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Development of a functional approach in a grassland vegetation sub-model

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ABSTRACT. To improve our understanding of grassland dynamics under different levels of utilization, a functional description of the vegetation was introduced in a deterministic model. The selected traits and their parameterization were based on the results of a long-term experiment in which temperate grasslands were managed for 12 years with three levels of herbage use: high, medium and low. The integration of functional attributes of the community species within the model's parameters can be seen as a new step in the study of the grassland ecosystem. With this tool, it is possible to decrease the number of interconnections in the system and consequently decrease the complexity. In this work a, functional definition of three different grassland communities was introduced into the sub-vegetation model. This was done by interchanging the model's parameters with the functional attributes of the communities. From the conceptual point of view, the sub-vegetation model works adequately and it seems suitable to simulate the dynamic of grassland vegetation described by functional traits. The model fits experimental data well for high levels of utilization, but was poorly adjusted at medium and low levels of herbage use. We believe this is due to a better simulation of green biomass fluxes than for senescence or reproductive fluxes. Some possible improvements of the model are discussed.

Key words: extensification, grassland vegetation, models, simulation, functional attributes, vegetation communities.

RESUMO. Desenvolvimento de uma abordagem funcional em um submodelo vegetal campestre. Para aumentar a nossa compreensão sobre a dinâmica da vegetação campestre em diferentes níveis de utilização, foi introduzido num modelo determinístico uma descrição funcional da vegetação. Os atributos funcionais escolhidos e suas parametrizações foram baseados em resultados de experimento de longo prazo, no qual pastagens temperadas foram manejadas por 12 anos com três níveis de utilização: alto, médio e baixo. A integração de atributos funcionais da comunidade vegetal nos parâmetros do modelo pode ser vista como um novo passo no estudo de ecossistemas pastoris. Com essa ferramenta, é possível reduzir o número de interconexões no sistema e consequentemente diminuir sua complexidade. Neste trabalho uma definição funcional de três diferentes comunidades vegetais campestres foi introduzida num submodelo vegetal. Isso foi feito pelo intercambio de parâmetros do modelo com atributos funcionais da comunidade. Do ponto de vista conceitual, o submodelo vegetal funciona bem e parece adequado para simular a dinâmica da vegetação campestre descrita por atributos funcionais. Os resultados do modelo mostram bom ajuste destes aos dados experimentais para o alto nível de utilização mas não para o médio ou baixo nível de utilização de forragem. Nós acreditamos que isto se deve a melhor simulação dos fluxos de biomassa verde do que da senescência ou dos fluxos reprodutivos. Algumas possibilidades de melhorias do modelo são discutidas.

Palavras-chave: extensificação, vegetação campestre, modelos, simulação, atributos funcionais, comunidades vegetais.

Introduction

To understand the relationship between the vegetation response to the intensity and frequency of grazing herbivores impact in relation to environmental conditions, simulation models have been developed. These are to provide a simplified framework to better understand grazing systems and to be able to simulate their complexity (Marriott and Carrère, 1998). The Institut National de la Recherche Agronomique (INRA) has developed a simulation model with the aim of building a spatial multi-agent simulator capable of conducting a

realistic representation of the management of permanent grassland vegetation under grazing regimes. It was conceived as a research tool to explore animal behavior in large heterogeneous spaces. Broad functional responses based on well-demonstrated biological laws and long developed theoretical frameworks were to be used to reach the target without creating an overly complicated model (Pérochon *et al.*, 2001; Baumont *et al.*, 2002; Carrère *et al.*, 2002). The role of such a model could be to explore a large number of hypotheses in the spatio-temporal heterogeneity in plant-animal interactions (Marriott and Carrère, 1998; Laca, 2000).

Recent researches in natural and semi-natural European grassland vegetation are focusing on the reduction of the intensity of grassland ecosystem utilization (Louault *et al.*, 2005). The main concerns of these works have been with those areas that have recently changed to a less intensive agricultural management. Some works concern low fertilizer application, others are pointing to the impact on decreasing the stocking rate. The principal question is to identify and quantify the process that drives plant communities in a system where the relationship between vegetation composition and grazing herbivores is dynamic in time and space (Taiton *et al.*, 1996). Grazing herbivores actions affect the structure and composition of the vegetation by changing the vertical and horizontal structure and quality of the vegetation, which in turn will affect the animal choices (Marriott and Carrère, 1998).

A grazed plant community consists of many populations coexisting in a meta-equilibrium between abiotic and biotic conditions (Bullock, 1996). It underlies dynamic processes where the number of individual plants in a population varies in time and space because some new individuals thrive and others die as a consequence of environmental variables or animal actions (Taiton *et al.*, 1996). The community composition depends on how these factors affect the performances and competitive abilities of each individual within the population. Many species can coexist in nature because they have some attributes that interact with the environment to affect the demographic performances and competitive abilities. Not all mechanisms which regulate the plant abundance in a grazed plant community ecosystem are understood (Bullock, 1996) and a full comprehension will expend a lot of effort, time and money: a complete understanding of population establishment and competition in a community would require a detailed study of each species, the interaction within

and between them, the environmental condition involved and the patterns of distribution in time and space of the species (Gordon, 2000).

One possibility to solve the problem has been the use of non-phylogenetic classification of plants responding in similar ways to a given factor. This kind of approach serves to complement the species-based classification with a more functional approach, facilitating the association of some plants characteristics with particular response to grazing, without the need to identify all the species (Landsberg *et al.*, 1999). Also it can provide a picture that could be applied to different regional floras. Several studies have attempted to identify functional groups of species with similar ecological roles. These groups are called functional types and can be defined as groupings of plants with similar functions and sharing common biologic characteristics (Díaz *et al.,* 2001), i.e. groups of populations in which the responses may not necessarily be plastic, but rather as substitutions of certain populations by other populations with different traits, more adapted to the new conditions or with the same functional effects in the ecosystem. Recent studies are trying to identify these linkages between the relation of the species contribution to the ecosystem process and the species response to changes in environment (Lavorel and Garnier, 2002). It means a new grouping of plants that will compose the vegetation community defining a mosaic in the landscape. The functional classification could be seen as a new scale of description of vegetation, used to simplify and improve the perception of the process by using the plants themselves as indicators (Pillar and Orlóci, 1993).

The vegetation patterns in grassland plots in an experimental area after 12 years of contrasting management was described by Louault *et al.* (2005), indicating marked differences in species composition among treatments. Three major plant functional types of response in relation to the level of herbage use (cutting and grazing) characterized the differences when the treatments were described by traits aggregated at the community scale. Two types co-dominated the high use plots and one type described the other treatments. In the high use treatment, one type is competitive (fast-growing), grazing tolerant and avoiding moderate grazing, while the other was assumed by the authors to be conservative and only avoiding moderate grazing. For the medium and low use treatments, the characteristic type is competitive to light but with little grazing avoidance and no grazing tolerance.

The aim of this work is to integrate the functional description at the community level in a

determinist model that simulates vegetation dynamic. A functional approach assumes that the plant species that develop in response to a given factor (e.g. herbage use efficiency, nutrient availability) display some converging traits, which in turn condition their performance in the community. The basic hypothesis is that the model can simulate different patterns of grassland vegetation response described by a functional approach. The work focuses particularly on the simulation of perennial grassland vegetation communities managed under three different levels of exploitation, described in Louault *et al*. (2005). We discuss how to integrate the traits description of each community in the model setup and its implications. We define the parameters in the grazing-vegetation model that can be used as links between the functional community description (*faciès*) and the vegetation community described by traits and determine the level of agreement of the simulation outputs with the experimental data when using a functional approach.

Model description

The prototype has been implemented with a Linux system and GNU C++. The vegetation sub-model was built using object-oriented analysis. At field scale, the spatial distribution of the vegetation is managed by an input file, which gives the position of different vegetation types (i.e. plant communities formed by a given mix of species) within the plot. Each vegetation type is associated with a cell. A simulation is driven by broad parameters determining the plot size, the simulation duration and climatic conditions. More specific parameters define a *faciès*. The climatic conditions are given by an environmental input file that allows the model to manage time using a thermal calendar based on the sum of average temperatures, which turns on or off the growth, flowering and senescence functions. These processes follow continuous functions, which are discrete in the sub-model using a daily iteration (Carrère *et al.*, 2002). The simulator was conceived as a spatial multi-agent model to be able to represent the different aspects of animal behavior and the heterogeneity of the vegetation. The simulator is composed of three sub-models: vegetation, animal, and spatial (herd displacement) (Baumont, 2002).

Vegetation Sub-model

According to Pérochon *et al.* (2001) and Carrère *et al.* (2002), the vegetation sub-model simulates dynamics of biomass flows in the vegetation in relation with the defoliation performed by animals. The grassland plot is divided into elementary hexagonal cells of 0.1 m², which correspond to the size of a feeding station for sheep. The defoliation process is considered homogeneous within the cell. The size of a cell is a trade-off between biological and modeling constraints, i.e. it has to be small enough to keep the homogeneity, but not too small to allow the modeling of a large area (e.g. up to ten hectares) avoiding an excessive number of cells. The use of a hexagonal cell facilitates the modeling of animal movements because the center of each cell is at equal distance of the center of the six adjacent cells.

Inside the cell, the vegetation is described by the following compartments: green leaves and shoots (GV), dry leaves and shoots (DV), green stems and ears (GR) and dry stems and ears (DR). Each of the four compartments is defined by state variables (biomass and height), two qualitative variables (fiber content and digestibility) and two allometric functions representing the relationships between state variables (vertical distribution of the biomass, and specific leaf area, which is the leaf area produced for each gram of biomass). Interactions between the four compartments are simulated by six functions which calculate the flow of biomass: one growth function, one reproductive function, two senescence functions, and two functions simulating abscission of dead tissues and their disappearance in the litter. Many equations are involved in those functions where time is managed using a thermal calendar, which determines activation or deactivation of these functions and therefore the vegetation development.

Only the above ground vegetation is simulated in the cell; soil activity is taken into account through a nutrition index representing soil fertility. The biomass produced in the GV compartment is then reallocated towards the three other compartments using reproductive (GV through GR) or senescence (GV through DV; GR through DR) functions. The biomass may be defoliated by an animal, by linking with the animal sub-module or by abscission of dead tissues, through a litter function not yet implemented. The spatial partition of the vegetation in the plot among the cells corresponds to the partition of the different plant community types called *faciès*. Each *faciès* is associated with a cell and described by a set of parameter values used by the cell functions. A set of parameters describing the vegetation and summarizing its properties defines a *faciès*. The parameters will complete the six functions of the vegetation sub-model and will allow the model to simulate different plant community dynamics. The growth of each cell is calculated in the GV compartment using three functions: the light dependent on radiation intensity function,

temperature function and fertility function. The biomass produced in the GV is then distributed between GV, GR or DV compartments, using flowering or senescence functions. The flowering function is driven by temperature and depends on soil fertility. The senescence flux varies with the average daily temperature and also considers biomass losses through respiration and through the abscission of shoot litter. Outputs of the vegetation sub-model consist in the state and qualitative variables of each compartment and weighted averages of the compartments for each cell. These output data for the vegetation sub-model are inputs data for the animal sub-model.

Material and methods

The experimental data to be used in the process of parameterization came from an experiment established in 1989 on permanent grassland located at Theix, (Auvergne, France). Six individual plots were subjected to three levels of herbage use in order to simulate a process of de-intensification of use. The three management regimes go from the mort (high H and medium M) to the least intensive (low L); all were first grazed in mid-April, and only H was cut for hay at mid-June. The H and M plots were also grazed three times, in late July, late September and late November. At each grazing period, eight ewes per plot performed grazing until the grassland height in the plots H reached 5.5 to 6.5 cm. There was no fertilization supply.

Since 1989, vegetation surveys were performed to observe the development of vegetation in the growing season. The proposal was to measure the biomass position and translocation year-round. This work was done in all herbage uses at the same time before and after each treatment was conducted. We chose the data from 1998 because it was closest to the year when the traits were measured (2000) and because the biomass partition sort data base was most complete for this year. Sampling was obtained within a 3.5 by 0.1 m sampling unit replicated three times in each herbage use and before each grazing or cutting treatment. The collected samples were sorted in green or dry leaves, ears, stems etc., and were dried and weighted. The experimental area has been described by Louault *et al.* (2005) as species-poor vegetation which was fully exploited by grazing and cutting with regular organic and inorganic fertilizer supply, before the experiment start in 1989. After 12 years (2000) of application of differential management, a vegetation survey and species traits measurements were performed in each of the six plots, one month after the early spring grazing. Plant

traits were measured on the most abundant species (i.e., those accounting for at least 85% of the vegetation biomass). Seventeen traits, including leaf traits, plant digestibility, plant height and phenology were evaluated with a method adapted from Weiher *et al.* (1999). The mean value for each trait was calculated at the community level for the three levels of herbage use, and significant differences between treatments were found for most of the traits (Louault *et al.*, 2002). The results (Louault *et al.*, 2005) suggest the possibility of describing the three different degrees of herbage use according to the following functional community approach:

H – high level of herbage use led the plant community to an increase in the abundance of short and early flowering plants with medium size lamina of low dry matter content.

L – low level of herbage use favored tall plants with medium date flowering and plants with medium size lamina of higher dry matter content when compared with H.

M – medium level of herbage use favored a mixed plant community composed of the two types already described above and a third type which is characterized by low height with early flowering an very small lamina of low dry matter content.

The environmental data corresponds to daily temperature and global radiation observations that were collected for the last 17 years by the meteorological station in St. Genest Champanelle. The global radiation data was previous transformed from Joule cm^2 to Megajoule cm^2 (PARi) using the formula $((X/100)\star0.47)$. After that, mean values for 17 years for both variables were calculated.

Functional parameters

Among the 43 parameters of the vegetation sub-model, some are predominantly functional and were considered as traits of the plant community, and some describe vegetation structure. Functional parameters are those that can be considered plant traits because they are related to some physiological or phenological aspect of the vegetation. In this first approach, parameters linked to the plasticity of the plant and their phenology and life cycles were considered. These parameters probably should best represent the adaptive responses of the communities to different disturbances or changes in aboveground biomass. Therefore, the parameters chosen are known to have an impact in the competitive abilities of the plants to the amount of light energy intercepted. The interception of light depends of the amount of dry material and its distribution in space, which determines the quantity of leaves by unit of

surface and its capacity of light interception. The light utilization efficiency is regulated for light conversion efficiency of the leaves and is controlled by the environment being dependent on radiation intensity, daily temperature and nutrition index. Based on this information, the first parameters are related to the life cycle of the plant community (earliness and duration of flowering) and to growth ability (SLA), and the second parameters inform us about vegetation state at the beginning of the simulation (beginning of the year) and concern the quantity, quality and vertical distribution of the biomass. For 17 parameters, values are given at the community level for the three levels of herbage use (Table 1), values of the remaining 26 staying the same for all three plant communities.

Simulation

Simulations were performed to describe the dynamics of the total biomass and of its four compartments for a one-year period, starting from the first of January. Input parameters describe plant communities under the three levels of herbage use. The environmental file corresponds to climatic (temperature and light) data of the year 1998 and the average of 17 years. A set of simulations was conducted including disturbance, i.e. biomass removal at each cutting or grazing event. It is important to stress that the spatial aspect was not considered in the simulations. All the work with the prototype was done in a single cell. The use of more cells is reasonable when the animal is present; otherwise it does not matter, since there is no interaction between cells.

The first simulations were done in order to comprehend the prototype functioning and to verify the basic set of data correction, i.e. to analyze whether the model works properly with the basic data prepared. The second set of simulations used the same files as above, including the 1998 environmental file during a period of a year starting from January 1st until the end of December. They did not consider the management of the treatments because the idea in this simulation was to observe the profile of each *faciès* along the year, comparing them in terms of the differences in biomass production, without any impact of different managements. In each sequence, the starting biomass for all compartments and the number of days simulated were based on the experimental data. The profiles were observed to identify similarities between the simulation and the experimental data. The estimated data based on the simulations performed above were compared with the empirical data to observe the level of adjustment. Graphics with both of these data sets were elaborated in order to examine the fitness of simulated data compared to the experimental data.

Results and discussion

Table 1 shows the parameters for the three *faciès* descriptions included in the input file. They correspond to the three levels of utilization in the experiment data, and the state variables total biomass (T) and biomass of each compartment were chosen as model outputs for further analysis.

Table 1. Values of parameters of the growth model for the three plant communities under the three levels of herbage use (High, Medium and Low).
Tabela 1. Valores dos parâmetros do modelo de crescimento para as três comunidades vegetais submetidas a três níveis de intensidades de uso (Alta, Média e Baixa).

Parameters (units) *Parâmetros (nidades)*	High *Alta*				Medium *Média*				Low *Baixa*				
Plant traits *Atributos das plantas*													
Specific leaf area (m² kg⁻¹ DM) *Área específica da folha (m² kg⁻¹ MS)*	0.0297				0.0298				0.0247				
Reproductive activation (day degree, °C) *Ativação da fase reprodutiva (grau dia, °C)*	883				992				1180				
Reproductive de-activation (day degree) *Desativação da fase reprodutiva (grau dia, °C)*	1274				1443				1833				
Vegetation State *Condição da vegetação*													
Height (1) (m) *Altura (1) (m)*	0.043				0.128				0.088				
Biomass (2) (g DM m⁻²) *Biomassa (2) (g MS m⁻²)*	T 56	gv 37	dv 0	gr 14	dr 5	T 345	gv 46	dv 0	gr 134	dr 165	T 438	gv 40	dv 0	gr 242	dr 157
Volumetric mass (2) (g DM m⁻³) *Massa volumétrica (2) (g MS m⁻³)*	gv 926	dv 291	gr 253	dr 207	gv 732	dv 192	gr 1269	dr 1002	gv 404	dv 72	gr 2979	dr 1652	
Neutral detergent fiber (1) (g DM kg⁻¹) *Fibra detergente neutra (1) (g MS m⁻¹)*	617				736				723				
Neutral detergent fiber digestibility (1) (%) *Digestibilidade fibra detergente neutral (1) (%)*	62				46				45				
Minimal % of leaves in biomass of gv *% mínimo de folhas na biomassa do gv*	68				33				55				
Maximal % of leaves in biomass of gv *% máximo de folhas na biomassa do gv*	72				77				67				

The first simulations of the prototype used as environmental variables the mean average of 17 years worth of data. This simulation was performed to observe whether the adjustment of the experimental data described by the three experimental *faciès* had been coherent with the standard. The results profile (Figure 1) shows a reasonable behavior for all *faciès* along the year despite the larger amount of total biomass (Wcell) produced (around 900 g m^{-2}) by the three experimental *faciès*. With the same basic *faciès* data, we tried to change the environmental data to see whether the results would keep coherence with the ones found using the 1998 environment data set. The idea was to compare the simulations results and choose one of then. The results (Figure 2) show that the maximum Wcell produced by the four *faciès* in 1998 based data was lower than the other. Also the total biomass of the cell (Wcell) started to grow earlier compared to the average of 17 years' data based simulation. We decided to work with the 1998 environmental data file.
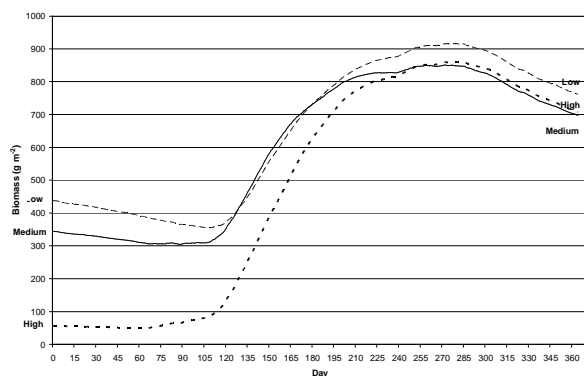
After that, the focus was to observe the model output performance along the year looking for the dynamic of total biomass without management. The profiles of simulation (Figure 2) show that the Wcell for each *faciès* started at different levels (point 1) and decreased during the ending winter time until the beginning of the growing season. It could be observed that the *faciès* high start to grow first (45 days) followed by the others *faciès* (point 2). From this point, the three curves showed a larger rate of biomass accumulation until they reach almost the same high-level plateau (point 3). For the last phase, the same pattern of biomass decreases could be observed in all *faciès* (point 4).

In Figure 3, experimental data is being compared with estimated data in terms of total biomass of the cell (Wcell). It can be observed that at high and medium levels of exploitation, the model agreed well with experimental data, but not at low level of herbage use. At the low level of exploitation, the simulated data estimate higher values (400 to 800 g m^{-2}) in comparison with experimental data (400 to 600 g m^{-2}). For each treatment alone, it is possible to observe that the simulation estimated better for the lower values of the most intensive management than for the higher ones. This fact could be linked to the fact that the model had problems to simulate the compartments Wdv and Wr (Figure 4). In these compartments, the model output showed a bad agreement with the experimental data, especially for the lower level of exploitation. However, in the green vegetative compartment (Wgv), the simulation data fit well with the experimental data at high and medium levels of exploitation, and performed not too badly in the most extensive treatment.

Figure 1. Profiles of **W cell** compartment for all *faciès* using the average of 17 years environmental data file.
*Figura 1. Perfis do compartimento **W** das células para todos os faciès utilizando arquivo de dados ambientais com a média de 17 anos.*
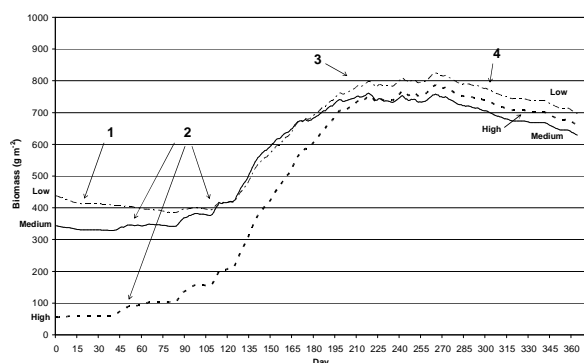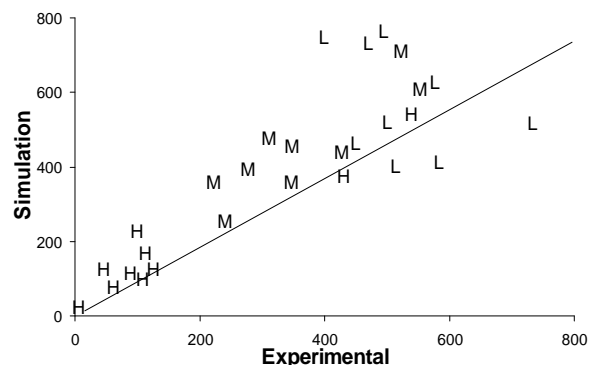

Figure 2. Profiles of **W cell** compartment for all *faciès* using the environmental data file of 1998. The numbers indicated important aspects of the profiles and are described in the text.
*Figura 2. Perfis do compartimento **W** das células para todos os faciès utilizando arquivo de dados ambientais do ano 1998. Os números indicam aspectos importantes dos perfis, e são descritos no texto .*

Figure 3. The experimental versus the simulated Wcell (g m^{-2}) for the three treatments (**H**, high; **M**, medium; **L**, low) considering the management. The diagonal line indicates the point where the estimate is equal to the experimental data.
*Figura 3. Valores experimentais versus simulados de Wcell (g m^{-2}) para os três tratamentos (**H**, alta; **M**, média; **L**, baixa intensidade). A linha diagonal indica os pontos onde os dados estimados são iguais aos experimentais.*
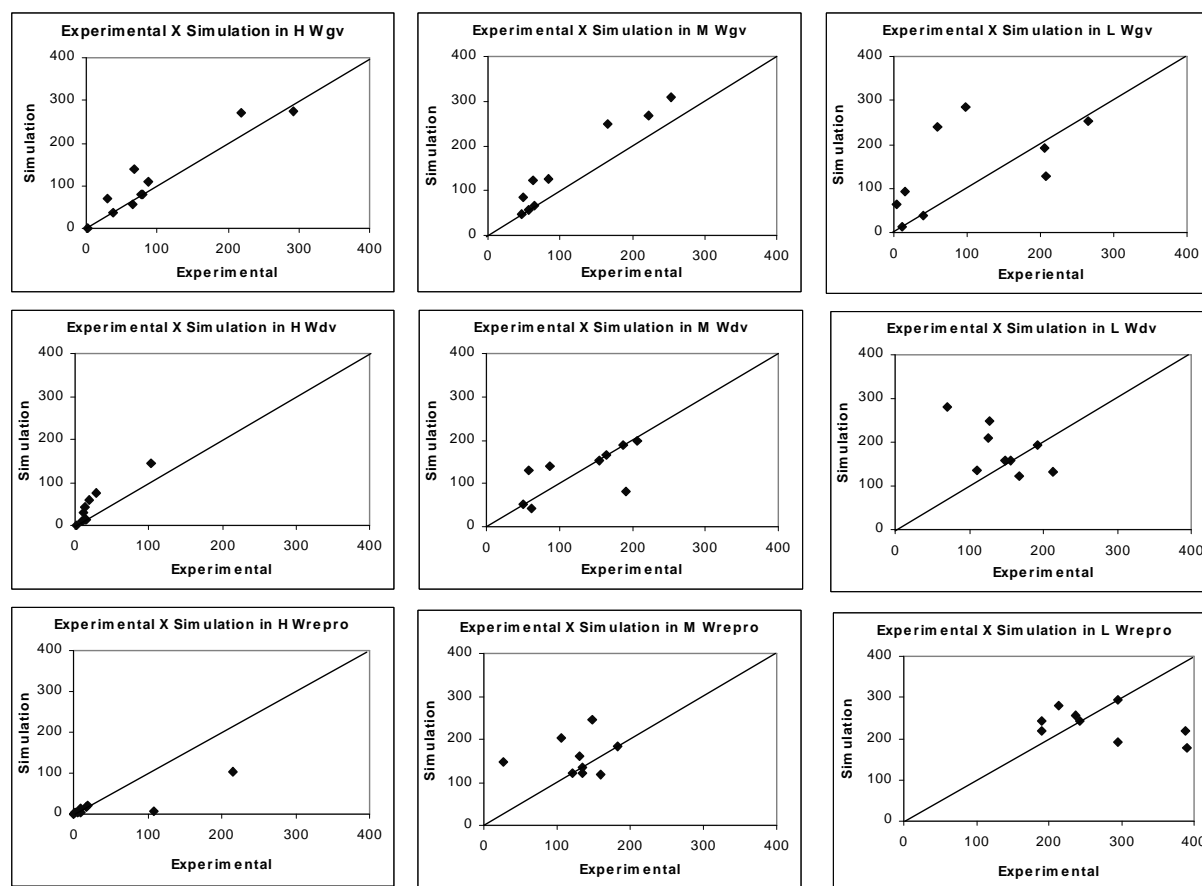
Figure 4. The experimental versus the simulated data for the compartments Wgv, Wdv, Wr (up to bottom) in the three treatments (left to right) considering the management. The diagonal line indicates the point where the estimate is equal to the experimental data.
Figura 4. Valores experimentais versus simulados para os compartimentos Wgv, Wdv, Wr (de cima para baixo) nos três tratamentos (esquerda para direita) segundo a intensidade do manejo. A linha diagonal indica os pontos onde os dados estimados são iguais aos experimentais.

The simulations performed with the community description based on the functional traits showed that the sub-vegetation model correctly estimated the dynamics of the vegetation. The model showed reasonable responses to the environmental variables, climate and fertility, performing a coherent profile for all *faciès* during the year. In the profile of the simulation without management, it can be observed that the vegetation followed the classical profile described in Lemaire and Chapman (1996). The biomass started from a lower level (point 1), in winter, and at the start of the warm season (point 2). The biomass grows until reaching an adequate plateau of total biomass production (point 3). After that, it begins to decrease according to the senescent rules (point 4). It can be observed that at the beginning of the simulation, the higher amount of biomass in the *faciès* L and M when compared to H is due to the accumulation of the dry and reproductive compartments, in accordance with the experimental data and the observations in Louault *et al.* (2005). Nearly 55% and 36% of the Wcell of

faciès L is given by the Wdv and Wr compartments, respectively, and the same proportion is found for the M *faciès*. From Louault *et al.* (2005) the experimental treatments of low herbage utilization lead to an increase in plant height with a significant correlation to later maturity. Nevertheless, the opposite was described for the *faciès* H where 66% of the total biomass was given by the Wgv compartment.

However, at the start of the growing season (point 2) it can be observed that the *faciès* H response was faster in terms of total biomass production than that of the others. The small proportion of senescent material from the last year in the well used treatments allowed for a net accumulation of herbage equals to the net assimilation rate of the canopy (Lemaire and Chapman, 1996). At this early stage of regrowth, there is little death of leaf material in H treatments, in contrast to the M and L treatments, where a high increase of death tissue can be observed. Yet, according to the same authors, the regrowth in highly used plots increases the leaf area index (LAI) by increasing leaf size and

appearance, which improves the light interception and gross photosynthesis. This can be translated into the model by *faciès* parameters linked to the biomass production (SLA) or the canopy structure of the community. In fact, these characteristics are attributes of the species interacting with the environmental to affect the demographic performances and competitive abilities of the plants (Bullock, 1996).

Referring to what has been discussed above, the net herbage accumulation rate will be at its maximum until the rate of senescent material equalizes it or the reproduction phase starts (Lemaire and Chapman, 1996). At this part of the simulation, other important traits related to the phenology and life cycle of the plants will affect the competitive abilities of the *faciès*. The reproductive activation attribute is a response to the start of the translocation of biomass produced in the Wr compartment, changing the pattern of the net accumulation rate and the reproductive activation deactivation for the duration of this period. It is later and longer in the L Faciès because maturity is reached later in tall plants than in short plants (Louault *et al.*, 2005).

In contrast with this first phase of the process, all the *faciès* showed the same dynamics of biomass production in the second part of the year. After a period of strong net accumulation of in the spring, the *faciès* likely equated in their rate of production and percentage of dead tissues (point 3). These results suggest a good adjustment of the model to the limit of production given by the environmental variables (climate and fertility).

Therefore, it can be observed in the simulation results that the dynamics of each *faciès* are consequence of a different structure of the community, determined by its level of exploitation i.e. by spatial and temporal heterogeneity of grazing (Laca, 2000). However, grazing or any kind of heterogeneous disturbance is not part of the model yet. While the temporal component should be further developed in the model, the spatial heterogeneity of the grassland vegetation is summarized in each *faciès* which represent a "functional" community description. The *faciès* reduce the spatial heterogeneity of the communities by means of the averages of the functional attributes of the plant community in homogeneous cells.

Conclusion

The traits of the plants in a community interact with the factors, altering the individual plants ability to compete. This ability is altered by the presence of

the animal increasing the number of different species by increasing the complexity of the system. Models are used to represent this complexity in a simpler manner. The sub-vegetation model was used to simulate grassland vegetation dynamic under three different levels of herbage use by grazers. These three communities were described by aggregates of traits involved in the response of the community to the level of use. These descriptions were introduced into the model concept by the *faciès* definition. Each *faciès* was related to a different community by defining their parameters according to the respective values of the community's traits. A correct simulation of the grassland vegetation dynamics described by functional traits was achieved by the sub-vegetation model. The model simulates well the dynamics of the different *faciès*, but performed better in the simulation of the growing flux than in phenology or the senescent flux. The structural aspect of the vegetation still is not being simulated well, especially in plots under low utilization and showing high spatial heterogeneity. The model needs to be improved to account for the complexity of the grazing system.

We suggest that the lack of agreement between observed and simulated results is due to a poor estimation of senescence and abscission fluxes. The largest discrepancies were shown for the winter period under high herbage use treatment. Under medium and low treatments, the large amounts of biomass were for long regrowth periods without disturbance, during which the tissues become old and start their senescence. Under high level of herbage use, the structure of the sward is more homogeneous than under low level of exploitation (Parsons *et al.*, 2000). We suggest that the discrepancies registered in our study partly arose because the errors of prediction were lower for a homogeneous structure than for a heterogeneous structure. One way to improve the model would be to use a stochastic and spatial approach, specifically combining plant and animal models. According to the changes of trait values observed in the vegetation at different levels of herbage use, the modification of the values of few parameters of the growth model (designated as traits), enable us to simulate contrasted biomass dynamics. Increases in the prediction performance of the model could be achieved through a better description of senescence mechanisms, and also by integrating a spatial approach.

Acknowledgements

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