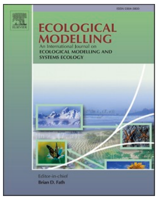
Ecological Modelling 439 (2021) 109345

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



DynaGraM: A process-based model to simulate multi-species plant community dynamics in managed grasslands

Thibault Moulin [a,b,*], Antoine Perasso [b], Pierluigi Calanca [a], François Gillet [b]

[a] *Agroscope, Agroecology and Environment, Reckenholzstrasse 191, CH-8046 Zurich, Switzerland*
[b] *Université Bourgogne Franche-Comté – CNRS, UMR 6249 Chrono-environnement, 16 route de Gray, 25030 Besançon cedex, France*

ARTICLE INFO

Keywords:
Grassland model
Hayfield
Interspecific competition
Pasture
Plant community dynamics
Process-based model
Vegetation dynamics

ABSTRACT

Permanent grasslands host a high plant diversity, which sustains many ecosystem services. Thus, understanding how composition of the plant community responds to different management practices under given soil and climatic conditions is crucial for making best use of grasslands. modeling approaches may be used to explain the manifold interactions involved to sustain this diversity. We developed the dynamic, process-based ecological model *DynaGraM* to simulate the seasonal aboveground vegetation dynamics of semi-natural grasslands. The model allows specifying plant community by any number of species. The predictive power of the model was assessed by simulating the dynamics of a virtual mountain grassland in response to four typical management scenarios under constant climatic conditions over several decades. In our experiments, we modelled an assemblage of seven species representing contrasted plant functional types. We compared model outputs to compositions inferred from floristic records conducted in the French Jura Mountains. Irrespective of initial conditions, the simulated community converged to four distinct compositions that primarily reflected management. Overall, the results matched the functional composition inferred for each of the scenarios from the botanical records. Convergence in functional composition was reached in less than 15 years under grazing scenarios, but not less than 50 years under mowing scenarios. At quasi-equilibrium, the highest vegetation diversity was obtained for extensive grazing and the lowest for extensive mowing. Overall, this study introduces a novel and relatively simple approach to model competition and adaptation processes in plant community dynamics, thus providing a response to the key challenge of modeling multi-species grasslands.

Introduction

Semi-natural permanent grasslands occupy a large fraction of European territories and are the milestone of agricultural practices in mountain areas (Gaujour et al., 2012). These ecosystems are often hotspots of biodiversity sustaining many ecosystem services and facing various disturbances of anthropogenic or natural origin. Species composition and diversity of the grassland plant communities are strongly influenced by their current and past management (Myers et al., 2000). While intensification or abandonment lead in many cases to severe reduction of plant diversity (Rosenthal, 2010; Van Calster et al., 2008), some temperate European grasslands managed for a long time with low intensity of mowing or grazing present the world record of species richness at fine scale (Wilson et al., 2012).

Models developed in the past to simulate the dynamics of vegetation composition in grasslands have mostly targeted the landscape scale, such as *WoodPaM* (Gillet, 2008; Peringer et al., 2013), or the global scale, such as *LPJmL* (Rolinski et al., 2018), rather than the field scale. Also, grassland models published so far focused on monospecific swards (Duru et al., 2009; McCall and Bishop-Hurley, 2003; Schapendonk et al., 1998), mixtures of a grass and a legume species (Lazzarotto et al., 2009; Thornley, 1998), or a multispecies community constant in time (Jouven et al., 2006a; Riedo et al., 1998). *LINGRA* is a sink/source model simulating the productivity of *Lolium perenne* in European grasslands (Schapendonk et al., 1998). *LINGRA* and *ModVege* (Jouven et al., 2006a) focus on the productivity dynamics of the plant community, whose composition is constant over time and described by one species or four functional types, respectively. Taubert et al. (2012) reviewed thirteen grassland models finding that only two described explicitly the plant community by more than three different species or functional types:

---

* Corresponding author.
E-mail addresses: thibault.moulin@posteo.net (T. Moulin), antoine.perasso@univ-fcomte.fr (A. Perasso), pierluigi.calanca@agroscope.admin.ch (P. Calanca), francois.gillet@univ-fcomte.fr (F. Gillet).

https://doi.org/10.1016/j.ecolmodel.2020.109345
Received 13 March 2020; Received in revised form 15 October 2020; Accepted 15 October 2020

GraS, a succession compartment model (Siehoff et al., 2011) and *STEPPE*, a gap model of semiarid grasslands (Coffin and Lauenroth, 1990). However, neither *GraS* nor *STEPPE* simulate plant biomass.

In a recent review, van Oijen et al. (2018) distinguished three categories of grassland models: empirical, integrated and process-based, the latter comprising ecological, biogeochemical and agricultural models. For all of them there is a need to incorporate biodiversity to, in particular, improve knowledge and predictions of the ecosystem services provided by permanent grasslands (van Oijen et al., 2020). Taubert et al. (2012) concluded that, in practice, only two contrasted formalisms have been explored so far to predict changes in the composition of grassland plant communities, following a gradient of complexity. On one hand, ecological grassland models, characterized by elegant mathematics, represent plant biomass or cover dynamics based on resource competition processes (Tilman, 1980, 1982) or tolerance to external disturbances, such as *GraS* (Siehoff et al., 2011). On the other hand, more complex, spatially explicit, individual-based grassland models may include a high number of plant species or plant functional types (PFTs). These models can consider above- and below-ground intra- and inter-specific competition among plant individuals or organs, allowing simulations of metacommunities of many PFTs. Typical examples are *IBC-grass* (Weiss et al., 2014) or *EcoHyD* (Lohmann et al., 2017), among other models falling into this category (May et al., 2009; Soussana et al., 2012; Taubert et al., 2012).

To be able to simulate in detail the interactions between the soil, the vegetation and the atmosphere, biogeochemical models tend to be rich in parameters and variables (van Oijen et al., 2018). Complexity can be reduced by resorting to plant functional types. In grassland models, PFTs are specified by combining parameters from a set of functionally related species, such as legumes, perennial grasses or erect forbs. Typically, a PFT is a group of species with similar functional traits and therefore similar responses to constraints and disturbances, such as management practices, and similar contributions to ecosystem services, such as forage production (Graux et al., 2016). In this context, incorporating an explicit description of vegetation diversity multiplies the dimension of the parameter space, leading to high complexity and models that could be difficult to control. A possible solution is to consider re-usable components that can be coupled with a single instance of a generic crop model to simulate explicitly seasonal changes in taxonomic and functional composition of managed grasslands. This approach has been implemented in CoS*Mo* (Confalonieri, 2014; Movedi et al., 2019).

As summarized by Moulin et al. (2018), very few grassland models have been designed to simulate both composition and biomass changes in multispecies, semi-natural grasslands used as pastures or/and hayfields, a requirement for understanding diversity-productivity-stability relationships. This gap has also been emphasized by Kipling et al. (2016). Currently few process-based models exist to explain or predict the intricacies of the relation between biodiversity, productivity and the long-term stability of the vegetation assemblage (van Oijen et al., 2018). Thus, it appears crucial to develop a dynamic grassland model of that includes an explicit description of diversity and addresses both plant composition and biomass growth for various forms of land use. Following the generic approach allowing the inclusion of any level of diversity introduced by Moulin et al. (2018), the aim of this paper is to provide a comprehensive description of the dynamic grassland model *DynaGraM* and to explore its behavior under different management conditions.

One important choice for building *DynaGraM* was to restrict the ecophysiological description to essential processes in order to minimize the dimension of the parameter space, hence to simplify species parameter estimations and to save computation time. In this respect, even if the purpose of *DynaGraM* appears very similar to that of CoS*Mo*, the approaches are different. As mentioned before, CoS*Mo* requires to be coupled with a complex biogeochemical model to run vegetation simulations. As opposed to this, *DynaGraM*, basically a mechanistic model of resource competition (Tilman, 1980), is a stand-alone solution. It represents the regulation of green biomass and plant competition from the standpoint of resource dynamics, but this approach is refined by integrating ecophysiological and biophysical details inherited from *ModVege* (Jouven et al., 2006a) and soil processes from *PROGRASS* (Lazzarotto et al., 2009). A recent adaptation of *ModVege*, the Moorepark St Gilles grass growth model (*MoSt-GG*), has been developed in the context of Irish pastures (Ruelle et al., 2018). This dynamic model describes the daily grass growth for grazing systems at the paddock level, including a spatially explicit structure and a soil nitrogen compartment. These models have been validated with real data (Calanca et al., 2016) and *MoSt-GG* is still the object of new developments (Ruelle et al., 2018). In contrast to *ModVege, MoSt-GG* and *GraS* (Siehoff et al., 2011), which assume a constant plant community composition, we integrated in *DynaGraM* a generic description of the vegetation as a set of any number of plant species or species groups (PFTs).

In a previous paper (Moulin et al., 2018), we compared simulation results from alternative instances of a preliminary version of *DynaGraM* that only differ by the identity and number of state variables (plant species or PFTs) describing the green biomass. In the present paper, we focus on a typical grassland plant community made of seven frequent and potentially dominant species representative of each PFT observed in European mid-mountain mesic grasslands. We explore the response of the functional composition of this modelled plant community to various management scenarios under realistic climatic conditions.

The overarching goal of this paper is to present the model formalism and to discuss model behavior with selected simulation experiments that we conducted for illustrative purposes only. In these experiments we address the following research questions:

1. How are diversity and composition of the plant community affected by several years or decades of constant land use (grazing or mowing) and management intensity (extensive or intensive)?
2. To what extent do management-induced differences in the simulated plant community reflect differences in relative cover of species or PFTs inferred from floristic records of mesic grasslands?
3. How does the initial composition of the plant community influence its adaptation to management conditions?
4. Does the response time of the simulated community dynamics depend on management type and intensity?

Methods

Model description

DynaGraM is a mechanistic, process-based model for simulating the seasonal growth of the aboveground biomass and the seasonal course of the botanical composition in mixed, temperate grasslands, under various conditions of climate, soil and management (Moulin et al., 2018). It consists of three submodels, with state variables (Table 1) and forcing variables connected as shown in Fig. 1. In this section, we present the key assumptions and the main equations of the model. A comprehensive description of *DynaGraM* is given in Appendix A (Online Supplementary Material).

Overview and main assumptions

The climate submodel contains four forcing variables defined as the daily records of mean temperature T [°C], precipitation P [mm], photosynthetic active radiation PAR [MJ m^{-2}] and potential evapotranspiration PET [mm]. The second submodel addresses grassland vegetation in terms of n state variables B_i representing the green biomass of each species or PFT i [kg DM ha^{-1}]. As species and PFTs are alternatives to the same variables, the term "species" will be used hereafter to refer to either species or PFTs. Plant growth and senescence are formulated in a similar manner as in the *LINGRA* model (Schapendonk et al., 1998) with adaptations as implemented in *ModVege* (Jouven et al.,

Table. 1
State variables and forcing climatic variables implemented in *DynaGraM*.

State variables	*Symbol*	*Description*	*Forcing climatic variables*	*Symbol*	*Description*
Green biomass	B_i	Green biomass of plant species or PFT *i*	Temperature	T	Daily average surface temperature acting on plant growth rate and mineralization rate of *No* to *Nm*
Organic nitrogen	No	Amount of organic nitrogen in the soil	Precipitations	P	Daily rainfall, the supply to the water reserve
Mineral nitrogen	Nm	Amount of mineral nitrogen in the soil, available for plant growth	Photosynthetically active radiation	PAR	Solar radiations activating the photosynthesis, driver of potential plant growth
Water reserve	WR	Amount of water in the soil, available for the plants	Potential evapotranspiration	PET	A loss in the water reserve due to evaporation and transpiration

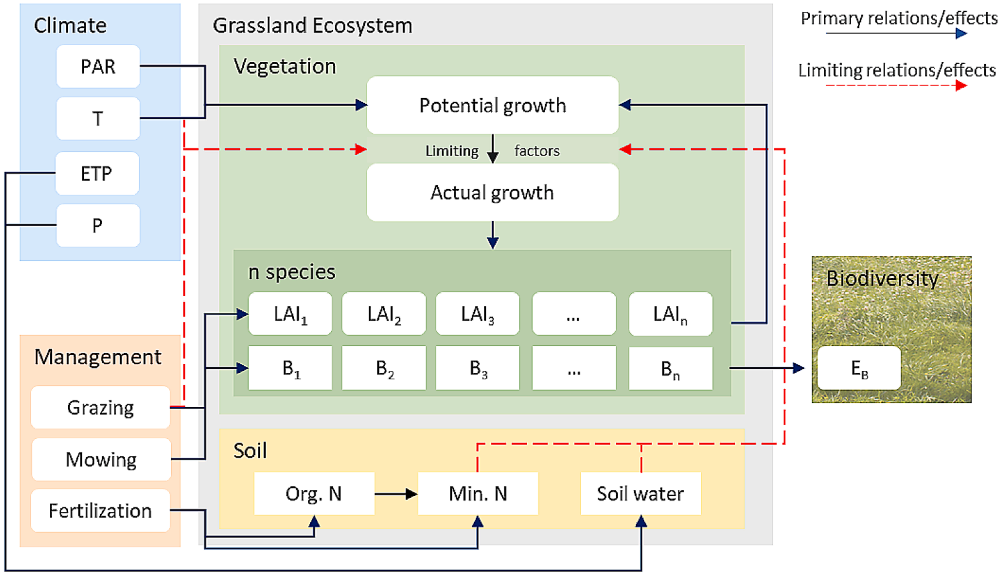


Fig. 1. Structure of the *DynaGraM* model. Rectangular plain boxes denote state variables (plant biomass, nitrogen and water reserve); rounded rectangles account for forcing variables (climate and management), intermediate variables (LAI, growth rates) or synthetic index of diversity (Simpson evenness E_B); blue plain lines denote primary relations or effects and red dashed lines denote reducer effects limiting the plant growth. The model can simulate any number of species, denoted in the figures with subscripts 1, 2, 3, …, n.

2006a). Plant growth is driven by radiation, with interception depending on the leaf-area index (LAI), and limited by temperature, soil water and radiation intensity. Senescence is a function of the age of the sward. The LAI is calculated diagnostically from the aboveground biomass.

The soil submodel contains three state variables. Two of them describe the amount of available soil resources, namely mineral nitrogen *Nm* [kg N ha^{-1}] and water reserve *WR*. The third corresponds to a pool of soil organic nitrogen *No* [kg N ha^{-1}], supplied by the senescence of standing biomass and litter decomposition. This soil organic nitrogen is mineralized to soluble mineral nitrogen *Nm* (nitrate or ammonium) that becomes available for plant uptake, according to the formulation used in *PROGRASS* (Lazzarotto et al., 2009) and introduced by previous authors (Kirschbaum, 2000; Paul et al., 2003; Schwinning et al., 1999). This loop of consumption-degradation of nitrogen (implicitly present in three forms: mineral in the soil solution, organic in the soil and in the biomass) is an important feature of *DynaGraM* as it directly supports interspecific resource competition.

Overall, the model consists of a non-linear system of $n + 3$ ordinary differential equations (ODEs), built under simplifying assumptions introduced to limit to a minimum the dimensions of the parameter space. Herbaceous vegetation is only described by green biomass (mainly leaves), thus implicitly excluding belowground biomass (roots, storage organs) and the reproductive parts of the plants (flowers, fruits). Hence, the model does not account for seed production and recruitment from the seedbank, and for allocation strategies. Although maximal canopy height is taken into account to contrast mowing impact on species, the model ignores the time-dependent height distribution of plants (assuming that the competition for light within the canopy only depends on the relative proportions of the leaf area index; see below), and considers a very simplified representation of the aging processes inherited from *ModVege*. Moreover, the model neglects symbiotic fixation of atmospheric nitrogen by legumes and denitrification in the soil.

Plant biomass dynamics

For a given species *i*, green biomass dynamics is described by the following equations (for clarity reason, only the dependence on state and forcing variables is indicated):

$$\frac{dB_i}{dt} = gr_i - \mu_i\ SEN(T) - mow_i(B_i) - graz_i(B_i) \tag{1}$$

$$gr_i = Gr_i(B_i, PAR)\ SEA(T)\ Rred(PAR)\ Nred_i(Nm)\ Tred_i(T)\ Wred_i(WR,\ PET)\ Ared_i \tag{2}$$

where gr_i expresses the actual growth rate of a given species *i*, $Gr_i(B_i, PAR)$ expresses potential growth as a function of standing biomass B_i and photosynthetic active radiation *PAR* and $SEA(T)$ is an empirical representation of the seasonal pattern of shoot growth (Jouven et al., 2006a). In addition, $Rred$,$Nred_i$, $Tred_i$, $Wred_i$ and $Ared_i$ are the growth reducers associated with radiation, soil mineral N availability, temperature, soil water status and cattle trampling, respectively; $\mu_i\ SEN(T)$ is the seasonal sink associated with senescence; $mow_i(B_i)$ and $graz_i(B_i)$ are the biomass removal rates due to mowing and grazing, respectively.

As in *LINGRA* and *ModVege*, potential growth is described by an Ivlev function of the total leaf area index (LAI_{tot}) weighted according to the proportion of LAI accounted for by the individual species (Thornley and Johnson, 1990). Setting

$$LAI_i(B_i) = SLA_i \frac{B_i}{10} LAM \tag{3}$$

$$LAI_{tot} = \sum_{j=1}^{n} LAI_j(B_j) \tag{4}$$

we have:

$$Gr_i(B_i, PAR) = 10\ PAR\ RUE_{\max}\ (1 - \exp(-\alpha\ LAI_{tot})) \frac{LAI_i(B_i)}{LAI_{tot}} \tag{5}$$

In Eqs. (3) to (5), $RUE_{\max}$ is the maximum radiation use efficiency of the whole canopy, α the extinction coefficient, SLA_i the specific leaf area of species i, and LAM the percentage of laminae. For the sake of simplicity and following *ModVege*, we assume the same values of LAM, α and $RUE_{\max}$ for all species. The factor 10 in Eq. (5) ensures unit consistency.

Growth limitation associated with soil mineral N availability is modelled as a Holling type III function:

$$Nred_i(Nm) = \frac{Nm^2}{k_i^2 + Nm^2} \tag{6}$$

where k_i is the half saturation term, corresponding to the amount of mineral N resource for which the vegetation growth rate could reach half its maximum (if the other resources are not limiting). This parameter k_i traduces for a given species i its nutrient requirement for its growth.

For the sake of compactness, details concerning other reducers and functions involved in Eqs. (1) and (2), viz. $Rred$, $Tred_i$, $Wred_i$, $Ared_i$, SEA and SEN, can be found in Appendix A (Online Supplementary Material).

The last two terms on the right-hand side of Eq. (1) are the rates of defoliation associated with mowing and grazing. Both are modelled as pulse-wise functions. Removal of aboveground biomass by mowing is assumed proportional to the standing green biomass of each species, whereby the proportionality factor λ_i also varies among species to account for differences in the vertical distribution of biomass. λ_i has been estimated according to the maximal canopy height H_i of the given species i and a cutting height of 5 cm, as expressed by: $\lambda_i = (H_i - 0.05)/H_i$.

$$mow_i(B_i) = \lambda_i\ B_i \tag{7}$$

The approach adopted to model removal of aboveground biomass by grazing is based on the assumption that each livestock unit consumes a predefined amount of biomass, in such a way that the loss of biomass by each species depends on appetence ρ_i and relative abundance of the species. Denoting by SD the stocking density, expressed in adult bovine units per hectare (ABU ha^{-1}), where 1 ABU is equivalent to a dairy cow, by κ the daily consumption of an adult bovine unit (kg DM ABU^{-1} d^{-1}) and again assuming a Holling type III functional response, we have:

$$graz_i(B_i) = \kappa\ SD \frac{\rho_i\ B_i^2}{1 + \sum_{j=1}^{n} \rho_j\ B_j^2} \tag{8}$$

In the model, growth competition among species occurs at different levels. Competition for light depends on LAI_i Eq. (5)), competition for nutrients on δi and k_i (Eq. (6), more details in Appendix A, Online Supplementary Material). In addition, different responses to environmental constraints (Appendix A, Online Supplementary Material, Fig. A.1) also provide advantages or disadvantages under specific conditions, as well as impacts of moving and grazing (Eqs. (7) and ((8)).

Soil nitrogen and water dynamics

The dynamics of soil organic N (*No*), soil mineral N (*Nm*) and soil water reserve (*WR*) is described by the following differential equations:

$$\frac{dNo}{dt} = \sum_{i=1}^{n} (\delta_i c_o \mu_i\ SEN(T)\ B_i) + Nd\ SD + \Phi_o - \theta\ Tmin(T)\ Wmin(WR)\ No \tag{9}$$

$$\begin{aligned} \frac{dNm}{dt} = {} & \theta\, Tmin(T)\ Wmin(WR)\ No + Nu\, SD + \Phi_m - \Lambda(Nm) \\ & - \sum_{i=1}^{n} \delta_i\ c_m\ Gr_i(B_i, PAR)\ Rred(PAR)\ Nred_i(Nm)\ Tred_i(T)\ Wred_i(WR,\ PET)\ Ared_i\ SEA(T) \end{aligned} \tag{10}$$

$$\frac{dWR}{dt} = P - AET(B_i,\ WR,\ PET) - \Delta(B_i,\ WR,\ PET,\ P) \tag{11}$$

The first term on the right-hand side of Eq. (9) represents the input of organic N through plant residues (as determined by senescence), the second is the input through dung deposition from grazing cattle, the third the input by organic fertilizer, and the last negative one the rate of mineralization as modulated by temperature and soil water availability.

The mineralization rate appears again in Eq. (10) with the opposite sign, representing here an input of mineral N. The second term on the right-hand side of Eq. (10) is the input through urine deposition from grazing cattle, the third the input from mineral N fertilizer, the fourth the loss by leaching, whereas the last one represents plant N-uptake. Finally, Eq. (11) gives the soil water budget as the difference between precipitation and evapotranspiration plus deep percolation.

Eqs. (9) and (10) follow the approach adopted in *PROGRASS* (Lazzarotto et al., 2009), whereas Eq. (11) is consistent with the solution implemented in *ModVege* (Jouven et al., 2006a). Details concerning the functions *Tmin, Wmin, SEN,* Λ, *AET* and Δ can be found in Appendix A (Online Supplementary Material).

Community diversity

To measure community diversity, *DynaGraM* uses Simpson evenness index, that is inverse Simpson diversity divided by the number of species n (Hill, 1973; Moulin et al., 2018):

$$E_B = \frac{1}{n} \left(\sum_{i=1}^{n} \left(\frac{B_i}{B_{tot}} \right)^2 \right)^{-1} \tag{12}$$

where $B_{tot} = \sum_{i=1}^{n} B_i$ is the total green biomass of the whole community.

Parameterization

DynaGraM includes 36 global parameters along with $9 \times n$ species-specific parameters and $n + 3$ initial condition values for state variables. Appendix B (Online Supplementary Material, Table B1) provides a complete list of the parameters, including definition, units, default values and references. We obtained values of the global parameters from literature. In addition, we estimated species parameters based on various sources (see Appendix A, Online Supplementary Material).

Numerical integration

We implemented *DynaGraM* in R language (R Core Team, 2020). We numerically solved the ODE system with the function 'ode' in the R package 'deSolve' (Soetaert et al., 2010) using the Euler method and an integration time step of one day. The appropriateness of the time step was verified by comparing standard outputs with those obtained from running the model with a smaller time step. The pertinence of the numerical solution scheme was further tested by replacing 'ode' with the function 'lsoda' in the same R package, the latter being an ODE solver that automatically switches between stiff and non-stiff methods. No sensible difference in the solution was detected.

However, the choice of a discrete-time integration method (Euler solver with $dt = 1$) can lead to negative biomass values after defoliation events. To prevent the inadvertent, definitive loss of species, we introduced a minimal residual amount of biomass remaining after any disturbance, $B_{min} = 1.5$kg DM ha^{-1}.

Model variables and parameters

To show the model ability to capture the response of grassland communities to management practices, we considered a fictitious grassland illustrative of European mountain pastures and hayfields. This theoretical grassland does not correspond to a real specific site, but vegetation, climate, soil, and land-use have been specified to be characteristic to those commonly observed in the Pontarlier region (French Jura Mountains, at 900 m a.s.l. elevation). In this region, permanent grasslands represent a large fraction of the agricultural area. They are extensively to intensively managed to sustain dairy farming for PDO cheese production (Mauchamp et al., 2014).

We retrieved climatic data for Pontarlier from the E-OBS v19.0e database (Cornes et al., 2018). We selected, within this climatic time series covering the period 1981 to 2018, the year 2004 to be representative of the climatic conditions in this area. We designed the climate forcing variables as repetitions of the daily records for this standard year 2004. It results that interannual variation of weather conditions is neglected in this study to avoid confounding effects of specific years on the response of vegetation to management scenarios. However, the considered climate forcing variables impact the seasonal dynamics of the state variables.

Table. 2
Four management scenarios used for the simulations: extensive and intensive grazing, extensive and intensive mowing. *ncut* denotes the number of mowing events, *SD* the livestock density expressed in number of Adult Bovine Units per hectare, Φ_m and Φ_o mineral and organic fertilization, respectively.

Forcing variables		*Extensive Grazing*	*Intensive Grazing*	*Extensive Mowing*	*Intensive Mowing*
ncut	Mowing events	–	–	2	3
	Days	–	–	June 26, September 23	June 10, August 9, October 3
SD	Stock density	0.5 ABU ha^{-1}	1.5 ABU ha^{-1}	–	–
	Grazing period	May 21 to October1	May 21 to October 1	–	–
Φ_m	Mineral N fertilization	–	90 kg Nm ha^{-1} a^{-1}	–	180 kg Nm ha^{-1} a^{-1}
	Spreads	–	4 from April 30 to July 29	–	5 from May 11 to September 8
Φ_o	Organic N fertilization	–	–	80 kg No ha^{-1} a^{-1}	80 kg No ha^{-1} a^{-1}
	Spreads	–	–	May 16, July 1	May 16, July 1

Soil properties are controlled by five parameters in the model: initial amount of mineral and organic N, maximal mineralization rate θ and levels of the permanent wilting point *PWP* and the water holding capacity *WHC*; values were estimated from the Soil Atlas of Europe (European Soil Bureau Network, 2005) and Maps of indicators of soil hydraulic properties for Europe (European Soil Data Centre, 2016). Soil parameter values are given in Appendix B (Online Supplementary Material, Table B1).

Anthropogenic disturbances were modelled by four agricultural management scenarios typical of the French Jura Mountains, differing by the type of defoliation and by the intensity of agricultural practices, including fertilization: extensive or intensive grazing and extensive or intensive mowing (Table 2).

Based on a theoretical assessment of the impact on *DynaGraM* simulations of the number of state variables describing the vegetation (Moulin et al., 2018), we chose $n = 7$ state variables to describe the plant community, corresponding to seven PFTs. We considered the four PFTs of grasses (Cruz et al., 2002; Duru et al., 2009) built on plant functional traits for nutrient acquisition and tolerance to defoliation: PFT A corresponds to early and fast-growing grasses in fertile and frequently disturbed grasslands whereas at the opposite PFT D describes late and slow-growing grasses in infertile and unfrequently disturbed grasslands. We added three lifeforms of dicots: tall erect forbs E, small rosette and creeping forbs R and legumes L.

Then, to specify values for each of the nine species-specific parameters (Table 3), we selected a single representative species for each of the seven PFTs, among the most frequent and abundant species in the Pontarlier region according to previous botanical surveys (Perronne et al., 2014). Details on the estimation of values for the species-specific parameters are available in Appendix A (Online Supplementary Material). This selection of seven species represents a wide diversity of life strategies, as evidenced by their distribution in the CSR triangle shown in Fig. 2 (Grime, 1977; Pierce et al., 2017). The community dynamics simulated by *DynaGraM* is explained by tradeoffs among the three life strategies of Grime (1977): a competitive ability C leading to high potential growth Gr_i (function of SLA_i), the tolerance to a stress on resources S mainly determined by $Nred_i$ (function of k_i) or $Wred_i$ (function of η_i), and a resistance to defoliation events R (driven by ρ_i, σ_i and λ_i).

Numerical experiments

Two numerical experiments were performed with *DynaGraM*. They illustrate the potential application of the model and should be considered as a proof of concept of the proposed approach rather than a model validation. The results of a third one, related to the comparison of *DynaGraM* and *ModVege*, is available in Appendix D (Online Supplementary Material).

Impact of management on community composition

Effects of management practices on the simulated botanical composition (research question 1) were assessed by simulations under the four management scenarios described in Table 2, starting from the same initial composition. We defined the latter by an even distribution of all species. Seasonal biomass dynamics at final state was obtained after a repetition of the same management scheme and the same seasonal weather conditions (for the year 2004) over twenty years. For extensive grazing and intensive mowing management, we also compared the seasonal dynamics of the four plant growth reducers introduced in Eq. (1). Reducer values were computed at the community level by averaging the seven species' values, weighted by their relative

Table. 3
List of the seven species representative of seven plant functional types (PFTs) selected in *DynaGraM* to describe the community composition, with their CSR strategy (Pierce et al., 2017) and values of the nine species-specific parameters: *SLA* specific leaf area (Kattge et al., 2011); λ proportion of biomass removed by a mowing event, estimated from canopy height (Perronne et al., 2014); ρ appetence for cattle (Kühn et al., 2004); σ trampling tolerance (Kühn et al., 2004); δ leaf nitrogen content (Soussana et al., 2012); k half-saturation constant of the nitrogen resource, estimated from nitrogen requirement (Julve, 2019); μ leaf senescence rate (Ryser and Urbas, 2000); T_1 lower limit of optimal growth temperature (Al Haj Khaled et al., 2005); η water requirement (Julve, 2019).

Symbol	Species name	PFT	CSR	*SLA*	λ	ρ	σ	δ	k	μ	T_1	η
Lol.per	*Lolium perenne*	A	R/CR	0.0286	0.82	9	8	0.0291	15.00	0.0134	10.0	1.0
Poa.tri	*Poa trivialis*	B	CSR	0.0331	0.81	7	6	0.0236	14.75	0.0130	12.7	1.3
Tri.fla	*Trisetum flavescens*	C	SR/CSR	0.0205	0.78	7	4	0.0272	8.00	0.0085	13.5	1.0
Des.ces	*Deschampsia cespitosa*	D	S/SR	0.0170	0.82	2	4	0.0168	9.00	0.0065	15.0	1.3
Ran.acr	*Ranunculus acris*	E	CR	0.0228	0.81	2	6	0.0197	11.50	0.0105	12.5	1.0
Tar.off	*Taraxacum officinale*	R	CR	0.0324	0.82	7	7	0.0291	17.00	0.0164	9.2	1.0
Tri.pra	*Trifolium pratense*	L	R/CSR	0.0228	0.80	8	4	0.0377	6.50	0.0120	12.5	1.0

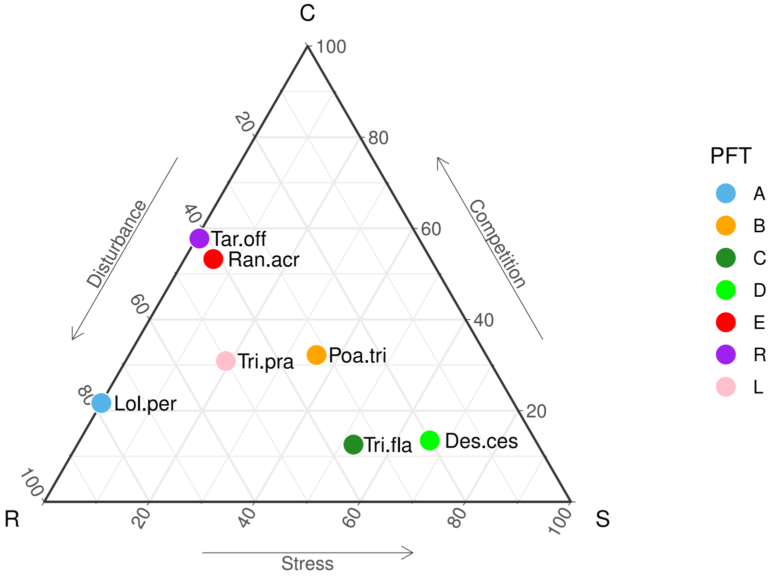


Fig. 2. Ternary plot of the CSR triangle indicating the life strategy of the species selected as representative of the seven plant functional types (PFTs) (Pierce et al., 2017).

biomass.

Because soil organic nitrogen showed a very slow dynamics (Fig. C2, Online Supplementary Material, Appendix C), the whole system would require a very long simulation time to reach equilibrium. However, we expect community composition to reach more rapidly a quasi-stable state characterized by very low variations simulated in the community structure due to its faster dynamics. To check this, we complemented this first experiment by an analysis, for each of the four management regimes, of the convergence time necessary to reach a community structure close to the cyclic attractor. Thus, we introduced a measure of stability by comparing a synthetic index of community diversity (Simpson evenness E_B) between successive years for each Julian day t. We computed relative differences as the ratio $(E_B(t) - E_B(t-365))/E_B(t-365)$. Mean year-to-year changes were computed for the vegetation period, i.e. from April 1 to September 30, over 100 years.

To assess the realism of the simulated functional composition (research question 2) we compared model simulation outputs to observed data in the selected case study area. We extracted from *Phytobase*, a phytosociological database (Gillet, 2015), 68 floristic relevés of permanent grasslands sampled at 800–900 m a.s.l. elevation in the French Jura Mountains, i.e. under the climatic conditions close to those at Pontarlier. We classified the relevés into four management categories deduced from their phytosociological classification (Ferrez et al., 2011): *Gentiano luteae – Cynosuretum cristati* was assigned to extensive grazing (9 relevés), *Lolio perennis – Plantaginetum majoris, Lolio perennis – Cynosuretum cristati* and *Alchemillo monticolae – Cynosuretum cristati* to intensive grazing (13 relevés), *Euphorbio brittingeri – Trisetetum flavescentis* to extensive mowing (18 relevés), and *Alchemillo monticolae – Brometum hordeacei* to intensive mowing (28 relevés). These 68 floristic relevés of mesic permanent grasslands have been recorded at different sites, seasons and years. Each of the observed 195 species was assigned to a PFT and we computed the mean relative cover of each PFT in each management category. In addition, we compared the relative cover of the seven species selected in the model simulations among the four management categories. Thus, we obtained two representations of the observed functional composition in response to four contrasted land-use types, directly comparable to previous *DynaGraM* simulation outputs.

Sensitivity to initial conditions

In a second simulation experiment, we assessed the impact of the initial community composition on vegetation dynamics under contrasted management practices (research question 3). For this purpose, we performed an analysis of the model sensitivity to the initial quantitative composition of the plant community, by varying the relative proportion of each species at the beginning of each simulation (the 1st of January at year 1). Eight initial compositions were considered: seven of them were defined by a strong dominance (half of the initial total biomass) of each one of the species in turn; the last one was built from an even distribution of all species, as in our first experiment. Sensitivity to the eight initial conditions were assessed under the four contrasted management scenarios described in Table 2, repeated every year. Identical soil and climatic conditions were considered for all these

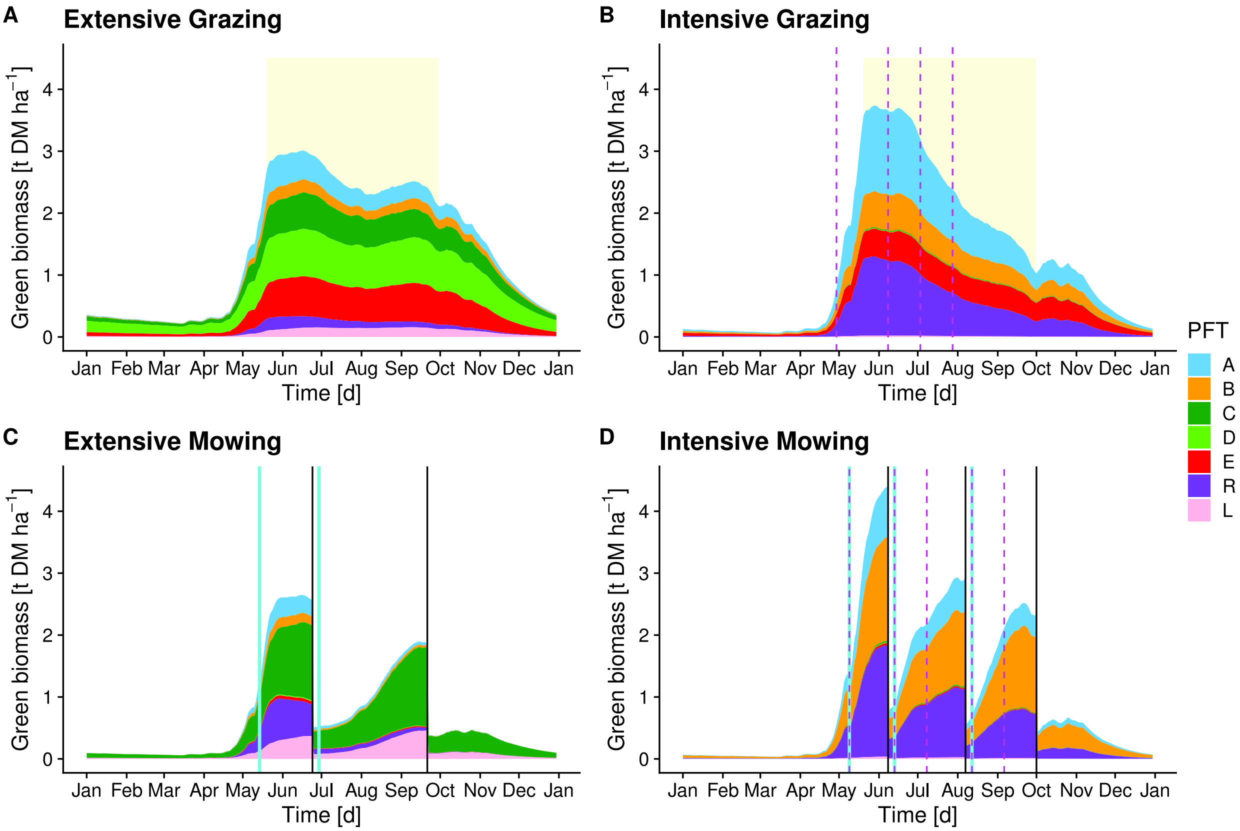


Fig. 3. Seasonal composition changes in a 7-PFT community, starting from the same initial conditions ($\forall\ i\ B_i\ (0) = 40$ kg DM ha^{-1}), after 20-year simulations under four management scenarios: (A) extensive grazing; (B) intensive grazing; (C) extensive mowing and (D) intensive mowing. Yellow areas represent the grazing period, black solid lines mowing events, magenta dashed lines mineral fertilization events and cyan solid lines organic fertilization events. Filled areas correspond to the contribution of each PFT to the green biomass.

simulations, as explained above in Section 2.2. We compared the simulated compositions obtained respectively at years 10 and 50, by representing mean biomass values of each species within the vegetation period (from April 1 to September 30).

Then, to address the question of the impact of management on the convergence time (research question 4), a 100-year time horizon was considered. Assuming for a given practice that all initial assemblages converge to the same final state, we summarized each community structure by its Simpson evenness. We compared time series of mean and standard deviation of the Simpson evenness obtained from the eight initial community structures under the four management scenarios within the vegetation period.

Results

Impact of management on community composition

Markedly distinct community patterns emerged after 20-year simulations for the four management scenarios (Fig. 3), despite the same initial conditions in all four cases. This result indicates that the simulated community composition was strongly influenced by management, both in term of intensity and type of defoliation. It highlights the ability of *DynaGraM* to express the chief influence of management practices on community dynamics.

As extensive grazing and intensive mowing resulted in very contrasted biomass and community patterns (Fig. 3A and 3D), we chose these two management scenarios to show how they differ in terms of seasonal change of the weighted-mean stress (reducers) and disturbance (defoliation) factors (Figs. 4A and 4B) and net growth rates of the different PFTs (Figs. 4C and 4D). Dominance of species in Fig. 3 resulted inherently from high actual growth rates in Figs. 4C and 4D.

Nitrogen availability played a key role among the limiting factors (Fig. 4A and B), in contrast to limitations associated with temperature and water, which did not differ between the two management scenarios. Thus, the sigmoid Holling III functional response appears as a key function in our model to describe competition for limiting resources among species and to explain the observed shift of dominant species with land-use intensification. This function explains how the shortage in mineral N resource affects negatively the growth rate of each species, as each unit of biomass produced requires the consumption of a certain amount of mineral N. The dependence on *Nm* in Eq. (6), along with differences in the value of the half-saturation constant k_i, explain how species compete and share the resource once it becomes limiting.

Under intensive mowing, fertilization can prevent mineral N stress, leading to values of *Nred* close to 1 for all species in summer (Fig. 4B). Nevertheless, mineral fertilization led to higher total biomass values, associated with a dominance of the competitive and productive PFTs A, B and R, (Fig. 3B and 3D). Alleviation of nutrient stress following each fertilization event (Fig. 4B) hence favored the growth of PFTs A, B and R (Fig. 4D). Higher *SLA* values provided an additional competitive advantage to PFTs B and R under high nutrient availability (Table 3).

Extensive management scenarios led to a dominance of PFTs C and D, as expected for grasslands established in poor environments and subject to low defoliation intensity (Fig. 3A and 3C). The highest diversity was reached under extensive grazing, corresponding to an intermediate level of disturbance. When comparing the two grazing regimes, the higher total biomass simulated in spring under intensive grazing (Fig. 3B) may be explained by the first fertilization event that restricted effects of the nutrient reducer. In this circumstance, the overall net growth rate in spring was higher than the daily forage

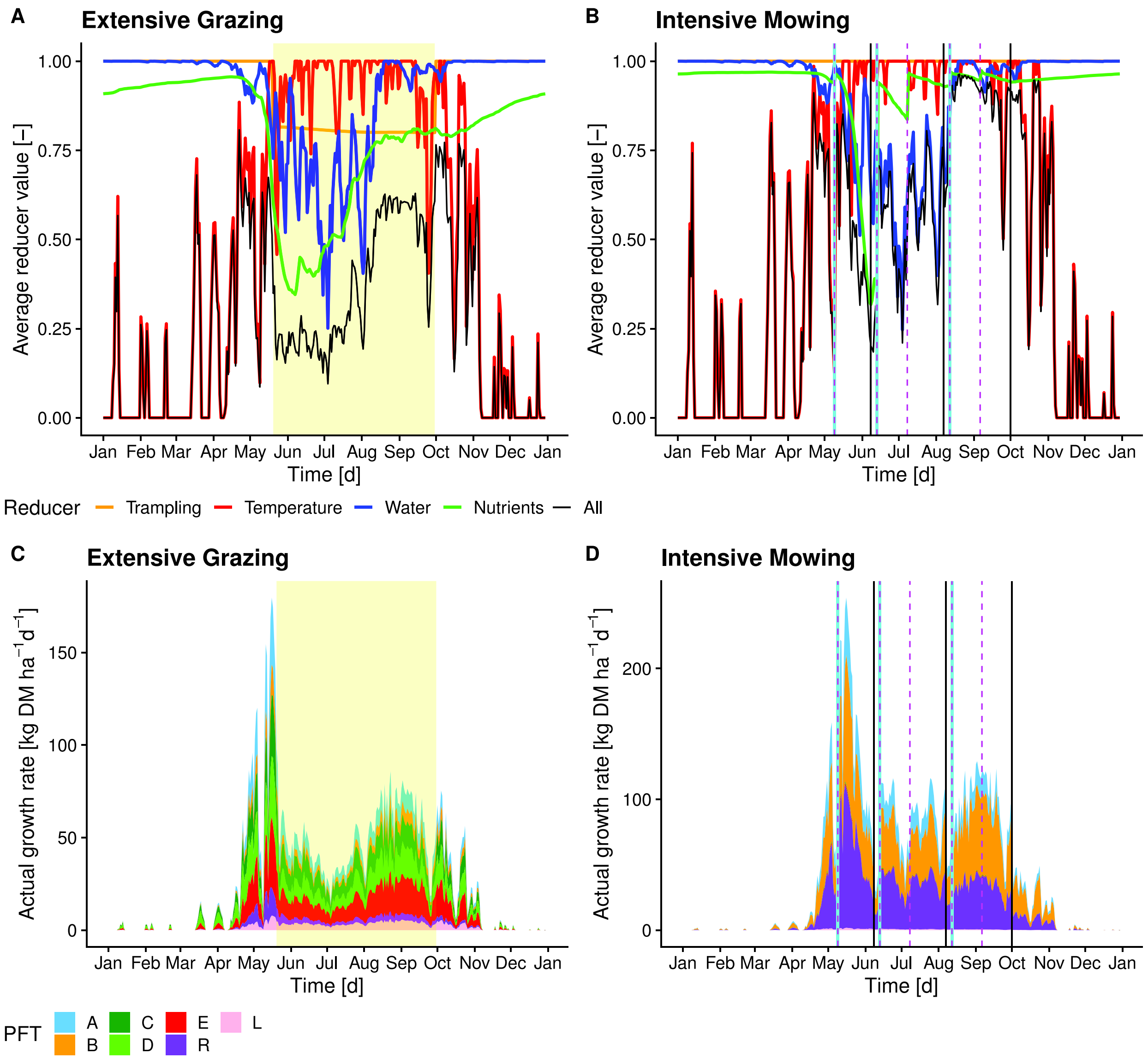


Fig. 4. Seasonal pattern of a 7-PFT community after 20-year simulations starting from the same initial conditions, under extensive grazing (left) and intensive mowing (right). (A) and (B) show the dynamics of four plant growth reducers: colored lines represent the daily weighted means of the trampling, temperature, water and nutrient reducers; the black thin curve corresponds to the product of the four reducers. A value of 1 for a reducer means that it has no effect on the biomass growth, whereas a value of 0 completely stops the growth. (C) and (D) represent the daily actual growth rate of each PFT. Yellow areas show the grazing period, black solid lines mowing events, magenta dashed lines mineral fertilization events and cyan solid lines organic fertilization events.

consumption by cattle, κ *SD* (Fig. 4C). The opposite process occurred in summer, with forage consumption higher than biomass production, leading at the end of the grazing period to a standing biomass twice as low for the intensive than the extensive scenario.

In the model simulations, time to convergence to a quasi-periodic state from a given initial community structure was primarily determined by the land-use type (grazing or mowing) and only secondarily by the intensity of the management practices (Fig. 5). For both grazing scenarios, the interannual rate of change of the diversity index decreased to below 0.1% within 20 simulation years. By contrast, under extensive and intensive mowing the rate of change of the diversity index increased to a maximum between 20 and 25 years before decreasing to less than 0.1% only after 40 or 50 years. The rate of change after 100 simulation years remained slightly higher for the intensive than for the extensive management scenarios, whatever the landuse type. This was due to the slow accumulation of organic nitrogen in the soil in case of intensive fertilization, which caused a slow but continuous adaptation of the plant community even after many decades.

In addition to these differences among management scenarios, the system dynamics was characterized by: (i) transient patterns with relatively high interannual rate of change (rate of change $>$ 0.5%) in the short term (5 years); (ii) a quasi-periodic state, with an interannual rate of change $<$ 0.1% in the medium term (50 years); and, (iii) an asymptotic cyclic state in the long term (more than 250 years, not shown). A thorough investigation of interannual changes in the system is provided in Appendix C (Online Supplementary Material).

The comparison of model outputs to expected species or functional compositions revealed, in spite of obvious divergences in the details, common overall features (Fig. 6). PFTs A, B and R showed higher relative biomass or cover in intensive than in extensive pastures and meadows, at the expense of C and D, which are stress-tolerant but less competitive in fertile and frequently disturbed grasslands. Extensive grazing was the best management practice to sustain the coexistence of all PFTs at long term. Among grass species, PFT A (e.g., *Lolium perenne*) was favored by intensive grazing, PFT B (e.g., *Poa trivialis*) by intensive mowing, and PFT C (e.g., *Trisetum flavescens*) by extensive mowing.

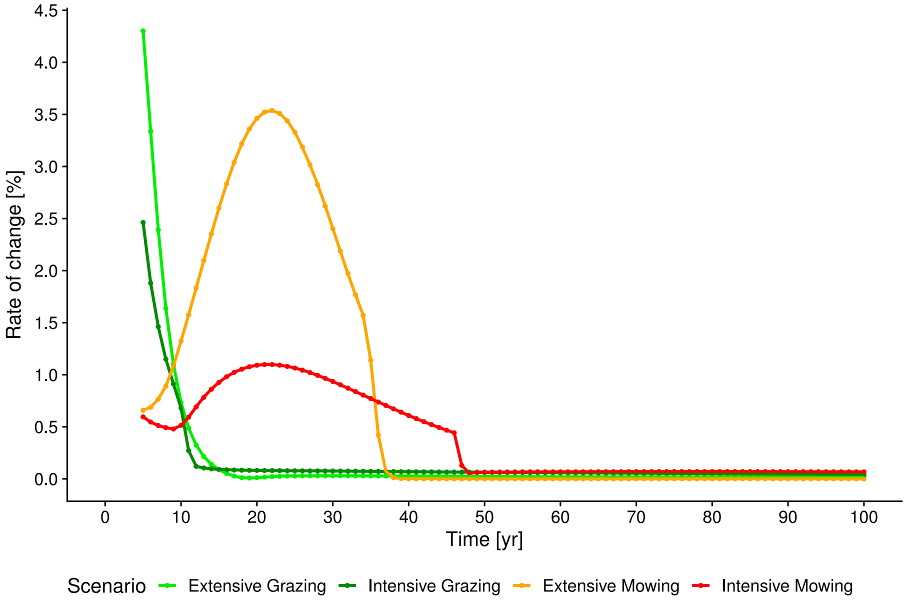


Fig. 5. Simulations of the interannual rate of change of the Simpson evenness E_B starting from an even initial species distribution under four management scenarios (described in Table 2). The interannual rate of change is the mean of year-to-year differences between the same Julian days in the vegetation period (from April 1 to September 30). Early values for years 1 to 4 are not plotted.

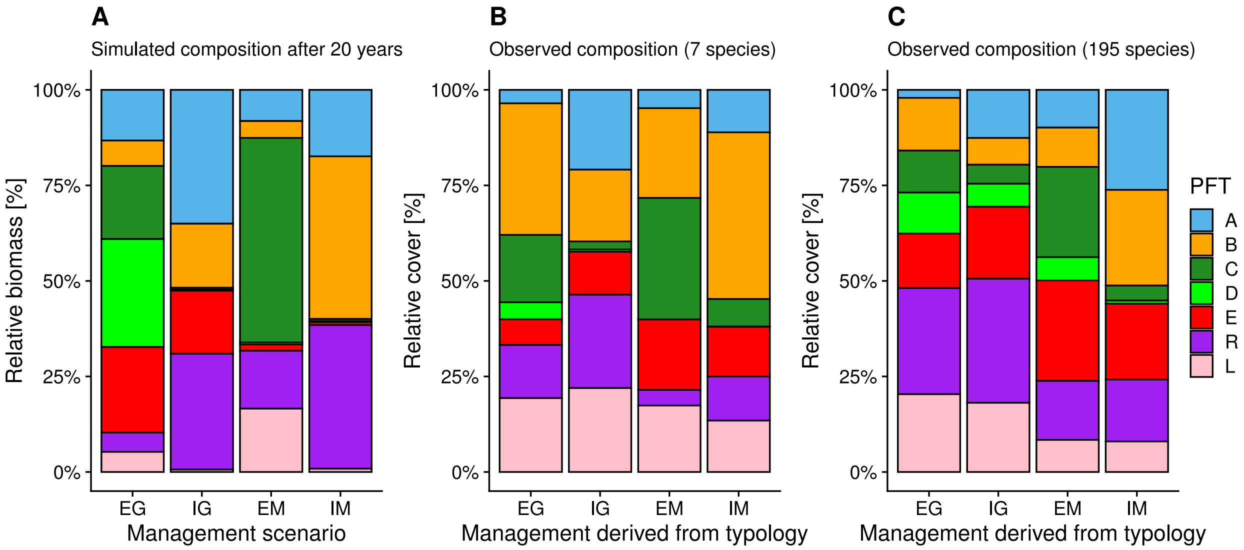


Fig. 6. Comparison of simulated and observed composition of grassland communities in response to four management schemes. Simulated relative biomass of each species (A) was extracted from model outputs after 20 years, starting from a same even initial distribution of PFTs. The observed relative cover of the same species (B) or of all species of each PFT (C) was averaged from 68 floristic relevés grouped in the four management types according to their phytosociological classification. EG: extensive grazing; IG: intensive grazing; EM: extensive mowing; IM: intensive mowing.

Differences between simulated and expected composition were due partly (1) to the uncertainty of the management conditions deduced from the typology of the observed vegetation, and (2) to the heterogeneity of response to management type and intensity among species of each PFT. Deviations were pronounced in particular in relation to the relative cover of legumes (*Trifolium pratense* in Fig. 6B or all species of PFT L in Fig. 6C) and erect forbs (*Ranunculus acris* in Fig. 6B or all species of PFT E in Fig. 6C). Grasses belonging to PFT D disappeared in simulated intensive grazing and extensive mowing scenarios (Fig. 6A) but not in intensive pastures and extensive hayfields (Fig. 6C). This was due to the choice of *Deschampsia cespitosa* as representative species for PFT D, this species being relatively rare in mesic managed grasslands but dominant in wet abandoned grasslands (Fig. 6B). Other species belonging to this PFT D were more frequently observed, such as *Cynosurus cristatus*, a diagnostic species of extensive pastures (Nicod et al., 2019). This could explain an under-representation of the PFT D in Fig. 6B.

Model sensitivity to initial conditions

After ten years of any grazing regime (extensive or intensive), all assemblages converged to a same composition (Fig. 7B) regardless of initial community structures (Fig. 7A). By contrast, under any mowing regime (extensive or intensive), the initial composition was still reflected in the plant community after 10 years of simulation (Fig. 7B). More specifically, for a sward initially dominated by one of the three PFTs A, B or R (assemblages S1, S2 and S6), which we identified as codominant in the long term for an intensive mowing management

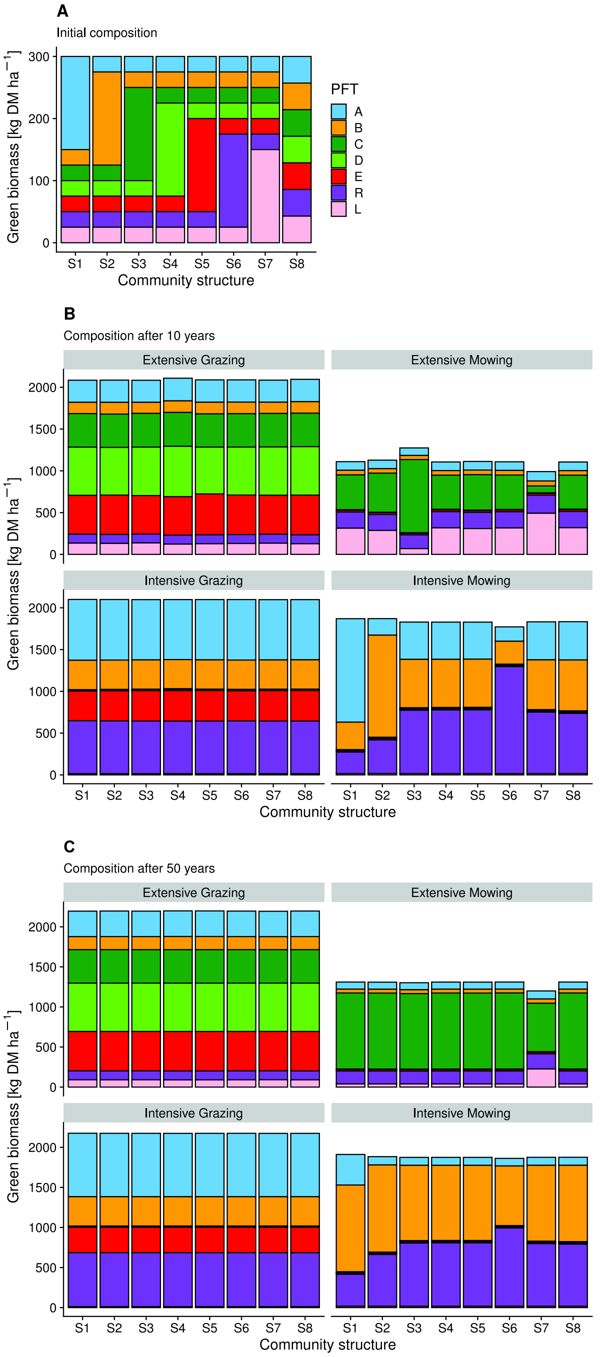


Fig. 7. Simulations of the model's sensitivity to (A) eight initial community structures (S1 to S8) after 10 years (B) and after 50 years (C). In (B) and (C), standing biomass values were averaged for each PFT over the vegetation period (between April 1 and September 30).

scenario (Fig. 3D), the state after 10 years was still transient. The latter was characterized by significantly higher values of the relative biomass of each of these PFTs than specified in the initial conditions (Fig. 7B). A similar behavior was observed for the extensive mowing scenario, where an initial dominance of the PFTs C or L (assemblages S3 and S7) led after 10 years to an over-representation of these PFTs (Fig. 7B). After 50 years of simulation, most differences vanished, except for assemblage S7 under extensive mowing (higher biomass of *Trifolium pratense*) and for S1 (higher biomass of *Lolium perenne*), S2 (larger dominance of *Poa trivialis*) and S6 (higher biomass of *Taraxacum officinale*) under intensive mowing (Fig. 7C). The total green biomass averaged over the vegetation period was only slightly affected by the initial composition, with comparably low values under mowing than under grazing after 50 years.

As all eight initial community assemblages tended to converge to a single final state (Fig. 7), we used Simpson evenness E_B as a synthetic descriptor of community diversity to compare convergence dynamics. The standard deviation of E_B values obtained for each management scenario was used to show when the impact of these initial structures on transient community diversity were vanishing (Fig. 8). As assemblages S1 to S7 described a same uneven PFT diversity pattern, they presented an equal initial evenness ($E_B = 0.49$). Assemblage S8 was built from a perfectly even PFT distribution, corresponding to a maximal initial evenness ($E_B = 1$).

Under both grazing management scenarios, plant community converged rapidly (~10 years) toward a same composition (vanishing standard deviation of the Simpson evenness). Eventually, this diversity index remained constant for extensive grazing and tended to slightly decrease for intensive grazing, likely due to the previously mentioned slow increase in soil organic nitrogen. In contrast, the simulation time required for convergence from various initial species distributions under mowing was considerably longer (> 50 years). Convergence was fully achieved after 65 years for the extensive mowing scenario but only at the end of the simulation period (~100 years) for the intensive mowing scenario despite low differences in E_B values among the eight community structures. Being as it is, this result nevertheless confirms that under constant climate forcing all assemblages explored for a given management converged to the same final seasonal pattern. From a theoretical perspective, this guarantees the independence of the equilibrium state from initial community composition.

In addition, after 100 years of simulation the Simpson evenness values obtained for extensive grazing were more than twice higher as those found with intensive mowing. Interestingly, this final diversity index was higher for extensive than for intensive grazing but was lower for extensive than for intensive mowing.

Discussion

With *DynaGraM* we introduce a relatively simple modeling solution to include the key notion of community dynamics in grassland models, by defining a generic structure in which interspecific interactions rely on resource competition and life strategies. Another approach has been proposed with the Co*SMo* module by Confalonieri (2014), Co*SMo* can coupled to any biogeochemical crop model, providing means for incorporating biodiversity in grassland models. Co*SMo* has been recently validated with experimental data (Movedi et al., 2019). However, the absence of state variables to describe the herbaceous species prevents the model to explicitly reproduce the competition within the assemblage, a point that we tackled with *DynaGraM.*

The results support our strategy of choosing a common formulation of growth for all species, and indicate that the formulation of a potential growth reduced by environmental limitations, introduced by Schapendonk et al. (1998), can provide realistic simulations. They also highlight the model capacity to predict a multi-species sward dynamics with a composition substantially explained by land use (Fig. 3), the latter having been identified as an important driver of biodiversity by Botkin et al. (2007) and Van Calster et al. (2008), addressing the research question 1. By comparing impacts of contrasted management scenarios, we highlight the importance of soil nutrient availability in determining the seasonal community pattern (Fig. 4). The latter showed a clear response to grassland management (type and intensity), which was eventually reflected in contrasting values of the nutrient reducer term *Nred*. This finding is in agreement with results obtained with the *PROGRASS* model (Lazzarotto et al., 2009).

We examined the realism of the simulated community dynamics in terms of taxonomic and functional composition. Due to the difficulty to access repeated measurements of green biomass for individual species in semi-natural permanent grasslands, we relied on floristic relevés from a

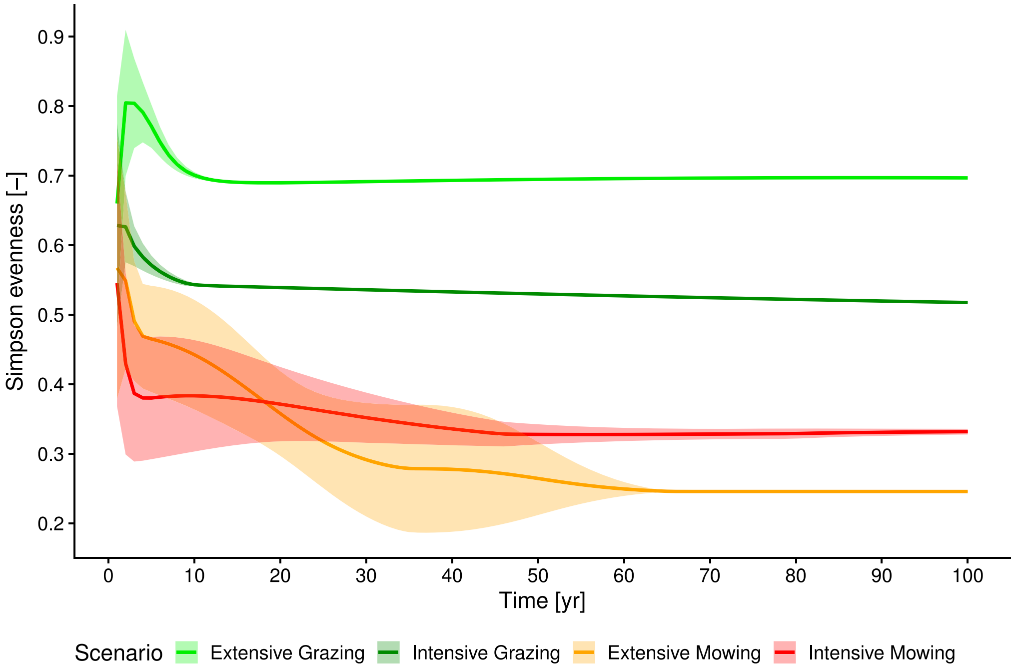


Fig. 8. Simulations of the Simpson evenness E_B dynamics (mean ± sd) obtained from the eight initial community structures (S1 to S8) described in Fig. 7A and computed for four management scenarios.

phytosociological database (Gillet, 2015) and a phytosociological classification (Ferrez et al., 2011) to define typical grassland compositions for management categories comparable to those defined in our four scenarios. It turns out that a fine tuning of some uncertain species-specific parameters was required to get simulation results close to observed vegetation structures. After that, *DynaGraM* was able to reflect management-induced differences in relative cover or PFTs (research question 2).

Regardless of the management scenario, the initial composition of the plant community had a small impact on the long-term functional composition (research question 3), confirming the key role of land-use type and intensity and complementing the answer to research question 1. However, simulations revealed that, in the short- to medium-term, the diversity of the plant community was far more sensitive to the initial composition under mowing than under grazing management (Fig. 7). Moreover, starting from an even initial species distribution, the interannual rate of change of Simpson evenness peaked between 20 and 25 years in case of extensive or intensive mowing, contrasting the relatively fast decline under the grazing scenarios (Fig. 5). The faster stabilization of functional composition and diversity predicted for grazing suggests that pastures could be more stable than hay meadows. On the other hand, management intensity had only a minor impact on the convergence speed. Our results suggest that response time of the simulated community dynamics is more affected by the management type than by its intensity, answering to our last research question 4.

The time required for the community to reach a quasi-periodic state ranged from 10 to more than 50 years, that is much longer than the twelve months reported for other process-based grassland models, e.g. Confalonieri (2014). Higher diversity levels considered in this study, implying a higher number of complex interactions among species, could explain the longer time required in *DynaGraM* to stabilize the composition. The ODE system at the core of *DynaGraM* is highly non-linear with many influences of the state variables on the dynamics of each other. As highlighted by Eq. (5), growth rate of one PFT i depends directly on its biomass B_i but also of the biomass of the n - 1 other PFTs, which impact (i) its potential growth according to the relative contribution of LAI_i to LAI_{tot}, and (ii) the available mineral N, which is necessarily consumed to produce any amount of biomass B_i, as shown in Eqs. (6) and (10). Whatever the initial composition, the model predicts that extensive grazing maximizes community diversity (highest values of the evenness index E_B) in the long term whereas extensive mowing results in the lowest evenness (Fig. 8). This is in accordance with the observation that grazing tends to be more beneficial to biodiversity than mowing (Tälle et al., 2016). This result also matches the expectations of the intermediate disturbance hypothesis (Dengler et al., 2014; Siehoff et al., 2011): under an extensive grazing management, the absence of fertilization (of mineral or organic origin) prevents competitive exclusion, while the low level of defoliation allows an even coexistence of all functional types in the plant community. Defoliations could thus explain the long-term coexistence of more species than expected from the availability of essential resources, contrary to the predictions of the tradeoff-based niche theory rooted on a simple resource-reduction competition model (Tilman, 1980).

As stressed in the model description (section 2), in terms of model formalism *DynaGraM* inherited many of the approaches implemented in *ModVege*. With respect to growth, a comparison of *DynaGraM* and *ModVege* at the community level is provided in Appendix D (Online Supplementary Material). Results showed the capacity of *DynaGraM* to simulate accurately the seasonal dynamics of herbage growth and standing biomass even after relaxing the assumptions of constant species composition and constant nutrient availability implicit in *ModVege* (Fig. D1). This implies that *DynaGraM* is able to capture key mechanisms of forage production defined by (Jouven et al., 2006a). *ModVege* has been validated with respect to field observations from Massif Central (France) (Jouven et al., 2006b), the Jura Mountains and the Swiss central plateau (Switzerland) (Calanca et al., 2016). In addition, a modified version of *ModVege*, in which nitrogen and soil water components were included, was validated with experimental data in UK (Ruelle et al., 2018). Therefore, the model comparison presented in Appendix D (Online Supplementary Material) can also be seen as an indirect verification of the performance of *DynaGraM*. Moreover, further support concerning the appropriateness of *DynaGraM* to simulate the dynamics of managed temperate grasslands comes from a comparison of model outputs and field measurements from the Oensingen field experiment (Ammann et al., 2020) conducted by Moulin (2018).

Conclusion

Compared to structurally more complex grassland models, we developed *DynaGraM* with few processes. This resulted in a parsimonious and flexible model that permits describing grassland vegetation by any number of species or species groups. The choice a minimalistic description of grassland dynamics allowed minimizing the computational requirements: only a few seconds of computational time are needed to run a 10-year simulation on a standard personal computer. However, the simple structure of *DynaGraM* has limitations. By considering only the green aboveground biomass and focusing on leaf functional traits, we neglected belowground biomass dynamics (roots and reserve organs) and associated processes, including processes involved in the nutrient cycling. The lack of allocation strategies from the equations describing plant growth implies that the simulated green biomass of some species can be under- or over-represented. Moreover, by assuming parameters LAM, α and $RUE_{\max}$ to be the same for all species, specificity of potential growth function for each species only stands on the SLA_i values.

Vegetative reproduction plays a major role in mountain permanent grasslands largely dominated by perennial species (Perronne et al., 2014). Yet, seed reproduction may be important, especially in case of severe disturbances (McIntyre et al., 1995). Omission of the processes governing seed bank dynamics in *DynaGraM* could be one of the reasons for the discrepancies between simulated and observed community composition.

Despite these limitations, we expect that *DynaGraM* can contribute to better understand the relationship between biodiversity and productivity and, in turn, the one between plant diversity and ecosystem services, matching one of the challenges for grassland models identified by van Oijen et al. (2018) and Kipling et al. (2016).

To date, three approaches have been followed to incorporate diversity in grassland models: (1) associate plant diversity to a constant or dynamic metric; (2) considering assemblages of multiple species or plant functional types without an explicit formulation of competition and selection processes, as in Co*SMo*; (3) representing multi-species community dynamics based on an explicit formulation of resource competition and tolerance to stress and disturbance. In this study, we followed the latter strategy. The formulation of *DynaGraM* complies with five out of six criteria given by Taubert et al. (2012) with respect to modeling of complex communities. The criteria met by *DynaGraM* refer to (1) species richness, (2) resource limitation (light, nutrients, water), (3) management practices (mowing, grazing, fertilizing), (4) model simplicity, and (5) interspecific competition for resources. To keep the model simple, we did not comply with the sixth criterion, which concerns the representation of belowground competition processes. For the same reason, we did not follow the individual-based approach proposed by Taubert et al. (2012), which includes for a high number of species above- and below-ground intra- and inter-specific competition.

By explicitly modeling the dynamics of a key nutrient (nitrogen) and by describing plant community diversity with dedicated state variables, *DynaGraM* provides answers to perspectives raised by Confalonieri (2014) and Jouven et al. (2006b). Recently, Ruelle et al. (2018) presented a very interesting refinement of *ModVege* with a component describing soil resource dynamics and integrating plant growth into a spatially explicit structure. The success of these last developments stresses the value of relatively simple models for advancing our understanding of how grasslands respond to management and environmental forcing.

Finally, the model described in this paper provides a promising basis for future work. Further developments of *DynaGraM* are already ongoing to address specific questions and practical problems, such as, for instance, interactions between fossorial vole outbreaks and vegetation dynamics in the context of climate change.

Credit author statement

This document will be send when the paper will be accepted for publication. Without any Credit of Author Statement, you may please consider that all authors have contributed in equal way for this paper.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research takes place in the Long-Term Ecological Research (LTER) site Jurassian Arc (http://zaaj.univ-fcomte.fr/?lang=en), which supports long-term interdisciplinary research on the dynamics of mountain social-ecological systems in the Jura Mountains. Our work will be integrated and will contribute to a wide range of activities co-ordinated by the National centre for Climate Services, NCCS (https://www.nccs.admin.ch), aiming at establishing a web-based knowledge hub that supports climate-smart decision-making.

Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.ecolmodel.2020.109345, including four Appendices:

Appendix A: Full description of the dynamic grassland model *DynaGraM*.

Appendix B: Model variables and parameters.

Appendix C: Convergence of the system to a quasi-periodic state.

Appendix D: Comparison of community-level *DynaGraM* and *ModVege* outputs.

The R code used to perform the numerical integration of the *DynaGraM* model and to generate the figures of this article, including supplementary figures in the Online Supplementary Material, are available online. The code is divided in several scripts, allowing the reader to reproduce all the exposed figures, and is available at: https://github.com/fgillet3/DynaGraM.

References

Al Haj Khaled, R, Duru, M, Theau, J.P., Plantureux, S., Cruz, P., 2005. Variation in leaf traits through seasons and N-availability levels and its consequences for ranking grassland species. J. Veg. Sci. 16, 391. https://doi.org/10.1658/1100-9233(2005)016 [0391:VILTTS]2.0.CO;2.

Ammann, C., Neftel, A., Jocher, M., Fuhrer, J., Leifeld, J., 2020. Effect of management and weather variations on the greenhouse gas budget of two grasslands during a 10-year experiment. Agric. Ecosyst. Env.. 292, 106814 https://doi.org/10.1016/j.agee.2019.106814.

Botkin, D.B., Saxe, H., Araújo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R., Faith, D.P., Ferrier, S., Guisan, A., Hansen, A.S., Hilbert, D.W., Loehle, C., Margules, C., New, M., Sobel, M.J., Stockwell, D.R.B., 2007. Forecasting the Effects of Global Warming on Biodiversity. Bioscience 57, 227–236. https://doi.org/10.1641/B570306.

Calanca, P., Deléglise, C., Martin, R., Carrère, P., Mosimann, E., 2016. Testing the ability of a simple grassland model to simulate the seasonal effects of drought on herbage growth. F. Crop. Res. 187, 12–23. https://doi.org/10.1016/j.fcr.2015.12.008.

Coffin, D.P., Lauenroth, W.K., 1990. A gap dynamics simulation model of succession in a semiarid grassland. Ecol. Modell. 49, 229–266. https://doi.org/10.1016/0304-3800(90)90029-G.

Confalonieri, R., 2014. CoSMo: a simple approach for reproducing plant community dynamics using a single instance of generic crop simulators. Ecol. Modell. 286, 1–10. https://doi.org/10.1016/j.ecolmodel.2014.04.019.

Cornes, R.C., van der Schrier, G., van den Besselaar, E.J.M., Jones, P.D., 2018. An Ensemble Version of the E-OBS Temperature and Precipitation Data Sets. J. Geophys. Res. Atmos. 123, 9391–9409. https://doi.org/10.1029/2017JD028200.

Cruz, P., Duru, M., Therond, O., Theau, J.P., Ducourtieux, C., 2002. Une nouvelle approche pour caractériser les prairies naturelles et leur valeur d'usage. Fourrages 172, 335–354. https://hal.archives-ouvertes.fr/hal-02683047.

Dengler, J., Janišová, M., Török, P., Wellstein, C., 2014. Biodiversity of Palaearctic grasslands: a synthesis. Agric. Ecosyst. Environ. 182, 1–14. https://doi.org/10.1016/j.agee.2013.12.015.

Duru, M., Adam, M., Cruz, P., Martin, G., Ansquer, P., Ducourtieux, C., Jouany, C., Theau, J.P., Viegas, J., 2009. Modelling above-ground herbage mass for a wide range of grassland community types. Ecol. Modell. 220, 209–225. https://doi.org/10.1016/j.ecolmodel.2008.09.015.

European Soil Bureau Network - European Commission, 2005. Soil Atlas of Europe, Office for Official Publications of the European Communities. ISBN 92-894-8120-X. https://esdac.jrc.ec.europa.eu/content/soil-atlas-europe.

European Soil Data Centre (ESDC) - European Commission, 2016. Maps of indicators of soil hydraulic properties for Europe, esdac.jrc.ec.europa.eu.

Ferrez, Y., Bailly, G., Beaufils, T., Collaud, R., Caillet, M., Fernez, T., Gillet, F., Guyonneau, J., Hennequin, C., Royer, J., Schmitt, A., Vadam, J., Vuillemenot, M., 2011. Synopsis des groupements végétaux de Franche-Comté. Nouv. Arch. la Flore Jurassienne du Nord. la Fr. N.S 1, 1–282. http://cbnfc-ori.org/sites/cbnfc-ori.org/files/synopsis-fc.-NAFJ-11.pdf.

Gaujour, E., Amiaud, B., Mignolet, C., Plantureux, S., 2012. Factors and processes affecting plant biodiversity in permanent grasslands. A review. Agron. Sustain. Dev. 32, 133–160. https://doi.org/10.1007/s13593-011-0015-3.

Gillet, F., 2015. Phytobase: a tool for the integrated synusial approach of vegetation classification at regional to national scale. In: Chytrý, M, Zeleny, D, Hettenbergerova, E (Eds.), Phytobase: a tool for the integrated synusial approach of vegetation classification at regional to national scale. Understanding Broad-Scale Vegetation Patterns 136. https://hal.archives-ouvertes.fr/hal-01211283.

Gillet, F., 2008. Modelling vegetation dynamics in heterogeneous pasture-woodland landscapes. Ecol. Modell. 217, 1–18. https://doi.org/10.1016/j.ecolmodel.2008.05.013.

Graux, A.-I., Klumpp, K., Ma, S., Martin, R., Bellocchi, G., 2016. Plant trait-based assessment of the Pasture Simulation model, in: Sauvage, S., Sánchez-Pérez, J., Rizzoli, A.. (Eds.), Proceedings of the 8th International Congress on Environmental Modelling and Software, July 10-14, Toulouse, France. Toulouse, France, pp. 518–525. https://hal.archives-ouvertes.fr/hal-01511982.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111, 1169–1194. http://www.jstor.org/stable/2460262.

Hill, M.O., 1973. Diversity and Evenness: a Unifying Notation and Its Consequences. Ecology 54, 427–432. https://doi.org/10.2307/1934352.

Jouven, M., Carrère, P., Baumont, R., 2006a. Model predicting dynamics of biomass, structure and digestibility of herbage in managed permanent pastures. 1. Model description. Grass Forage Sci 61, 112–124. https://doi.org/10.1111/j.1365-2494.2006.00515.x.

Jouven, M., Carrère, P., Baumont, R., 2006b. Model predicting dynamics of biomass, structure and digestibility of herbage in managed permanent pastures. 2. Model evaluation. Grass Forage Sci 61, 125–133. https://doi.org/10.1111/j.1365-2494.2006.00517.x.

Julve, P., 2019. Baseflor: index botanique, écologique et chorologique de la flore de France [WWW Document]. URL http://www.tela-botanica.org/projets/18/telechargement/24229.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., Bodegom, P.M.v., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernández-Mendez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R.V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B., Messier, J., Moles, A.T., Müller, S.C., Nadrowski, K., Naeem, S., Niinemets, U., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V.G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W.A., Patiño, S., Paula, S., Pausas, J.G., Peñuelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E., Wirth, C., 2011. TRY – a global database of plant traits. Glob. Chang. Biol. 17, 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x.

Kipling, R.P., Virkajärvi, P., Breitsameter, L., Curnel, Y., De Swaef, T., Gustavsson, A.M., Hennart, S., Höglind, M., Järvenranta, K., Minet, J., Nendel, C., Persson, T., Picon-Cochard, C., Rolinski, S., Sandars, D.L., Scollan, N.D., Sebek, L., Seddaiu, G., Topp, C. F.E., Twardy, S., Van Middelkoop, J., Wu, L., Bellocchi, G., 2016. Key challenges and priorities for modelling European grasslands under climate change. Sci. Total Environ. 566–567, 851–864. https://doi.org/10.1016/j.scitotenv.2016.05.144.

Kirschbaum, M.U.F., 2000. Will changes in soil organic carbon act as a positive or negative feedback on global warming? Biogeochemistry 48, 21–51. https://doi.org/10.1023/a:1006238902976.

Kühn, I., Durka, W., Klotz, S., 2004. BiolFlor - A new plant-trait database as a tool for plant invasion ecology. Divers. Distrib. 10, 363–365. https://doi.org/10.1111/j.1366-9516.2004.00106.x.

Lazzarotto, P., Calanca, P., Fuhrer, J., 2009. Dynamics of grass–clover mixtures—An analysis of the response to management with the PROductive GRASsland Simulator (PROGRASS). Ecol. Modell. 220, 703–724. https://doi.org/10.1016/j.ecolmodel.2008.11.023.

Lohmann, D., Guo, T., Tietjen, B., 2017. Zooming in on coarse plant functional types—Simulated response of savanna vegetation composition in response to aridity and grazing. Theor. Ecol 1–13. https://doi.org/10.1007/s12080-017-0356-x.

Mauchamp, L., Mouly, A., Badot, P.-.M., Gillet, F., 2014. Impact of management type and intensity on multiple facets of grassland biodiversity in the French Jura Mountains. Appl. Veg. Sci. 17, 645–657. https://doi.org/10.1111/avsc.12116.

May, F., Grimm, V., Jeltsch, F., 2009. Reversed effects of grazing on plant diversity: the role of below-ground competition and size symmetry. Oikos 118, 1830–1843. https://doi.org/10.1111/j.1600-0706.2009.17724.x.

McCall, D.G., Bishop-Hurley, G.J., 2003. A pasture growth model for use in a whole-farm dairy production model. Agric. Syst. 76, 1183–1205. https://doi.org/10.1016/S0308-521X(02)00104-X.

McIntyre, S., Lavorel, S., Tremont, R.M., 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. J. Ecol. 83, 31. https://doi.org/10.2307/2261148.

Moulin, T., 2018. Modélisation mathématique de la dynamique des communautés herbacées des écosystèmes prairiaux. https://hal.archives-ouvertes.fr/tel-02096315.

Moulin, T., Perasso, A., Gillet, F., 2018. Modelling vegetation dynamics in managed grasslands: responses to drivers depend on species richness. Ecol. Modell 374. https://doi.org/10.1016/j.ecolmodel.2018.02.013.

Movedi, E., Bellocchi, G., Argenti, G., Paleari, L., Vesely, F., Staglianò, N., Dibari, C., Confalonieri, R., 2019. Development of generic crop models for simulation of multi-species plant communities in mown grasslands. Ecol. Modell. 401, 111–128. https://doi.org/10.1016/j.ecolmodel.2019.03.001.

Myers, N., Mittermeier, R., Mittermeier, C., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities 403, 853–858. 10.1038/35002501.

Nicod, C., Leys, B., Ferrez, Y., Manneville, V., Mouly, A., Greffier, B., Hennequin, C., Bouton, Y., Prévost-bouré, N.C., 2019. Towards the assessment of biodiversity and management practices in mountain pastures using diagnostic species ? Ecol. Indic 107, 105584. https://doi.org/10.1016/j.ecolind.2019.105584.

Paul, K.I., Polglase, P.J., O'Connell, A.M., Carlyle, J.C., Smethurst, P.J., Khanna, P.K., 2003. Defining the relation between soil water content and net nitrogen mineralization. Eur. J. Soil Sci. 54, 39–47. https://doi.org/10.1046/j.1365-2389.2003.00502.x.

Peringer, A., Siehoff, S., Chételat, J., Spiegelberger, T., Buttler, A., Gillet, F., 2013. Past and future landscape dynamics in pasture-woodlands of the Swiss Jura Mountains under climate change. Ecol. Soc 18. https://doi.org/10.5751/ES-05600-180311 art11.

Perronne, R., Mauchamp, L., Badot, P.-.M., Gillet, F., 2014. Contrasted taxonomic, phylogenetic and functional diversity patterns in semi-natural permanent grasslands along an altitudinal gradient. Plant Ecol. Evol. 147, 165–175. https://doi.org/10.5091/plecevo.2014.885.

Pierce, S., Negreiros, D., Cerabolini, B.E.L., Kattge, J., Díaz, S., Kleyer, M., Shipley, B., Wright, S.J., Soudzilovskaia, N.A., Onipchenko, V.G., van Bodegom, P.M., Frenette-Dussault, C., Weiher, E., Pinho, B.X., Cornelissen, J.H.C., Grime, J.P., Thompson, K., Hunt, R., Wilson, P.J., Buffa, G., Nyakunga, O.C., Reich, P.B., Caccianiga, M., Mangili, F., Ceriani, R.M., Luzzaro, A., Brusa, G., Siefert, A., Barbosa, N.P.U., Chapin, F.S., Cornwell, W.K., Fang, J., Fernandes, G.W., Garnier, E., Le Stradic, S., Peñuelas, J., Melo, F.P.L., Slaviero, A., Tabarelli, M., Tampucci, D., 2017. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. Funct. Ecol. 31, 444–457. https://doi.org/10.1111/1365-2435.12722.

R. Core Team, 2020. R: a language and environment for statistical computing. http://www.r-project.org/index.html.

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

Rolinski, S., Müller, C., Heinke, J., Weindl, I., Biewald, A., Leon Bodirsky, B, Bondeau, A, Boons-Prins, E.R., Bouwman, A.F., Leffelaar, P.A., Roller, J.A.T., Schaphoff, S., Thonicke, K., 2018. Modeling vegetation and carbon dynamics of managed grasslands at the global scale with LPJmL 3.6. Geosci. Model Dev. 11, 429–451. https://doi.org/10.5194/gmd-11-429-2018.

Rosenthal, G., 2010. Secondary succession in a fallow central European wet grassland. Flora - Morphol. Distrib. Funct. Ecol. Plants 205, 153–160. https://doi.org/10.1016/j.flora.2009.02.003.

Ruelle, E., Hennessy, D., Delaby, L., 2018. Development of the Moorepark St Gilles grass growth model (MoSt GG model): a predictive model for grass growth for pasture based systems. Eur. J. Agron. 99, 80–91. https://doi.org/10.1016/j.eja.2018.06.010.

Ryser, P., Urbas, P., 2000. Ecological significance of leaf life span among Central European grass species. Oikos 91, 41–50. https://doi.org/10.1034/j.1600-0706.2000.910104.x.

Schapendonk, A.H C M, Stol, W., Van Kraalingen, D.W.G., Bouman, B.A.M., 1998. LINGRA, a sink/source model to simulate grassland productivity in Europe. Eur. J. Agron. 9, 87–100. https://doi.org/10.1016/S1161-0301(98)00027-6.

Schwinning, S., Parsons, A.J., 1999. The stability of grazing systems revisited: spatial models and the role of heterogeneity. Funct. Ecol. 13, 737–747. https://doi.org/10.1046/j.1365-2435.1999.00382.x.

Siehoff, S., Lennartz, G., Heilburg, I.C., Roß-Nickoll, M., Ratte, H.T., Preuss, T.G., 2011. Process-based modeling of grassland dynamics built on ecological indicator values for land use. Ecol. Modell. 222, 3854–3868. https://doi.org/10.1016/j.ecolmodel.2011.10.003.

Soetaert, K., Petzoldt, T., Setzer, R.W., 2010. Package deSolve : solving Initial Value Differential Equations in R. J. Stat. Softw. 33, 1–25. https://doi.org/10.18637/jss.v033.i09.

Soussana, J.-.F., Maire, V., Gross, N., Bachelet, B., Pagès, L., Martin, R., Hill, D., Wirth, C., 2012. Gemini: a grassland model simulating the role of plant traits for community dynamics and ecosystem functioning. Parameterization and evaluation. Ecol. Modell. 231, 134–145. https://doi.org/10.1016/j.ecolmodel.2012.02.002.

Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L., Milberg, P., 2016. Grazing vs. mowing: a meta-analysis of biodiversity benefits for grassland management. Agric. Ecosyst. Environ 222, 200–212. https://doi.org/10.1016/j.agee.2016.02.008.

Taubert, F., Frank, K., Huth, A., 2012. A review of grassland models in the biofuel context. Ecol. Modell. 245, 84–93. https://doi.org/10.1016/j.ecolmodel.2012.04.007.

Thornley, J.H.M., 1998. Grassland dynamics: an ecosystem simulation model. CAB International.

Thornley, J.H.M., Johnson, I.R., 1990. Plant and Crop Modelling: A Mathematical Approach to Plant and Crop Physiology. Oxford, Clarendon.

Tilman, D., 1980. Resources: a graphical-mechanistic approach to competition and predation. Am. Nat. 116, 362–393. https://doi.org/10.1086/283633.

Tilman, D., 1982. Resource Competition and Community Structure. Monographs in Population Biology (17), ISBN: 9780691083025.

Van Calster, H., Vandenberghe, R., Ruysen, M., Verheyen, K., Hermy, M., Decocq, G., 2008. Unexpectedly high 20th century floristic losses in a rural landscape in northern France. J. Ecol. 96, 927–936. https://doi.org/10.1111/j.1365-2745.2008.01412.x.

van Oijen, M., Barcza, Z., Confalonieri, R., Korhonen, P., Kröel-Dulay, G., Lellei-Kovács, E., Louarn, G., Louault, F., Martin, R., Moulin, T., Movedi, E., Picon-Cochard, C., Rolinski, S., Viovy, N., Wirth, S.B., Bellocchi, G., 2020. Incorporating biodiversity into biogeochemistry models to improve prediction of ecosystem services in temperate grasslands: review and roadmap. Agronomy 10, 1–24. https://doi.org/10.3390/agronomy10020259.

van Oijen, M., Bellocchi, G., Höglind, M., 2018. Effects of climate change on grassland biodiversity and productivity: the need for a diversity of models. Agronomy 8, 14. https://doi.org/10.3390/agronomy8020014.

Weiss, L., Pfestorf, H., May, F., Körner, K., Boch, S., Fischer, M., Müller, J., Prati, D., Socher, S.A., Jeltsch, F., 2014. Grazing response patterns indicate isolation of semi-natural European grasslands. Oikos 123, 599–612. https://doi.org/10.1111/j.1600-0706.2013.00957.x.

Wilson, J.B., Peet, R.K., Dengler, J., Pärtel, M., 2012. Plant species richness: the world records. J. Veg. Sci. 23, 796–802. https://doi.org/10.1111/j.1654-1103.2012.01400.x.