An L-system based model of a ryegrass heterogeneous population.

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Introduction

Grasslands, natural and cultivated, are one of the major sources of forage in European agricultural systems where they are exploited via grazing and mowing. In the European changing political context regarding environmental questions, social perception of grasslands has shifted. Grasslands are now seen as important due to two main functions: forage production (use value) and environmental roles (biodiversity preservation, carbon sequestration, soil conservation). They are well inserted in the multifunctional paradigm. In addition, compared with other crops, grasslands present some particularities that justify their specific study. For example, they are perennials populations repeatedly exploited via defoliation-regrowth cycles while growing under changing conditions. Grasslands also show high intra and inter specific variability.

Both the canopy structure and the genotypic composition of the population are the determinants of the grassland agricultural use value (quantity and quality of the harvested biomass) as well as of its environmental roles. Canopy structure and the genotypic composition of the population are emergent properties resulting from the behaviour of individual plants and their interactions during the grassland lifespan. Thus, the study of the morphogenesis of the individual is a relevant element to better understand the dynamics of the canopy structure and the population composition.

Several major environmental factors affect plant morphogenesis such as: light resource (trophic and photomorphogenetic signals), intensity and frequency of defoliation, nutrients supply, water availability and temperature dynamics. However, it is difficult to quantify the contribution of each of these factors to the phenotypic plasticity because of their multiple interactions.

Objectives

Our aim is to build up an individual-based Functional-Structural Model of a heterogeneous mini-population of perennial ryegrass, using L-systems. This model is built so that the morphogenesis of the individual is directly affected by its environment. It should allow us to better understand how the use-value of grasslands is modified by the behaviour of individuals under variable management regimes. Furthermore, the analysis of both i) the ryegrass genotypes responses and ii) the ability of genotype to compete under changing environments is a key-point that could help us to understand the genotypic changes in species mixture and opens perspectives towards ecological studies.

Material and method

The described model is based on the L-system formalism (Lindenmayer, 1968; Prusinkiewicz, 1999) using the L-Studio LPFG simulation platform (Karkowski, 2002). The model in itself will be constituted of a model of a sward canopy, along with a light environmental program.

Plant model

Structure and function

The plant model simulates the 3D development of the aerial parts of plants in the vegetative phase. Grasses have the particularity, in the vegetative phase, of not elongating their internodes so that the plant is mainly constituted of tillers, which are themselves made of leaves emitted at the basis of the plant by the apical meristems. Consequently, a realistic representation of the architecture can be obtained by a description of the topology of the plant and of the leaf dynamics (e.g. growth kinetic, lifespan, geometry) at different levels of organisation. The main criterions (not all comprehensive) that have been identified, at each organisation level, as essential to properly model the structure of a ryegrass canopy are listed in figure 1, along with the corresponding process that must be taken into account.
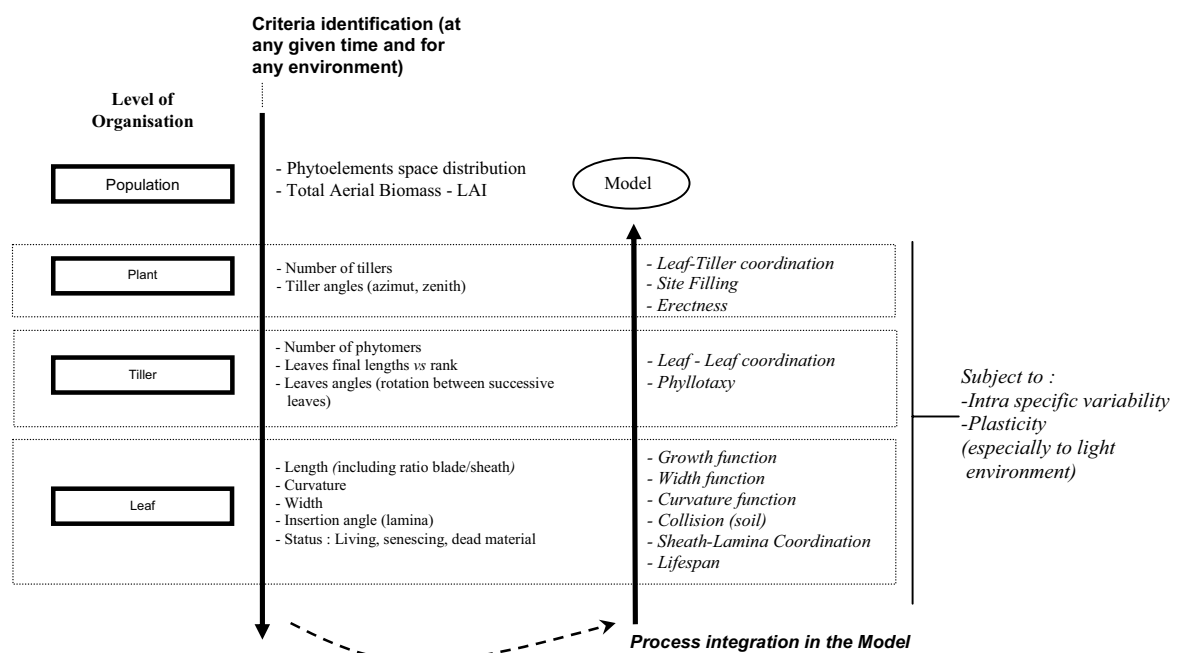

Fig. 1. Criteria identification and processes taken into account, each level of organisation, for building the population model. Basically, a realistic representation of the architecture relies on properly describing the number of leaves and tillers, space orientation and shape of the phyto-elements, at any given time and environment.

From a functional point of view, the processes controlling the triggering, coordination and kinetic of leaves and tillers growth are of utmost importance. The main static (e.g. final leaf length) and dynamic (growth rate, elongation duration) characteristics of the leaves can be described as a function of their phytomer relative number (Evers *et al*., 2005). They are input into the model to obtain realistic, but deterministic simulations of the gradients observed on a given axis. On the other hand, several author (e.g. Fournier *et al*., 2007) suggested that some events are controlled, in an indirect manner, by the pre-existing architecture. For example, the growth of a given leaf is triggered when the older leaf emerges out of the pseudostem cylinder. In our work, to test these hypotheses, we designed a model that is as "self-regulated" as possible, i.e. the only descriptive input is the general form of the growth function of the leaves. The values of the parameters of this function are modified by the current state of the plant. Furthermore, this approach actually allows simulating the impact of structural modifications, such as cutting, on the subsequent development of the plant architecture (Fig. 2). This is unavoidable to reach our objective.

Topology

In our model, the topological description of the plant relies on virtual phytomers that are created at the apices, as described by Fournier *et al*. (2007). The creation of a new phytomer is determined by the detection of a specific event: the emergence of a leaf out of the whorl formed by the sheaths of older leaves. When a phytomer is created, the elongation of its own leaf is triggered. Thus, the plant model does not emit organs according to a clock in order to obtain a given phyllochron, but creates its own phyllochron according to the kinetic of the growth of the leaves.

Leaf growth

The values of the parameters such as the elongation duration, the elongation rate and the final length are not given *a priori* as a function of the leaf rank on the axis, but are self-determined by the model according to the local growth conditions. For instance, the final leaf length is determined by the time that the leaf spends growing within the whorl. In other words, it is indirectly determined by the actual length of the sheath of the previous leaf.

Management methods: simulation of cutting regimes

As cited above, grasslands are grazed and/or mowed (cut). Cutting can be characterized by its intensity and its frequency. Combinations of these two factors affect mono-species grasslands productivity (Hernandez Garay *et al*., 1999) and could also modify the genotypic composition of heterogeneous populations (Hazard and Ghesquiere, 1995). Thus, we are aiming to simulate the modification of the canopy structure under different cutting regimes in order to better understand how the individual and the group of plants will react to the modification of their own structure and of their access to light, especially for shaded plants and organs.

Results

By dynamically adjusting the values of the various parameters, the model satisfactorily captures the evolution of the patterns and time kinetics of major architectural traits such as the final lengths and appearance rates of leaves (Fig. 2a, 2b). In its present state, the model also mimics the response of the plant to structural perturbations induced by differential cutting heights (Fig. 2c, 2d).
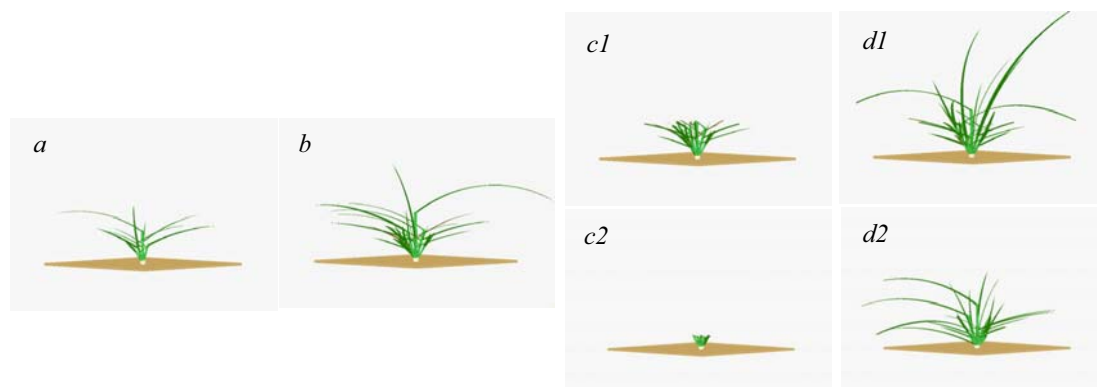

Fig. 2. Sequence illustrating the simulation of a plant at two developmental stage (a, b), defoliated (c1 and c2) and during regrowth after a cutting event at two different heights(d1 and d2).

Conclusion

Several hypotheses have been proposed to explain the dynamics of ryegrass population canopy structure and genotype composition (in the case of heterogeneous communities) under competition for light and different cutting regimes. However, we are lacking proper understanding of what are the utmost explanations: trophic responses, morphogenetic responses to signals, genotypic competing ability. Furthermore, we face difficulties when trying to design and conduct experiments allowing answering these questions. The FS approach could be a particularly well adapted tool to investigate these topics.

Perspectives

Some improvements of the model are needed, especially to properly simulate both the tillering and the behaviour of different genotypes.

Environmental programs. Site filling and other plant architectural traits are determined by the light environment. Thus, in a next stage, a radiation model will be coupled with the plant/population model, enabling us to simulate light micro-environment in the neighbourhood of each organ (Evers *et al*. 2005).

Genotypic heterogeneity. Another goal of our work is to characterize the behaviour of architectural traits of different genotypes under competition for light and under different management regimes. Populations constituted of two different simulated genotypes will be created, based on the characteristics of the short-leaved and long-leaved types selected by Hazard *et al*. (1996). Different mixtures will be artificially "sowed" and their evolution monitored, under the constraints cited above.

Acknowledgments

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