Modelling vegetation dynamics in managed grasslands: Responses to drivers depend on species richness

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

[a] *Université Bourgogne Franche-Comté, UMR CNRS 6249 Chrono-environnement, Besançon, France*
[b] *Ecole Polytechnique Fédérale de Lausanne, Ecological Systems Laboratory, Lausanne, Switzerland*

ABSTRACT

In mathematical grassland models, plant communities may be represented by a various number of state variables, describing biomass compartments of some dominant species or plant functional types. The size of the initial species pool could have consequences on the outcome of the simulated ecosystem dynamics in terms of grassland productivity, diversity, and stability. This choice could also influence the model sensitivity to forcing parameters.

To address these issues, we developed a dynamic grassland model, DynaGraM, designed to simulate seasonal changes in both aboveground biomass production and species composition of managed permanent grasslands under various soil, climate and management conditions. We compared simulation results from alternative instances of DynaGraM that only differ by the identity and number of state variables describing the green biomass, here plant species. We assessed the sensitivity of each instance of the model to key forcing parameters for climate, soil fertility, and defoliation disturbances, using univariate and multivariate regression trees and dynamic trees.

Results of 10-year simulations under various climate, fertility and defoliation conditions showed that the final total biomass was tending to increase with the size of the species pool, while species evenness and the proportion of surviving species was tending to decrease. We found a positive correlation between the species survival ratio and the defoliation intensity, and this correlation increased with the initial species richness. The sensitivity to forcing parameters of community structure and species evenness differed markedly among alternative models, showing a progressive shift from high importance of soil fertility (fertilisation level, mineralization rate) to high importance of defoliation (mowing frequency, grazing intensity) as the size of the species pool increased. By contrast, the key drivers of total biomass production were independent of species richness and only linked to resource supply (nitrogen and water).

These results highlight the need to take into account the role of species diversity to explain the behaviour of grassland models.

1. Introduction

Semi-natural permanent grasslands present important ecological, cultural and economic values, and support many ecosystem services due to their biodiversity (Gaujour et al., 2012; Mauchamp et al., 2012). Some temperate European grasslands, managed for a long time with low-intensity grazing or mowing, are the plant communities with the world records for species richness at fine scale (Wilson et al., 2012).

Various diachronic studies have revealed recent changes in the structure and composition of grassland plant communities in Europe (Gillet et al., 2016; Homburger and Hofer, 2012; Mitchell et al., 2017; Wesche et al., 2012). The causes of these changes are related to climatic (warming, extreme events) and anthropogenic (technical and socio-economic changes in management) constraints and disturbances. Land-use intensification or abandonment may lead to a severe reduction of species diversity with adverse impacts on ecosystem services. Fertilisation and defoliation regimes have been identified as the main drivers of plant species richness in productive grasslands (Gaujour et al., 2012; Mauchamp et al., 2016, 2014).

According to field observations, local species richness of temperate natural and semi-natural grasslands shows unimodal relationship with productivity, with a maximum biodiversity for intermediate productivity (Dengler et al., 2014). This questions how grassland ecosystem stability and productivity are influenced by vascular plant

species richness. Field observations and experiments on semi-natural grasslands suggest that the most productive communities are the least diverse, but also the least resilient. By contrast, field experiments based on artificial species mixtures showed a positive correlation between species richness and productivity (Hector et al., 1999; Reich et al., 2012). A recent meta-analysis of experimental studies on such artificial species assemblages revealed that species richness generally improves resistance of grassland productivity to climatic extreme events, but not its recovery rate (Isbell et al., 2015). Increasing species richness in such artificial communities stabilizes whole community biomass but destabilizes the dynamics of constituent populations (de Mazancourt et al., 2013; Gross et al., 2013).

Since experimental studies have not been able to provide a general explanation to the relationships observed between grassland diversity and their productivity and stability, dynamical models are powerful tools for testing predictions of ecological theories. A lot of mathematical models of grassland dynamics based on explicit ecological processes have been developed. Some non-exhaustive reviews of grassland models are available (Snow et al., 2014; Taubert et al., 2012; Wiegand et al., 2008). Grassland models published so far have targeted 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., 2006; Riedo et al., 1998). In a review of thirteen grassland models (Taubert et al., 2012), only two considered more than three different species or plant functional types: GraS, a succession compartment model (Siehoff et al., 2011) and STEPPE, a gap model of semiarid grasslands (Coffin and Lauenroth, 1990); however, none of them simulate biomass. So far, 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. Indeed, most of current grassland models focus on the impact of agricultural practices on forage production with many ecophysiological and biophysical details inherited from crop models but do not consider temporal changes in taxonomic and functional composition. An attempt (Lauenroth et al., 1993) to couple individual-based gap models describing changes in species composition (STEPPE) and ecosystem models describing nutrient cycling and biomass production (CENTURY) or water balance (SOILWAT) led to the development of the ECOTONE model, able to simulate transitions between biomes (Peters, 2002). Several biophysical pasture models can be used to simulate growth of composite pasture types of several species under various management strategies, such as CLASS-PGM, a generic pasture growth model (Vaze et al., 2009), or DairyMod and the SGS Pasture Model (Johnson, 2016), but these models are rather complex, limited to five "species" and not optimized for mowing management. Gemini (Soussana et al., 2012) is another very detailed biophysical model of grassland ecosystems that explicitly simulates competition among any number of clonal populations for two key resources (light and nitrogen) along vertical canopy and soil profiles; plant functional traits are used to explain the response of aboveground net primary production and of plant community structure to various soil, climate and management conditions, including grazing, cutting and fertilization. Some recent mathematical models are based on stochastic differential equations adapted from the Lotka-Volterra equations to simulate changes in aboveground biomass of plant species mixtures and to explain community dynamics by environmental and demographic stochasticity (de Mazancourt et al., 2013; Lohier et al., 2016).

Taking into account the whole species diversity of grasslands in a mathematical model is quite impossible, given the large number of vascular plant species that may potentially co-occur in such ecosystems. For example, the regional species pool in permanent grasslands of the French Jura Mountains exceeds 1000 and the average number of species per local grassland is about 30, ranging from 3 to 92 (Mauchamp et al., 2012). To reduce the number of state variables describing the

plant community in the model, a common solution is to consider plant functional types (PFTs) instead of individual species. PFTs can be viewed as theoretical "average species" combining parameters from a set of more or less functionally related species, such as legumes, perennial grasses or erect forbs. Typically, a PFT is a group of species with similar functional traits explaining their response to constraints and disturbances, such as management practices, and their effect on ecosystem function, such as forage production (Cruz et al., 2010, 2002; Duru et al., 2009; Graux et al., 2016). The GraS model (Siehoff et al., 2011) simulates the succession of both dominant species and PFTs described by their cover dynamics, contrary to most agronomic grassland models, such as ModVege (Calanca et al., 2016; Jouven et al., 2006), which simulate seasonal changes in one or several biomass compartments, assuming a constant assemblage of species or PFTs. Individual-based, spatially explicit community grassland models such as IBC-grass (Weiss et al., 2014) are able to simulate metacommunities of many PFTs over hundred years, but at the price of a simplified representation of edaphic and climatic drivers. By contrast, (Confalonieri, 2014) suggested a model of plant community dynamics based on a single instance of a generic crop simulator, state variables being only simulated for the whole community. EcoHyD (Lohmann et al., 2017) is an ecohydrological model of semi-arid grasslands and savannas, able to simulate cover dynamics of a large number of PFTs, but focuses on hydrological processes and does not implement nutrient stress.

In this paper, we address a general issue that could be raised in any modelling study: the appropriate choice of the level of detail of the model, i.e. the number of state variables and associated parameters to be taken into account for describing the dynamical system, here the plant community. Although this choice is usually motivated by model objectives (e.g., with a focus on forage production or on biodiversity conservation) and by technical constraints (e.g., data availability, model performance), what are its consequences on the simulated dynamics of the virtual community in terms of grassland productivity, diversity, and stability? This question is especially relevant for permanent grasslands used for grazing or mowing and subject to seasonal changes in species composition and forage production, because of the high number of species coexisting in such ecosystems.

Thus, the first aim of the present study is to examine the consequences of increasing the number of state variables (i.e. the size of the local species pool) describing plant community composition on model behaviour, regarding grassland productivity, diversity and stability. Specifically, we formulated four hypotheses: (H1) the inclusion of more species in the model increases its *productivity*, hence the final total biomass after ten-year simulations with various values of control parameters; (H2) the inclusion of more species in the model decreases its final species evenness, the component of community *diversity* measuring equitability in biomass and resource partitioning among species; (H3) the inclusion of more species in the model decreases its *stability*, hence the final proportion of surviving species (species survival ratio); (H4) species survival ratio increases with intensity and frequency of disturbances, and this positive correlation increases with the size of the species pool.

The second purpose is to assess the consequences of increasing the size of the species pool on the model sensitivity to key control parameters regarding climate, soil fertility and defoliation. We hypothesized that (H5) the hierarchy of influential parameters depends on species identity but not on the size of the species pool.

For these purposes, we need a simple mechanistic model in which the main ecological processes are implemented (seasonal mechanisms of plant growth, soil resource competition, response to climatic constraints and agricultural management) and in which we can vary the number and the identity of species in the initial plant community. As no such model was available, we developed DynaGraM, a simple and flexible dynamical model based on ordinary differential equations (ODEs), able to simulate various combinations of climate, soil and management conditions. The aim of this paper is not to present this