

Draft

Clément Viguier

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## Introduction

### State of the art

Large scale empirical studies (wright, reich), databases (try) and meta-analysis (poorter mouais, other meta-analysis) have greatly improve our understanding of functional traits in plants. Both trade-of between traits (wright and reich) and trait variations with climatic conditions have been studied, and general patterns could be drawn. This understanding of plant functional traits is key in the study of plant communities. Functional trait can be used to better assess the functioning of a community, its diversity, and the services it offers (lavorel and others: diaz ?). More importantly they offer the opportunity to study very different species together and their interactions.

Classical community models (gemini and others) often consider species as unique entities with particular functioning determined by their parameters values, extracted from empirical studies. Such approaches required a lot of species specific data, and can only be used in the same context as the data. This dependency from specific (species and habitat) data make difficult generalization of the obtained results. Dynamic global vegetation models (DGVMs) have been generalizing the plant behaviour for a while, using shared traits evolutionary dynamics to predict global ecosystems dynamics. These approaches can now be strengthened by the contribution from functional trait based studies. Recently trait based models have been developed to investigate community dynamics. The use of functional trait enables the modelling of multiple species with different strategies to question the role of trade-of in species coexistence in an evolutionary model.

General framework for plant functioning through traits and trade-of allows the investigation of plant coexistence mechanisms at large scales (falster). Coexistence mechanisms and community dynamics should also be interrogated at a finer scale where other mechanisms may be involved. This interest for large temporal and spatial scale may be explained by the greater interest of community ecologists for forest than for other type of vegetation communities. There are indeed few models interested in multi-species grasslands. Changing the scope of plant community ecology could benefit to the whole field of community ecology thanks to a better understanding of finer scale interactions and mechanisms.

General framework for plant functioning through traits

and trade-of allows the investigation of plant coexistence mechanisms at large scales (falster). Coexistence mechanisms and community dynamics should also be interrogated at a finer scale where other mechanisms may be involved.!!! **No link between these sentences !!!** Empirical studies have used the community weighted mean trait values to assess the functioning of plant communities. However there is a growing interest in intra-specific variability (diaz) as it represents a relatively high portion of total trait variation (albert) and can have great impact on community response to drivers 'need references). In addition to potentially change the values of community realised trait means (compared to means computed with species mean trait values)(jung) and so affect the ecosystem services provided, intra-specific variability could also change the output of community composition mechanisms (jung, diaz?). Effect on inter- and intra-specific interactions and coexistence mechanisms are also questioned, with various conclusions (theoretical model and empirical study of plasticity). New plant community models should take intra-specific variations into account to better understand its impact on plant interactions, community composition and ecosystem services.

Incorporating intra-specific variation in vegetation model can be challenging as there are many sources for such variations: genetic variations, epigenetic variations and phenotypic plasticity as the three main sources. Genetic variation does not match the finer scope we suggest to investigate to better understand plant interaction and community dynamics. Epigenetic variation has a great potential to change the community dynamics, but it requires first phenotypic plasticity to be already incorporated. From that, phenotypic plasticity seems to be the first source of variation that should be studied. Phenotypic plasticity is a powerful but complex concept that is detailed in box 1. Integrating the phenotypic plasticity to the model using a framework of generic traits and trade-ofs is necessary to improve our understanding of plant interactions, responses to drivers and impact on community dynamics.

We developed with *MountGrass* a agent-based grassland model integrating phenotypic plasticity in a general multi-strategy framework based on carbon pools and trade-ofs. The general framework of carbon pools and trade-of allows to study different species and diverse communities within a generic set of rules. The phenotypic plasticity relies on the possibility for plants to change the carbon allocation scheme to the different carbon pools based on

their species specific strategy and their individual experience of external conditions. The following paper describes the keys elements of the model and how they integrate to model from single plant growth to multiple plant mixture community dynamic.

### Box 1: plant phenotypic plasticity

"What's in da box !?" - Brad Pitt

#### Sources of variations

between individuals (genetic, epigenetic, plasticity), and in time (performance, ontogeny, plasticity)

#### What is phenotypic plasticity ?

Phenotypic plasticity is often defined as the capacity of individual from the same genotypes to express different phenotypes. trait variation from same genotype (includes epigenetic here, we don't). Capacity for a plant to actively change its organization scheme to match its own individual perception of external conditions.

#### Phenotypic plasticity in plant models

relative plasticity (depends on the focus), not a plant physiological model -> that means some real plastic traits may be fixed, but change the focus, these fixed traits are lower level, the traits that determine the functional trait values – coherence to the plasticity, not only variation, or hadhoc function with species specific parameters.  
plant size at maturity vs time for flowering  
Perception of conditions  
Plasticity cost:

duced resource on growth, survival and reproduction.

flexibility to address multiple questions on plasticity and coexistence, and extentionnality, strategy space, etc... but it comes with the cost of complexity, slowness and difficulty of parametrization.

### General framework and carbon pools

Plants in *MountGrass* are defined by their species, position, carbon pool size and environment perception. Carbon pools are divided between preservation pools (i.e. storage and reproduction pools) and development pools that constitute stem, leaves and roots. Leaves and roots are the exchange surfaces of the plant and critical trade-of between their structure and function have been enlighten. LES, eventual root similar spectrum (paper in favour, paper againts). These trade-offs can be partly explain by the structure of the organs that result from allocation between two distinct complementary carbon pools: active tissues and structural tissues (Shipley). Changes in the ratio of active over structural tissues induce changes in exchange area per mass unit (because of differences in density), over-all respiration and lifespan, these relationships are detailed in figure ??.

Individual belonging to the same species share the same strategy. A species specific strategy is defined by its position within the multidimensional strategy space made of axis like: seed mass, shoot height-radius ratio, height at maturity, fast-slow resource acquisition, annual-perennial, etc.

All plants physiological mechanisms are ruled by the same functions and parameters. Differences between organic repartition between pools are translated in differences in exchange area, lifespan and relative equilibrium between shoot and root activity.

### Daily cycle and competition for resources

Cycle - pseudo code. Competition for light and water are handled in similar way. Light competition is computed pixel by pixel. Each pixel is divided in layer of homogeneous density between two consecutive individual height of overlapping plants in the pixel. In each layer the average density and the top incident light allows the integration of potential photosynthesis supposing light transmission follows Beer Lambert's law and an homogeneous vertical leaf area distribution. The potential photosynthesis is summed up for all layers of all pixel for each plants, and converted into water demand thanks to WUE parame-

## 1 Model

### Overview

*MountGrass* is an agent based, spatially explicit model of mountain grassland. Individual plants compete on a torus grid for light and water. Competition is indirect and result from resource partitioning based on exchange rates derived from individual traits. Above- and below-ground competition result in production of organic matter that is then distributed between the different plant carbon pools according to species strategy and individual experience. Fitness of individual plants, and so community dynamics, emerge from the impact of allocation of the newly pro-

ter.

Water competition is also computed by pixel, where all water in the pixel is equally accessible to the root in the said pixel. The water demand may limit the water competition if the potential root water uptake in the focus pixel is greater than the water demand relative to the pixel. If total potential water uptake of plants in the pixel exceeds the available water, water absorption is then proportional to the relative potential water uptake of each plant compared to the total potential uptake.

The growth production is computed from the water uptake and the water use efficiency. Maintenance respiration of active tissues only is subtracted to the growth production, and if positive the result is reduced by the growth respiration. Competition for light  
competition for water  
production

#### Allocation of carbon and plasticity

Once produced the organic matter is allocated to the stem to reach the minimal mechanical support. The remaining OM is divided between preservation pools, if the plant is mature, and plant leaves and root development. Only the leaves and roots pools are plastic, that means that the fractions allocated to the two pools of leaves and the two pools of roots can change over time. These changes lead to different shoot:root ratio and eventually different functional trait values. Active modifications of the size of the pools (increase only, no reallocation) are driven by the following hypothesis: *plants adjust their phenotype to improve the carbon return in an hypothetical future estimated from genetic memory and individual experience, by particularly maintaining the equilibrium between above- and below-ground activity*. This hypothesis contains multiple key elements that we will try to explain in the following paragraphs.

conditions of competition  
future estimation: memory, maximize return over time...  
objective functions  
plasticity cost  
algorithms

## 2 Results

### One plant growth and development

hypothesis: coordination, pot, same thickness.  
fast-slow effect  
different plasticity mechanisms effects on individual growth  
plasticity - strategy interaction: plasticity capacity.

### Monoculture: competition and plasticity

comparison of no plasticity - plasticity productivity  
play with scales: time and space resolution.

### Mixed community: competition

## 3 Discussion

## References