), leading to the increase in the persistent carbon stock.*

When a sufficiently high herbivore-induced root exudation rate is considered in the model, simulated increases in soil carbon storage under low and moderate grazing fall within the range reported in empirical meta-analyses. Specifically, SOM_c^* increased by 5.77% under low grazing intensity, which lies between the +0.78% reported by Zhou et al. (2017) and the +10.8% reported by Lai and Kumar (2020). At moderate grazing intensity, SOM_c^* increased by 10.24%, slightly below the +16.1% observed under dry climates in Abdalla et al. (2018). In contrast, SOM_c^* declined by 14.62% under high grazing intensity, somewhat exceeding the average reductions reported in meta-analyses (− 7.5% in Hao et al., 2024; − 9.92% in Zhou et

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

al., 2017; – 10.8% in Lai and Kumar, 2020). Our simulated root exudation responses to grazing intensity are also broadly consistent with empirical estimates. In the model, root exudation increased by 56.64%, 118.16%, and 66.32% under low, moderate, and high grazing intensity, respectively. These values are slightly lower than the average increases reported by Yang et al. (2026) (+82%, +146%, and +70%, respectively). This difference suggests that the effect of herbivores on root exudation could be slightly underestimated in our model. However, because empirical data on grazing-induced changes in root exudation are still limited, more studies are needed to better quantify this mechanism.

4.2. Grazing optimization and carbon storage

Our model provides a mechanistic framework to disentangle one of the cascading processes through which carbon storage can increase with grazing intensity (h) (Fig. 7). It suggests that for such an increase to occur, NPP has to increase by more than 5% with grazing intensity (Fig. 4). The grazing optimization hypothesis (GOH) predicts a bell-shaped response of grassland NPP to increasing grazing intensity under certain conditions (McNaughton, 1979; Hilbert et al., 1981; Dyer et al., 1986; Chen et al., 2025). While several mechanisms have been proposed to explain such responses, the role of root exudation has received little attention so far. Our results (Fig. 3a) indicate that the emergence and magnitude of this bell-shaped response strongly depends on the herbivore-induced root exudation and its impact on SOM decomposition by rhizosphere priming effect. In line with de Mazancourt et al. (1998), grazing can enhance plant production when it effectively imports or mobilizes a limiting nutrient. In our model, plant growth is nitrogen-limited, such that NPP depends on nitrogen uptake from the mineral stock. Herbivore-induced increases in root exudation stimulate microbial activity and SOM decomposition, thereby enhancing nitrogen mineralization and making additional nitrogen available to plants. This pathway effectively constitutes an indirect nutrient input

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

providing a mechanistic basis for grazing-induced increase in NPP. However, consistent with recent studies (e.g., Zhang et al., 2025), increased NPP does not necessarily translate into higher carbon storage (Figs. 4a, 4e). In our model, increase in NPP arises primarily as a compensatory response required to maintain plant carbon stock at steady state. Because plant carbon inputs and outputs must be equal at steady state, grazing-induced increase in plant carbon losses induce a corresponding increase in NPP. Consequently, elevated NPP does not inherently imply greater carbon sequestration; rather, it may simply reflect an acceleration of the carbon cycling through the ecosystem. NPP alone is therefore an insufficient indicator of ecosystem carbon sequestration. Overall, our results point out herbivore-induced root exudation as a potential, yet underexplored, mechanism contributing to grazing optimization. They also highlight the fact that NPP and soil carbon storage have different dynamics, hence, NPP is not a valuable proxy for soil carbon storage.

4.3. Evolution of soil nitrogen stock with grazing intensity

In our model, the increase of the total carbon stock is associated with the decrease of the total nitrogen stock (Fig. 3b, 3d) resulting in an increase in the soil C:N ratio at low to medium grazing intensities. Interestingly, this pattern is consistent with empirical evidence. Two meta-analyses reporting a bell-shaped response of ecosystem carbon stocks to grazing intensity also observed increases in soil C:N ratios under low to moderate grazing intensity (Zhou et al., 2017; Lai & Kumar, 2020). However, these studies found that total nitrogen stocks either increased or remained unchanged under light grazing, contrasting with our model simulations. This discrepancy likely arises from processes not represented in our model. For grazing to have a neutral or positive effect on nitrogen stocks, the additional losses generated by grazing (e.g. urine volatilization, nitrogen storage, enhanced leaching caused by enhanced mineral nitrogen) must be compensated by increased nitrogen inputs or reduced outputs. Such compensatory mechanisms may include enhanced biological nitrogen fixation (e.g., via

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

increased legume abundance) or improved synchrony between nitrogen mineralization and plant or microbial uptake (Fontaine et al., 2024), which reduces nitrogen leaching. Because these processes are not included in our model, nitrogen losses associated with enhanced mineralization are not offset, leading to a systematic decline in total nitrogen stocks with increasing grazing intensity. This suggests that incorporating additional nitrogen input and retention pathways would be necessary to capture the full range of observed ecosystem responses to grazing.

4.4. Perspectives

Herbivore-induced root exudation, which allows carbon stocks to increase with grazing intensity in our model, operates only under the assumption that decomposers are carbon-limited. This condition is required for plants and decomposers to coexist at a stable steady state. Under alternative conditions where decomposers are nitrogen-limited, increased root exudation and enhanced nitrogen mineralization from soil organic matter (SOM) by rhizosphere priming effect could stimulate decomposer growth by alleviating nitrogen limitation. Because nitrogen limitation of decomposers is not represented in the current model structure, this mechanism cannot be evaluated here. Incorporating nitrogen limitation would therefore represent an important extension of the model. However, doing so would likely require revisiting the temporal framework. In particular, introducing seasonal dynamics may be necessary to avoid unrealistic competitive exclusion between plants and decomposers (Daufresne and Loreau, 2001) and to better capture temporal niche partitioning in nutrient uptake. Some studies (e.g., Soussana and Lemaire, 2014; Stanley et al., 2024) suggest that herbivores may also influence decomposer growth, and thus carbon storage, by altering the C:N ratio of fresh organic matter (FOM). However, under carbon-limited conditions, changes in FOM C:N ratio associated with increasing grazing intensity do not directly affect decomposer growth in our model, and therefore do not contribute to increased carbon storage. For this reason, this pathway is not explicitly represented. In addition, the carbon use efficiency (CUE)

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

of decomposers is assumed to be constant. While this assumption simplifies the model, empirical evidence linking grazing intensity to variations in microbial CUE remains limited, preventing robust parameterization of such dynamics.

5. CONCLUSION

Our exploration of the model's outcomes with different realistic parameter sets suggests that the increase in carbon storage at steady state with increasing grazing intensity can occur, but that it is more of an exception than the rule. Increasing grazing intensity can lead to an increase in grassland carbon stocks at steady state if the increase in NPP is sufficient to compensate for the increase in carbon output by herbivores. As a result, net primary production alone is not a reliable proxy for carbon sequestration. One pathway that could lead to a sufficient increase in NPP is the increase in herbivore-induced root exudation following defoliation by the herbivores. The increase in root exudates can increase nitrogen mineralization from the soil by rhizosphere priming effect allowing plants to grow. When NPP compensates for the carbon losses caused by increased grazing intensity, the increased flow of fresh organic matter to the soil stimulates the growth of soil decomposers, which eventually leads to an increase of the SOM formation by FOM decomposers. Ultimately, the increase in root exudate and SOM formation by FOM decomposers generates an increase in the persistent carbon stock of the grassland ecosystem. To conclude, our model suggests that increasing carbon storage through grazing is possible in ecosystems in which grazers promote root exudation and so mineralization by rhizosphere priming effect. It is then necessary to identify grazing management practices (timing, duration, intensity, frequency of grazing) that maximize these mechanisms.

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

Code availability

The R script used to produce the manuscript's figures in the paper can be found at https://forge.inrae.fr/emma.escoffier/grassland_publi_1

Author contributions

Emma Escoffier : Conceptualization, Methodology, Software, Writing - Original Draft

Céline Casenave : Methodology, Writing - Review & Editing, Supervision

Tanguy Daufresne : Methodology, Writing - Review & Editing, Supervision, Funding acquisition

Competing interests

The authors declare there are no conflicts of interest for this manuscript.

Acknowledgements

This research project was funded by the French National Research Agency (ANR) under the grant agreement C-cos2 (ANR-23-CE32-0001).

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

REFERENCES

Abdalla, M., Hastings, A., Chadwick, D. R., Jones, D. L., Evans, C. D., Jones, M. B., Rees, R. M., and Smith, P.: Critical review of the impacts of grazing intensity on soil organic carbon storage and other soil quality indicators in extensively managed grasslands, Agriculture, Ecosystems & Environment, 253, 62–81, https://doi.org/10.1016/j.agee.2017.10.023, 2018.

Abramoff, R., Xu, X., Hartman, M., O'Brien, S., Feng, W., Davidson, E., Finzi, A., Moorhead, D., Schimel, J., Torn, M., and Mayes, M. A.: The Millennial model: in search of measurable pools and transformations for modeling soil carbon in the new century, Biogeochemistry, 137, 51–71, https://doi.org/10.1007/s10533-017-0409-7, 2018.

Allard, V., Soussana, J.-F., Falcimagne, R., Berbigier, P., Bonnefond, J. M., Ceschia, E., D'hour, P., Hénault, C., Laville, P., Martin, C., and Pinarès-Patino, C.: The role of grazing management for the net biome productivity and greenhouse gas budget (CO2, N2O and CH4) of semi-natural grassland, Agriculture, Ecosystems & Environment, 121, 47–58, https://doi.org/10.1016/j.agee.2006.12.004, 2007.

Angst, G., Mueller, K. E., Nierop, K. G. J., and Simpson, M. J.: Plant- or microbial-derived? A review on the molecular composition of stabilized soil organic matter, Soil Biology and Biochemistry, 156, 108189, https://doi.org/10.1016/j.soilbio.2021.108189, 2021.

Austrheim, G., Speed, J. D. M., Martinsen, V., Mulder, J., and Mysterud, A.: Experimental Effects of Herbivore Density on Aboveground Plant Biomass in an Alpine Grassland Ecosystem, Arctic, Antarctic, and Alpine Research, 46, 535–541, https://doi.org/10.1657/1938-4246-46.3.535, 2014.

Bardgett, R. D., Bowman, W. D., Kaufmann, R., and Schmidt, S. K.: A temporal approach to linking aboveground and belowground ecology, Trends in Ecology & Evolution, 20, 634–641, https://doi.org/10.1016/j.tree.2005.08.005, 2005.

Bernard, C.: Introduction à l'étude de la médecine expérimentale par m. Claude Bernard, Baillière, 460 pp., 1865.

Bloor, J. M. G., Jay-Robert, P., Le Morvan, A., and Fleurance, G.: Déjections des herbivores domestiques au pâturage : caractéristiques et rôle dans le fonctionnement des prairies, INRA Prod. Anim., 25, 45–56, https://doi.org/10.20870/productions-animales.2012.25.1.3196, 2012.

Bondeau, A., Smith, P. C., Zaehle, S., Schaphoff, S., Lucht, W., Cramer, W., Gerten, D., Lotze-Campen, H., Müller, C., Reichstein, M., and Smith, B.: Modelling the role of agriculture for the 20th century global terrestrial carbon balance, Global Change Biology, 13, 679–706, https://doi.org/10.1111/j.1365-2486.2006.01305.x, 2007.

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

Bork, E. W., Hewins, D. B., Lamb, E. G., Carlyle, C. N., Lyseng, M. P., Chang, S. X., Alexander, M. J., Willms, W. D., and Iravani, M.: Light to moderate long-term grazing enhances ecosystem carbon across a broad climatic gradient in northern temperate grasslands, Science of The Total Environment, 894, 164978, https://doi.org/10.1016/j.scitotenv.2023.164978, 2023.

Brilli, L., Bechini, L., Bindi, M., Carozzi, M., Cavalli, D., Conant, R., Dorich, C. D., Doro, L., Ehrhardt, F., Farina, R., Ferrise, R., Fitton, N., Francaviglia, R., Grace, P., Iocola, I., Klumpp, K., Léonard, J., Martin, R., Massad, R. S., Recous, S., Seddaiu, G., Sharp, J., Smith, P., Smith, W. N., Soussana, J.-F., and Bellocchi, G.: Review and analysis of strengths and weaknesses of agro-ecosystem models for simulating C and N fluxes, Science of The Total Environment, 598, 445–470, https://doi.org/10.1016/j.scitotenv.2017.03.208, 2017.

Cannon, W. B.: The wisdom of the body, 2nd ed, Norton & Co., Oxford, England, 1939.

Chandel, A. K., Jiang, L., and Luo, Y.: Microbial Models for Simulating Soil Carbon Dynamics: A Review, Journal of Geophysical Research: Biogeosciences, 128, e2023JG007436, https://doi.org/10.1029/2023JG007436, 2023.

Chang, Q., Wang, L., Ding, S., Xu, T., Li, Z., Song, X., Zhao, X., Wang, D., and Pan, D.: Grazer effects on soil carbon storage vary by herbivore assemblage in a semi-arid grassland, Journal of Applied Ecology, 55, 2517–2526, https://doi.org/10.1111/1365-2664.13166, 2018.

Chari, N. R., Tumber-Dávila, S. J., Phillips, R. P., Bauerle, T. L., Brunn, M., Hafner, B. D., Klein, T., Obersteiner, S., Reay, M. K., Ullah, S., and Taylor, B. N.: Estimating the global root exudate carbon flux, Biogeochemistry, 167, 895–908, https://doi.org/10.1007/s10533-024-01161-z, 2024.

Chen, Z., Zhao, D., Wang, S., Zhu, Y., Deng, S., Wang, K., Gao, X., Wu, X., Tian, D., and Zheng, D.: Single-peaked responses of grassland productivity to grazing intensity, Agriculture, Ecosystems & Environment, 387, 109630, https://doi.org/10.1016/j.agee.2025.109630, 2025.

Chertov, O., Kuzyakov, Y., Priputina, I., Frolov, P., Shanin, V., and Grabarnik, P.: Modelling the Rhizosphere Priming Effect in Combination with Soil Food Webs to Quantify Interaction between Living Plant, Soil Biota and Soil Organic Matter, Plants, 11, 2605, https://doi.org/10.3390/plants11192605, 2022.

Coleman, K. and Jenkinson, D. S.: RothC-26.3 - A Model for the turnover of carbon in soil, in: Evaluation of Soil Organic Matter Models, edited by: Powlson, D. S., Smith, P., and Smith, J. U., Springer Berlin Heidelberg, Berlin, Heidelberg, 237–246, https://doi.org/10.1007/978-3-642-61094-3_17, 1996.

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., and Paul, E.: The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

organic matter stabilization: do labile plant inputs form stable soil organic matter?, Global Change Biology, 19, 988–995, https://doi.org/10.1111/gcb.12113, 2013.

Daufresne, T.: A consumer-driven recycling theory for the impact of large herbivores on terrestrial ecosystem stoichiometry, Ecology Letters, 24, 2598–2610, https://doi.org/10.1111/ele.13876, 2021.

Daufresne, T. and Loreau, M.: Ecological Stoichiometry, Primary Producer–Decomposer Interactions, and Ecosystem Persistence, Ecology, 82, 3069–3082, https://doi.org/10.1890/0012-9658(2001)082[3069:ESPPDI]2.0.CO;2, 2001.

Deng, L., Shangguan, Z., Bell, S. M., Soromotin, A. V., Peng, C., An, S., Wu, X., Xu, X., Wang, K., Li, J., Tang, Z., Yan, W., Zhang, F., Li, J., Wu, J., and Kuzyakov, Y.: Carbon in Chinese grasslands: meta-analysis and theory of grazing effects, Carbon Res., 2, 19, https://doi.org/10.1007/s44246-023-00051-7, 2023.

Don, A., Seidel, F., Leifeld, J., Kätterer, T., Martin, M., Pellerin, S., Emde, D., Seitz, D., and Chenu, C.: Carbon sequestration in soils and climate change mitigation—Definitions and pitfalls, Global Change Biology, 30, e16983, https://doi.org/10.1111/gcb.16983, 2024.

Dyer, M. I., DeAngelis, D. L., and Post, W. M.: A model of herbivore feedback on plant productivity, Mathematical Biosciences, 79, 171–184, https://doi.org/10.1016/0025-5564(86)90146-X, 1986.

Elser, J. J., Fagan, W. F., Denno, R. F., Dobberfuhl, D. R., Folarin, A., Huberty, A., Interlandi, S., Kilham, S. S., McCauley, E., Schulz, K. L., Siemann, E. H., and Sterner, R. W.: Nutritional constraints in terrestrial and freshwater food webs, Nature, 408, 578–580, https://doi.org/10.1038/35046058, 2000.

Elser, J. J., Bracken, M. E. S., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom, E. W., Shurin, J. B., and Smith, J. E.: Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems, Ecology Letters, 10, 1135–1142, https://doi.org/10.1111/j.1461-0248.2007.01113.x, 2007.

Fang, J., Chen, B., Wang, F., Li, W., Zhang, H., Fang, J., Liu, S., Zheng, Z., Guo, M., and Niu, S.: Nitrogen, phosphorus, and potassium co-limitation in terrestrial ecosystems: A global meta-analysis, PLANTS, PEOPLE, PLANET, 6, 1329–1340, https://doi.org/10.1002/ppp3.10524, 2024.

Follett, R. F. and Reed, D. A.: Soil Carbon Sequestration in Grazing Lands: Societal Benefits and Policy Implications, Rangeland Ecology & Management, 63, 4–15, https://doi.org/10.2111/08-225.1, 2010.

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

Frank, D. A. and Groffman, P. M.: Ungulate Vs. Landscape Control of Soil C and N Processes in Grasslands of Yellowstone National Park, Ecology, 79, 2229–2241, https://doi.org/10.1890/0012-9658(1998)079[2229:UVLCOS]2.0.CO;2, 1998.

Fu, H., Chen, H., Ma, Z., Liang, G., Chadwick, D. R., Jones, D. L., Wanek, W., Wu, L., and Ma, Q.: Fungal Necromass Carbon Dominates Global Soil Organic Carbon Storage, Global Change Biology, 31, e70413, https://doi.org/10.1111/gcb.70413, 2025.

Fu, J., Gasche, R., Wang, N., Lu, H., Butterbach-Bahl, K., and Kiese, R.: Impacts of climate and management on water balance and nitrogen leaching from montane grassland soils of S-Germany, Environmental Pollution, 229, 119–131, https://doi.org/10.1016/j.envpol.2017.05.071, 2017.

Gavrichkova, O., Moscatelli, M. C., Grego, S., and Valentini, R.: Soil carbon mineralization in a Mediterranean pasture: effect of grazing and mowing management practices, 2008.

Gunina, A. and Kuzyakov, Y.: Sugars in soil and sweets for microorganisms: Review of origin, content, composition and fate, Soil Biology and Biochemistry, 90, 87–100, https://doi.org/10.1016/j.soilbio.2015.07.021, 2015.

Hafner, S., Unteregelsbacher, S., Seeber, E., Lena, B., Xu, X., Li, X., Guggenberger, G., Miehe, G., and Kuzyakov, Y.: Effect of grazing on carbon stocks and assimilate partitioning in a Tibetan montane pasture revealed by 13CO2 pulse labeling, Global Change Biology, 18, 528–538, https://doi.org/10.1111/j.1365-2486.2011.02557.x, 2012.

Hamilton, E. W. and Frank, D. A.: Can Plants Stimulate Soil Microbes and Their Own Nutrient Supply? Evidence from a Grazing Tolerant Grass, Ecology, 82, 2397–2402, https://doi.org/10.1890/0012-9658(2001)082[2397:CPSSMA]2.0.CO;2, 2001.

Hamilton, E. W., Frank, D. A., Hinchey, P. M., and Murray, T. R.: Defoliation induces root exudation and triggers positive rhizospheric feedbacks in a temperate grassland, Soil Biology and Biochemistry, 40, 2865–2873, https://doi.org/10.1016/j.soilbio.2008.08.007, 2008.

Hao, X., Yang, J., Dong, S., He, F., and Zhang, Y.: The influence of grazing intensity on soil organic carbon storage in grassland of China: A meta-analysis, Science of The Total Environment, 924, 171439, https://doi.org/10.1016/j.scitotenv.2024.171439, 2024.

Hilbert, D. W., Swift, D. M., Detling, J. K., and Dyer, M. I.: Relative growth rates and the grazing optimization hypothesis, Oecologia, 51, 14–18, https://doi.org/10.1007/BF00344645, 1981.

Hodgson, J.: Grazing management. Science into practice., UK, 203 pp., 1990.

Inselsbacher, E., Hinko-Najera Umana, N., Stange, F. C., Gorfer, M., Schüller, E., Ripka, K., Zechmeister-Boltenstern, S., Hood-Novotny, R., Strauss, J., and Wanek, W.: Short-term

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

competition between crop plants and soil microbes for inorganic N fertilizer, Soil Biology and Biochemistry, 42, 360–372, https://doi.org/10.1016/j.soilbio.2009.11.019, 2010.

2006 IPCC Guidelines for National Greenhouse Gas Inventories: https://www.ipcc-nggip.iges.or.jp/public/2006gl/french/pdf/4_Volume4/V4_06_Ch6_Grassland.pdf, last access: 5 August 2025.

Klumpp, K., Tallec, T., Guix, N., and Soussana, J.-F.: Long-term impacts of agricultural practices and climatic variability on carbon storage in a permanent pasture, Global Change Biology, 17, 3534–3545, https://doi.org/10.1111/j.1365-2486.2011.02490.x, 2011.

Kuzyakov, Y.: Review: Factors affecting rhizosphere priming effects, Journal of Plant Nutrition and Soil Science, 165, 382–396, https://doi.org/10.1002/1522-2624(200208)165:4<382::AID-JPLN382>3.0.CO;2-#, 2002.

Lai, L. and Kumar, S.: A global meta-analysis of livestock grazing impacts on soil properties, PLOS ONE, 15, e0236638, https://doi.org/10.1371/journal.pone.0236638, 2020.

Lecompte, P., Boval, M., Guerin, H., Ickowicz, A., Huguenin, J., and Limbourg, P.: Carbone et élevage de ruminants, Colloque international sur les influences de la gestion de la biomasse sur l'érosion et la séquestration du carbone, Montpellier, 2002.

Lefebvre, T. and Gallet, C.: Impacts des grands herbivores sur la végétation des prairies et conséquences sur la décomposition de la litière, INRAE Productions Animales, 30, 455–464, https://doi.org/10.20870/productions-animales.2017.30.5.2276, 2017.

Levins, R.: The Strategy of Model Building in Population Biology, American Scientist, 54, 421–431, 1966.

Li, S., Xing, T., Sa, R., Zhang, Y., Chen, H., Jin, K., Shao, Q., Tang, S., and Wang, C.: Effects of grazing on soil respiration in global grassland ecosystems, Soil and Tillage Research, 238, 106033, https://doi.org/10.1016/j.still.2024.106033, 2024.

Li, Z., Zeng, Z., Song, Z., Wang, F., Tian, D., Mi, W., Huang, X., Wang, J., Song, L., Yang, Z., Wang, J., Feng, H., Jiang, L., Chen, Y., Luo, Y., and Niu, S.: Vital roles of soil microbes in driving terrestrial nitrogen immobilization, Global Change Biology, 27, 1848–1858, https://doi.org/10.1111/gcb.15552, 2021.

Liang, C., Amelung, W., Lehmann, J., and Kästner, M.: Quantitative assessment of microbial necromass contribution to soil organic matter, Global Change Biology, 25, 3578–3590, https://doi.org/10.1111/gcb.14781, 2019.

Maestre, F. T., Le Bagousse-Pinguet, Y., Delgado-Baquerizo, M., Eldridge, D. J., Saiz, H., Berdugo, M., Gozalo, B., Ochoa, V., Guirado, E., García-Gómez, M., Valencia, E., Gaitán, J. J., Asensio, S., Mendoza, B. J., Plaza, C., Díaz-Martínez, P., Rey, A., Hu, H.-W., He, J.-Z.,

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

Wang, J.-T., Lehmann, A., Rillig, M. C., Cesarz, S., Eisenhauer, N., Martínez-Valderrama, J., Moreno-Jiménez, E., Sala, O., Abedi, M., Ahmadian, N., Alados, C. L., Aramayo, V., Amghar, F., Arredondo, T., Ahumada, R. J., Bahalkeh, K., Ben Salem, F., Blaum, N., Boldgiv, B., Bowker, M. A., Bran, D., Bu, C., Canessa, R., Castillo-Monroy, A. P., Castro, H., Castro, I., Castro-Quezada, P., Chibani, R., Conceição, A. A., Currier, C. M., Darrouzet-Nardi, A., Deák, B., Donoso, D. A., Dougill, A. J., Durán, J., Erdenetsetseg, B., Espinosa, C. I., Fajardo, A., Farzam, M., Ferrante, D., Frank, A. S. K., Fraser, L. H., Gherardi, L. A., Greenville, A. C., Guerra, C. A., Gusmán-Montalvan, E., Hernández-Hernández, R. M., Hölzel, N., Huber-Sannwald, E., Hughes, F. M., Jadán-Maza, O., Jeltsch, F., Jentsch, A., Kaseke, K. F., Köbel, M., Koopman, J. E., Leder, C. V., Linstädter, A., le Roux, P. C., Li, X., Liancourt, P., Liu, J., Louw, M. A., Maggs-Kölling, G., Makhalanyane, T. P., Issa, O. M., Manzaneda, A. J., Marais, E., Mora, J. P., Moreno, G., Munson, S. M., Nunes, A., Oliva, G., Oñatibia, G. R., Peter, G., Pivari, M. O. D., Pueyo, Y., Quiroga, R. E., Rahmanian, S., Reed, S. C., et al.: Grazing and ecosystem service delivery in global drylands, Science, 378, 915–920, https://doi.org/10.1126/science.abq4062, 2022.

Manzoni, S., Jackson, R. B., Trofymow, J. A., and Porporato, A.: The Global Stoichiometry of Litter Nitrogen Mineralization, Science, 321, 684–686, https://doi.org/10.1126/science.1159792, 2008.

Marks, E. A. N., Barbosa, J. M., García-Orenes, F., Mataix-Solera, J., Arcenegui, V., Albolafio, S., Velamazán, M., García-Carmona, M., and Sánchez-Zapata, J. A.: Ungulate herbivores promote contrasting modifications of soil properties and organic carbon stabilization in a grazed grassland versus rewilded woodland environment, Agriculture, Ecosystems & Environment, 367, 108983, https://doi.org/10.1016/j.agee.2024.108983, 2024.

de Mazancourt, C., Loreau, M., and Abbadie, L.: Grazing Optimization and Nutrient Cycling: When Do Herbivores Enhance Plant Production?, Ecology, 79, 2242–2252, https://doi.org/10.1890/0012-9658(1998)079[2242:GOANCW]2.0.CO;2, 1998.

McNaughton, S. J.: Grazing as an Optimization Process: Grass-Ungulate Relationships in the Serengeti, The American Naturalist, 113, 691–703, https://doi.org/10.1086/283426, 1979.

McNaughton, S. J., Banyikwa, F. F., and McNaugthon, M. M.: Promotion of the Cycling of Diet-Enhancing Nutrients by African Grazers | Science, 278, 1798–1800, 1997.

McSherry, M. E. and Ritchie, M. E.: Effects of grazing on grassland soil carbon: a global review, Global Change Biology, 19, 1347–1357, https://doi.org/10.1111/gcb.12144, 2013.

Monod, J.: THE GROWTH OF BACTERIAL CULTURES, Elsevier, 371–394 pp., 1949.

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

Niu, W., Ding, J., Fu, B., Zhao, W., and Eldridge, D.: Global effects of livestock grazing on ecosystem functions vary with grazing management and environment, Agriculture, Ecosystems & Environment, 378, 109296, https://doi.org/10.1016/j.agee.2024.109296, 2025.

Nosetto, M. D., Jobbágy, E. G., and Paruelo, J. M.: Carbon sequestration in semi-arid rangelands: Comparison of *Pinus ponderosa* plantations and grazing exclusion in NW Patagonia, Journal of Arid Environments, 67, 142–156, https://doi.org/10.1016/j.jaridenv.2005.12.008, 2006.

O'Mara, F. P.: The role of grasslands in food security and climate change, Ann Bot, 110, 1263–1270, https://doi.org/10.1093/aob/mcs209, 2012.

Osterholz, W. R., Rinot, O., Shaviv, A., Linker, R., Liebman, M., Sanford, G., Strock, J., and Castellano, M. J.: Predicting Gross Nitrogen Mineralization and Potentially Mineralizable Nitrogen using Soil Organic Matter Properties, Soil Science Society of America Journal, 81, 1115–1126, https://doi.org/10.2136/sssaj2017.02.0055, 2017.

Are grasslands under threat? https://www.fao.org/uploads/media/grass_stats_1.pdf, last access: 5 August 2025.

Parton, W. J., Hartman, M., Ojima, D., and Schimel, D.: DAYCENT and its land surface submodel: description and testing, Global and Planetary Change, 19, 35–48, https://doi.org/10.1016/S0921-8181(98)00040-X, 1998.

Pausch, J., Holz, M., Zhu, B., and Cheng, W.: Rhizosphere priming promotes plant nitrogen acquisition by microbial necromass recycling, Plant, Cell & Environment, 47, 1987–1996, https://doi.org/10.1111/pce.14858, 2024.

Perveen, N., Barot, S., Alvarez, G., Klumpp, K., Martin, R., Rapaport, A., Herfurth, D., Louault, F., and Fontaine, S.: Priming effect and microbial diversity in ecosystem functioning and response to global change: a modeling approach using the SYMPHONY model, Global Change Biology, 20, 1174–1190, https://doi.org/10.1111/gcb.12493, 2014.

Reeder, J. D. and Schuman, G. E.: Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands, Environmental Pollution, 116, 457–463, https://doi.org/10.1016/S0269-7491(01)00223-8, 2002.

Riedo, M., Grub, A., Rosset, M., and Fuhrer, J.: A pasture simulation model for dry matter production, and fluxes of carbon, nitrogen, water and energy, Ecological Modelling, 105, 141–183, https://doi.org/10.1016/S0304-3800(97)00110-5, 1998.

Risch, A. C., Zimmermann, S., Ochoa-Hueso, R., Schütz, M., Frey, B., Firn, J. L., Fay, P. A., Hagedorn, F., Borer, E. T., Seabloom, E. W., Harpole, W. S., Knops, J. M. H., McCulley, R. L., Broadbent, A. a. D., Stevens, C. J., Silveira, M. L., Adler, P. B., Báez, S., Biederman, L. A.,

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

Blair, J. M., Brown, C. S., Caldeira, M. C., Collins, S. L., Daleo, P., di Virgilio, A., Ebeling, A., Eisenhauer, N., Esch, E., Eskelinen, A., Hagenah, N., Hautier, Y., Kirkman, K. P., MacDougall, A. S., Moore, J. L., Power, S. A., Prober, S. M., Roscher, C., Sankaran, M., Siebert, J., Speziale, K. L., Tognetti, P. M., Virtanen, R., Yahdjian, L., and Moser, B.: Soil net nitrogen mineralisation across global grasslands, Nat Commun, 10, 4981, https://doi.org/10.1038/s41467-019-12948-2, 2019.

Risch, A. C., Zimmermann, S., Schütz, M., Borer, E. T., Broadbent, A. a. D., Caldeira, M. C., Davies, K. F., Eisenhauer, N., Eskelinen, A., Fay, P. A., Hagedorn, F., Knops, J. M. H., Lembrechts, J. J., MacDougall, A. S., McCulley, R. L., Melbourne, B. A., Moore, J. L., Power, S. A., Seabloom, E. W., Silviera, M. L., Virtanen, R., Yahdjian, L., and Ochoa-Hueso, R.: Drivers of the microbial metabolic quotient across global grasslands, Global Ecology and Biogeography, 32, 904–918, https://doi.org/10.1111/geb.13664, 2023.

Rocci, K. S., Cleveland, C. C., Eastman, B. A., Georgiou, K., Grandy, A. S., Hartman, M. D., Hauser, E., Holland-Moritz, H., Kyker-Snowman, E., Pierson, D., Reich, P. B., Schlerman, E. P., and Wieder, W. R.: Aligning theoretical and empirical representations of soil carbon-to-nitrogen stoichiometry with process-based terrestrial biogeochemistry models, Soil Biology and Biochemistry, 189, 109272, https://doi.org/10.1016/j.soilbio.2023.109272, 2024.

Roy, S., Naidu, D. G. T., and Bagchi, S.: Functional substitutability of native herbivores by livestock for soil carbon stock is mediated by microbial decomposers, Global Change Biology, 29, 2141–2155, https://doi.org/10.1111/gcb.16600, 2023.

Scurlock, J. M. O. and Hall, D. O.: The global carbon sink: a grassland perspective, Global Change Biology, 4, 229–233, https://doi.org/10.1046/j.1365-2486.1998.00151.x, 1998.

Selbie, D. R., Buckthought, L. E., and Shepherd, M. A.: The Challenge of the Urine Patch for Managing Nitrogen in Grazed Pasture Systems, Advances in Agronomy, 129, 229–292, https://doi.org/10.1016/bs.agron.2014.09.004, 2015.

Shi, T.-S., Collins, S. L., Yu, K., Peñuelas, J., Sardans, J., Li, H., and Ye, J.-S.: A global meta-analysis on the effects of organic and inorganic fertilization on grasslands and croplands, Nat Commun, 15, 3411, https://doi.org/10.1038/s41467-024-47829-w, 2024.

Sitters, J., Wubs, E. R. J., Bakker, E. S., Crowther, T. W., Adler, P. B., Bagchi, S., Bakker, J. D., Biederman, L., Borer, E. T., Cleland, E. E., Eisenhauer, N., Firn, J., Gherardi, L., Hagenah, N., Hautier, Y., Hobbie, S. E., Knops, J. M. H., MacDougall, A. S., McCulley, R. L., Moore, J. L., Mortensen, B., Peri, P. L., Prober, S. M., Riggs, C., Risch, A. C., Schütz, M., Seabloom, E. W., Siebert, J., Stevens, C. J., and Veen, G. F. (Ciska): Nutrient availability controls the impact of mammalian herbivores on soil carbon and nitrogen pools in grasslands, Global Change Biology, 26, 2060–2071, https://doi.org/10.1111/gcb.15023, 2020.

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

927 Sokol, N. W., Whalen, E. D., Jilling, A., Kallenbach, C., Pett-Ridge, J., and Georgiou, K.: Global
928 distribution, formation and fate of mineral-associated soil organic matter under a changing
929 climate: A trait-based perspective, Functional Ecology, 36, 1411–1429,
930 https://doi.org/10.1111/1365-2435.14040, 2022.

931 Soussana, J.-F. and Lemaire, G.: Coupling carbon and nitrogen cycles for environmentally
932 sustainable intensification of grasslands and crop-livestock systems, Agriculture, Ecosystems
933 & Environment, 190, 9–17, https://doi.org/10.1016/j.agee.2013.10.012, 2014.

934 Soussana, J.-F., Tallec, T., and Blanfort, V.: Mitigating the greenhouse gas balance of
935 ruminant production systems through carbon sequestration in grasslands, Animal, 4, 334–350,
936 https://doi.org/10.1017/S1751731109990784, 2010.

937 Stanley, P. L., Wilson, C., Patterson, E., Machmuller, M. B., and Cotrufo, M. F.: Ruminating on
938 soil carbon: Applying current understanding to inform grazing management, Global Change
939 Biology, 30, e17223, https://doi.org/10.1111/gcb.17223, 2024.

940 Sterner, R. W. and Elser, J. J.: Ecological Stoichiometry: The Biology of Elements from
941 Molecules to the Biosphere, Princeton University Press,
942 https://doi.org/10.1515/9781400885695, 2003.

943 Su, J., Xu, F., and Zhang, Y.: Grassland biodiversity and ecosystem functions benefit more
944 from cattle than sheep in mixed grazing: A meta-analysis, Journal of Environmental
945 Management, 337, 117769, https://doi.org/10.1016/j.jenvman.2023.117769, 2023.

946 Sulman, B. N., Phillips, R. P., Oishi, A. C., Shevliakova, E., and Pacala, S. W.: Microbe-driven
947 turnover offsets mineral-mediated storage of soil carbon under elevated CO2, Nature Clim
948 Change, 4, 1099–1102, https://doi.org/10.1038/nclimate2436, 2014.

949 Sun, G., Zhu-Barker, X., Chen, D., Liu, L., Zhang, N., Shi, C., He, L., and Lei, Y.: Responses
950 of root exudation and nutrient cycling to grazing intensities and recovery practices in an alpine
951 meadow: An implication for pasture management, Plant Soil, 416, 515–525,
952 https://doi.org/10.1007/s11104-017-3236-7, 2017.

953 Tilman, D.: Resource Competition and Community Structure, Princeton University Press, 312
954 pp., 1982.

955 Wang, C. and Kuzyakov, Y.: Energy use efficiency of soil microorganisms: Driven by carbon
956 recycling and reduction, Global Change Biology, 29, 6170–6187,
957 https://doi.org/10.1111/gcb.16925, 2023.

958 White, R. P., Murray, S., Rohweder, M., Prince, S. D., and Thompson, K. M.: Pilot Analysis of
959 Global Ecosystems: Grassland Ecosystems, World Resources Institute, ISBN 1-56973-461-
960 5, 2000.

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

Wilson, C. H., Strickland, M. S., Hutchings, J. A., Bianchi, T. S., and Flory, S. L.: Grazing enhances belowground carbon allocation, microbial biomass, and soil carbon in a subtropical grassland, Global Change Biology, 24, 2997–3009, https://doi.org/10.1111/gcb.14070, 2018.

Wutzler, T., Reimers, C., Ahrens, B., and Schrumpf, M.: Optimal enzyme allocation leads to the constrained enzyme hypothesis: the Soil Enzyme Steady Allocation Model (SESAM; v3.1), Geoscientific Model Development, 17, 2705–2725, https://doi.org/10.5194/gmd-17-2705-2024, 2024.

Xu, H., You, C., Tan, B., Xu, L., Liu, Y., Wang, M., Xu, Z., Sardans, J., and Peñuelas, J.: Effects of livestock grazing on the relationships between soil microbial community and soil carbon in grassland ecosystems, Science of The Total Environment, 881, 163416, https://doi.org/10.1016/j.scitotenv.2023.163416, 2023.

Yang, G., Gong, J., Zhang, S., Wang, R., Wang, T., Yu, Y., and Xie, Q.: Trade-offs between root exudation and root traits induced by coexisting species under a grazing gradient can mobilize available nitrogen to promote grassland productivity, Soil and Tillage Research, 260, 107108, https://doi.org/10.1016/j.still.2026.107108, 2026.

Yong-Zhong, S., Yu-Lin, L., Jian-Yuan, C., and Wen-Zhi, Z.: Influences of continuous grazing and livestock exclusion on soil properties in a degraded sandy grassland, Inner Mongolia, northern China, CATENA, 59, 267–278, https://doi.org/10.1016/j.catena.2004.09.001, 2005.

Zhan, T., Zhang, Z., Sun, J., Liu, M., Zhang, X., Peng, F., Tsunekawa, A., Zhou, H., Gou, X., and Fu, S.: Meta-analysis demonstrating that moderate grazing can improve the soil quality across China's grassland ecosystems, Applied Soil Ecology, 147, 103438, https://doi.org/10.1016/j.apsoil.2019.103438, 2020.

Zhang, M., Li, X., Wang, H., and Huang, Q.: Comprehensive analysis of grazing intensity impacts soil organic carbon: A case study in typical steppe of Inner Mongolia, China, Applied Soil Ecology, 129, 1–12, https://doi.org/10.1016/j.apsoil.2018.03.008, 2018.

Zhang, Y., Lavallee, J. M., Robertson, A. D., Even, R., Ogle, S. M., Paustian, K., and Cotrufo, M. F.: Simulating measurable ecosystem carbon and nitrogen dynamics with the mechanistically defined MEMS 2.0 model, Biogeosciences, 18, 3147–3171, https://doi.org/10.5194/bg-18-3147-2021, 2021.

Zhang, Y., Liang, J., He, J., Han, G., and Bai, Y.: Formation and regulation mechanisms of grassland productivity: A review, Chin. Sci. Bull.-Chin., 70, 1477–1485, https://doi.org/10.1360/TB-2024-0285, 2025.

Zhang, Z., Zhao, Y., Lin, H., Li, Y., Fu, J., Wang, Y., Sun, J., and Zhao, Y.: Comprehensive analysis of grazing intensity impacts alpine grasslands across the Qinghai-Tibetan Plateau: A meta-analysis, Front. Plant Sci., 13, https://doi.org/10.3389/fpls.2022.1083709, 2023.

https://doi.org/10.5194/egusphere-2026-4892
Preprint. Discussion started: 19 August 2026

996 Zhao, H., Sun, J., Xu, X., and Qin, X.: Stoichiometry of soil microbial biomass carbon and
997 microbial biomass nitrogen in China's temperate and alpine grasslands, European Journal of
998 Soil Biology, 83, 1–8, https://doi.org/10.1016/j.ejsobi.2017.09.007, 2017.

999 Zheng, M., Zhou, Z., Luo, Y., Zhao, P., and Mo, J.: Global pattern and controls of biological
1000 nitrogen fixation under nutrient enrichment: A meta-analysis, Global Change Biology, 25,
1001 3018–3030, https://doi.org/10.1111/gcb.14705, 2019.

1002 Zhou, G., Zhou, X., He, Y., Shao, J., Hu, Z., Liu, R., Zhou, H., and Hosseinibai, S.: Grazing
1003 intensity significantly affects belowground carbon and nitrogen cycling in grassland
1004 ecosystems: a meta- analysis, Global Change Biology, 23, 1167–1179,
1005 https://doi.org/10.1111/gcb.13431, 2017.

1006