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CLÉMENT VIGUIER

PHD THESIS

ABSTRACT

This is the abstract.

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INTRODUCTION

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INDIVIDUAL LEVEL
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Why the how: what makes these objectives valid
The machine
The results

II

BACKGROUND: COMMUNITY DYNAMICS, TRAITS AND PHENOTYPIC PLASTICITY

1 UNDERSTANDING COMMUNITY DYNAMICS: DRIVERS AND THEORIES OF COEXISTENCE

1.1 The mystery of coexistence

Other things being equal hypothesis (in models at least) does not allow the full diversity to emerge.

One mechanisms alone seams to not be enough to explain fantastic diversity explain in natural ecosystems. However there are multiple theoretical mechanisms that support species diversity and that should taken into account in community models: diversity of resources, spatial and temporal variability, frequency dependent effects, etc...

1.2 Abiotic and biotic factors: from potential to realised niche

Abiotic drivers main tnhing at global scale... Then interactions and competition.

The concept of ecological niche serves as a great tool for theoretical research on coexistence. It encompass in a convenient way both abiotic and biotic drivers of one species distribution. The Hutchitonian niche also captures the multidimensionality of persistence and reproduction.

1.3 The complexity of coexistence

From the multiple first attends to explain coexistence with one particular mechanism, scientific community realised that indeed multiple mechanisms are at work to make species diversity in ecological community. This multiplicity highlight the need for unifying framework able to cover this diversity of mechanisms and dimensions.

2 CONSIDERING STRATEGIES AND FUNCTIONAL TRAITS

2.1 The continuity of functional ecology

The paradigm shift toward functional ecology allowed the shift from discrete to continuous representation of species. This change make easier the representation and study of plant communities, especially along conditions or management gradient. Despite the advantages of functional traits, close comparisons and links with theoretical approaches should be used carefully, and underlying assumptions should be interrogated.

2.2 How trade-offs make strategy space

Diversity of mech: diveristy of strategies. more or less independent.

The multiplicity of mechanisms in these systems lead to similar diversity in plant strategies. These strategies are captured in a strategy space drawn by independent trade-offs. Such trade-offs can be captured and embodied thanks to functional traits.

2.3 Modelling diverse plant community

The use of strategy spaces in models allow the representation of high diversity in a common plant functioning framework requiring limited number of parameters. Such approaches are very useful to follow the dynamics of communities in a mechanistic framework.

3 THE IMPORTANCE OF INTRA-SPECIFIC VARIABILITY

3.1 Intra-specific variations change the rules

More interest in trait distribution, variability and diversity. $\rightarrow$ Get to look at intra-specific variability.
Jung: not always in the same way
Wellstein:

The intra-specific variability has been observed to be both an important part of community functional diversity, but also a way the community respond to changes in conditions. In addition to the empirical evidence of this importance, theoretical approaches support contrasting effects of such variations on coexistence mechanisms, evolutionary processes and community responses to climate event or invasion. It is crucial to disentangle different sources of intra-specific variability in order to their understand potential effect on ecosystem dynamics.

3.2 Phenotypic plasticity: a specific case

•

3.3 Beyond the mean and the bell-shape: for more mechanisms in intra-specific variability

The same way the neutral theory is simplifying and brings little understanding to underlying processes and relies on strong hypothesis, considering intra-specificity as a purely random mechanism is insufficient.
Bell shape do not appear in altitude gradient...
Strong theoretical hypothesis
Asymmetric and symmetric competition

As ecology shifted from species to traits syndroms, it seems that it needs to go from syndroms to distributions and drivers. The complexity of living communities requires to go further down and consider the individual scale. This is made possible by the acumulation of more and more numerous and detailed data, the improvement of statistical and simulation tools.

3.4 For an integrative framework of plant strategy and phenotypic plasticity

Bradshaw? Dewitt

New simulations tools for understanding community dynamics should try to both include multiple coexistence mechanisms and plant strategies, and focus on individual level mechanisms of competition, growth and survival. This can only be achieved an a constraint high dimensional strategy space based on physical and biological trade-offs. Individual level modelling allows the integration of multiple sources of intra-specific variability: genetic diversity and phenotypic plasticity. Phenotypic plasticity being driven by the perception of environment, it cannot be simply described by normal random distribution and should receive more attention. This focus is particularly important considering both the lack of understanding of this phenomena and the consequences for plant communities.

III

MODELLING ALPINE GRASSLANDS WITH MOUNTGRASS

A GENERIC FRAMEWORK INTEGRATING PHENOTYPIC

PLASTICITY

The objective of this chapter is to develop the core concepts of the model, introduced in previous chapter, and explain the structure and design choices made during the model development. The first part focuses on the general context of alpine grasslands and some coexistence mechanisms at stake. The following part details the definition of the strategy space and the modelling of phenotypic plasticity, while introducing the key concepts of species memory and individual experience. Finally, the last part is a detailed description of the model following Grimm recommendations [].

1 ALPINE ENVIRONMENT: CONDITIONS, RESOURCES AND PERTURBATIONS

1.1 The scale of alpine grasslands

1.2 Resources: light and water

1.3 Perturbations: frost, grazing and cutting

2 MULTI-DIMENSION STRATEGY SPACE, CARBON POOLS AND TRADE-OFFS

2.1 Multi-dimension strategy space and allocation pools

2.1.1 The strategy space in `MountGrass`

In an ecological agent-based simulation model a species will be defined by its values for the species specific parameters. They can be estimated from experimental data [,] or be picked from a strategy axis [,] composing a strategy space []. The diversity of the species pool will depend on the number of values for each of these specific parameters, or traits, and the number of these traits. Each trait increasing the dimension of the strategy space []. The ambition of this model being to simulated rich plant communities, the definition of these axis is crucial. Trade-offs between traits are excellent applicants for these specific pa-

WHAT IS A STRATEGY SPACE

rameters as they reduce the dimensionality of phenotypes to a small number of dimensions [,] while keeping the information of traits needed to describe the plant functioning. Trade-offs emerge from ecological and physical or biological constrains, by considering these constrains Darwinian demons are avoided.

Considering too many axis does not improve community description [], but a certain number is needed to have strategic diversity as they should be related to particular aspect of fitness and mechanisms for coexistence (*e.g.* reproduction, competitve ability, resistance to resource shortage, predation, etc.). In this model, multiple aspect of plant life are represented from germination with the germination rate for storage effect [,], dispersion with seed mass [] or tissue construction cost [,]. All main aspects of plant growth and life history being covered by such trade-offs and driven by mechanisms shared by all vegetation systems, the model has a great potential of genericity and diversity. It can be easily adapted to other plant communities with specific calibration, and extended with couples of biological process and differenciation axis (*e.g.* root herbivory and associated resistance carbon pool). The the trade-offs used in the model are detailed in the model description below. These differentiation axis should, in such models, be independent, (*i.e.* it is physically and biologically possible for a plant to take any position in the space drawn by the two axis) and result from physical or biological law (ensuring that impossible strategies are not tested). First, it is a condition for parsimony of the model. Second and more interesting reason is that any trade-off emerging from the model should have an ecological interpretation [].

One way of constraining plant strategies to certain axis is to consider allocation trade-offs [,]. An allocation trade-off is the translation of the mass conservation rule that prevent the use of the same biomass pool for distinct function. If biological functions are related to organic matter pools (photosynthesis to leaves, water and nutrient uptake to roots), then the sum of biomass to invest in each carbon pool cannot exceed the available biomass (from net production or stored biomass mobilisation). Allocation trade-offs have the advantage to be easily implemented and be intuitive. By design, a partitioning factor correspond to a position on the strategic axis. Five trade-offs take advantage of this in this version of the model: (1) partitioning between reproduction and maintenance of vegetative tissues (when plant is mature), (2) partitioning of reproduction biomass between persistence (storage) and production of new propagules (seed/clone production)[], (3) investment between shoot and root, [,](4) construction cost trade-offs between active and structural tissues in both shoot and root and (5) partitioning between stored biomass and frost resistance carbohydrates []. This last trade-off can be extended to other carbon pools of specific resistances, for example to herbivory. Modification of these coefficient during life history is a way to introduce plasticity in the model. The rules driving such changes for some of this partitioning parameters are described in the following section.

One of these trade-offs, (4), is key and related the construction cost of organs (independently leaves and roots). Highlighted at global scale and for leaves, the Leaf Economic Spectrum [] draws an strategic differentiation axis from conservative slow species and exploitive fast species. The construction cost, related to

the resource use strategy, has long been identify as a factor of strategic differentiation in plant communities. This strategic axis, being related to many functional traits: SLA, LDMC, LNC, leaf longevity, Amass, etc. is of crucial importance. First, these traits are closely related to the characterisation of plant communities and the assessment of services. Second, if some of these traits are soft traits, strong links and correlations can be made with physiological traits. Finally, a species resource use strategy is closely related to its responses and vulnerability to changing conditions. If it was mainly evidenced for leaves, there are empirical results that support similar axis for roots [**tjoelker_linking_2015**,]. The necessity for independent similar axis for leaves and root can be discussed with respect to coordination between shoot and root activities. Because perfect cannot be guaranteed in all conditions, strict coordination cannot taken as a principle for the reduction of strategy space. Moreover, empirical results suggest small deviations from coordination are common. The leaf economic spectrum being conserved at the intra-specific level [**freschet**,] is another reason to include such trade-of as it would be a good basis for phenotypic plasticity.

These trade-offs between highly productive tissues with low construction cost and short lifespan called exploitative, and more conservative strategy with longer lifespan but lower productivity are mainly observed thanks to soft traits such as SLA for LNC []. Mechanistic model require traits related to physiology and organ performance [,], but link can generally be done between these traits and soft traits. However traits such as SRL or SLA are composite traits emerging from different organ properties [,], where tissue density and organ thickness are the main determinants. "*A necessary trade-off between allocation to structural tissues versus liquid phase processes*" has been identified by Shipley et al. [] as one of the two main factors for the leaf economic spectrum to emerge. Such allocation trade-off can indeed explain differences in construction cost as the liquid phase corresponding to the "active" part of plant tissue, the cell content, have much lower dry volumetric mass than its "structural" counterpart, the cell-wall. Also active tissues containing the protein machinery for photosynthesis and water absorption, a higher proportion of high protein concentration tissue would be correlated to higher nitrogen concentration in the organ on the "fast-slow" spectrum, along with a higher mass-based photosynthetic rate []. On the other end, the structural tissues give the organ a higher lifespan [,] that compensate for lower productivity []. Such trade-off can be apply to both shoot and roots [,]. From that, the decomposition of organs between active and structural tissues constitutes a strong basis to model construction cost trade-offs as the main parts of the global strategy space.

The use of allocation trade-offs allows the construction of a generic multi-dimension strategy space where a high diversity of species can potentially coexist. Because this space is based on physic laws, it ensures the non existence of Darwinian demons and does not limit the species or individual plants to tested parameters and strategies. To be complete the link between carbon pool allocation and physiology must be determined within the respect of similar biological or physical laws.

2.2 Craft a trade-off: active and structural tissues

Allocation trade-offs offer great flexibility and are easily understood and imple-
mented. However, when they control the value of traits (SLA or SRL) involved
in multiple processes, a balance must be found to avoid that: (1) one process
is ignored because has a low relative importance on fitness (becoming useless
to the model), (2) the effects of processes involved show strong response curves
to the allocation and there is only one global[1] optimum. The idea behind a
trade-off is that multiple positions are viable in different conditions or in asso-
ciation with other strategies. The leaf-economic spectrum, in addition to rely
on the active-structural tissue trade-off, also requires "*an evolutionary tradeoff be-
tween leaf photosynthetic rates, construction costs, and leaf longevity*". This trade-off
is explore in this section of the document.

[1] I use the term global here to des-
ignate the multidimensional space
draw by the axis of interest and
other variables play a role in in-
volved process (e.g. resource avail-
ability, temperature etc...).

In the framework of the model, plants share the same global parameters, and
the maximum photosynthetic rate should be the same. Because photosynthesis
relies on the exchange of gases (CO_2, O_2 and H_2O) and the interception of light,
it is related to exchange area. Considering one shared parameter for maximum
area-based potential exchange rate satisfy both the need for a shared parameter
and a way for plant to vary their mass based exchange rate by changing its pro-
portion of active tissues. This is in agreement with the LES that describe strong
relationship between mass based traits and limited ones for area-based variables
[2], and explain the first part of the trade-off between photosynthetic rate and
construction cost. The second part is the relationship with the longevity. The
longevity is often correlated to SLA in empirical studies, however this is mainly
explained by differences in tissue density and toughness than in thickness (other
component of SLA) [3]. For this reason we can directly link the leaf longevity to
active tissue proportion. Respiration is also increased by the increase of pro-
portion of photosynthetic tissues [4]. We have now a trade-off between a gain
function (exchange area gain by changes in densities) and a cost function (tissue
turn over and respiration). This should be enough to explain different strategies
[5]. However the model need internal limits to avoid the gain function to lead to
only active tissue organ (or only structural). These limits are required to allow
individuals or species to change position along these axis (plasticity or strategic
shift). The convex shape of gain function in association with a minimal cost
(minimum turn-over cost above maximum potential gain) is enough to limit the
allocation to structural tissues only. To avoid allocation to only active tissue,
that would correspond to an organ made of protoplasts, the cost function need
higher than the potential gain. To acheive that an ... function is chosen. This
choice ensure that the potential gain function has an optimum different from the
borders. **(see figure)**.

[2]

[3]

[4] ; and

[5]

Active got closer to optimum, but less active and positive gain in more condi-
tions. Can I demonstrate this with formulas ? (gain = function(condition))

GAIN AS FUNCTION OF CONDI-
TIONS

The potential gain is not only function of active tissue proportion, but also de-
pends on resource availability. Changes in resource level imply changes in slope
of gain function and a shift of the organ optimum for tissue allocation. This shift
make more conservative strategies more interesting when resources are scarce,

while more exploitative allocation strategies are better for high resource availability. This link between optimum allocation and resource level could be used to define the best phenotype according to experience conditions, but the organ strategy cannot be disconnected from the whole plant strategy and allocation.

The phenotype (within the subspace of vegetative allocation) depends both on the individual efficiency of organs and the balance between shoot and root activity. This balance, often used to model plant plastic allocation and considered between light and nitrogen [1]. In the context of mountain grasslands and global change, the water... The integration of nitrogen as a limiting solution is discussed in latter chapter. The balance between shoot and root activity being key in overall performance, the root shoot ratio (RSR) will be determined as a function of estimated availability.

2.2.1 Species memory and phenotype determination

phenotype = ensemble of response trait values. Emerge from default trait + environment.
Composite traits are defined by the interaction of different, independent, driving traits. What is a driving traits ? Biology: genetic information. This genetic information is selected by climatic conditions. If we can make a link between optimum value for a trait and environmental conditions, then store external conditions and use link between.

MEMORY OF SPECIES: A DRIVING TRAIT

The decomposition of organs organic matter in active and structural carbon pools makes a link between allocation and physiology and draws a subspace within the strategy space where individuals can move and change their phenotype. Limiting mechanisms restraint the viable options to realistic values along these axis. Within this space, the resource availability and external conditions play a major role in the expression of the strategy.

Flexible, allocation based, diversity and movement

3 MODEL PHENOTYPIC PLASTICITY

3.1 Plasticity as a strategy: between species memory and individual experience

Plasticity: expected environment -> phenotype, here phneotype is equivalent to biomass partitioning, that means expected environement -> allocation coefficients. Then memory -> expectations -> allocation. Because low dimensions, and we want diversity, and the link between memory and allocation might not be a function (one memroy give exactly one optimum allocation), in the model

this relationship is not verified. Species specfic traits are used to allow for different strategies to be associated to a same memory (different plants won't have the same strat, despite sharing the projection)

Once the plasticity is introduced, talk about the memory. Now you can also talk about the mapping/consistency between both and the difficulties to use both.

3.1.1 Projection of external conditions: between species memory and individual experience

Or can a plant be plastic and unique ? The paradox of plasticity and diversity.

Plastic will neceseraly reduce the space (as there is convergence, unless different strategies of adaptation).

3.1.2 On the difficulty to match strategy and conditions.

Because the plasticity is a strategy and not a default behaviour, its effects on individual performance have to be tested. But it also opens a lot of interesting questions around the costs and benefits of plasticity, and the co-selection with the resource use strategy.

Moreover this particular implementation of plasticity limits risks of convergence while allowing plants to evolve in the strategy space defined earlier.

The projection of external conditions, driving the plastic allocation of organic matter, lies on a balance between species memory and individual experience. Its design make of plasticity an axis of strategic differentiation alongside the other strategy axis. Thanks to this innovative design, the model can be used to examine the ecological relevance of plasticity in different conditions and in association with different strategies. The effect of allocation rules and projection stability can be explore independently or conjointly for a better understanding of relative importance of allocation and plasticity.

3.2 Driving rules of allocation

... few words on the space ?

The driving rule of plasticity defines whether or not the choice of the phenotype is fully determined by the projection of external conditions or constrained by some species specific parameters. The effect of this balance between projection and parameters is crucial in the model behaviour. In any case the projection is the main control on individual plastic response to change in conditions, offering possibilities to modulate individual plasticity despite a shared mechanism.

4 THE MODEL

This document is a detailed description of the `MountGrass` model. This description is based on the ODD protocol of Grimm et al.. The model is inspired by multiple other forest and grassland models (for grassland models see particularly Taubert [1] and Lohier [2]). It differentiates itself from these models by the incorporation of phenotypic plasticity in a generalizing framework for plant functioning. This allows it to be used to both to explore the fundamental effects of phenotypic plasticity the dynamics of rich grass communities and the impact of the phenotypic plasticity on plant interactions. The general approach and the practical details are further detailed in this document.

4.1 Model overview

4.1.1 Model purpose

The development of `MountGrass` is motivated by the need for a flexible tool to explore the complex dynamics of mountain grassland communities, in the context of global change. This tool should, by a better understanding of community dynamics and representation of plant strategies and interaction, also help in the assessment of ecosystem services in new conditions. We believe that to capture the dynamic of such communities, we need to understand and represent first the individual response of plants to fluctuating levels of resources, and the impact of plants on the resources. Individual responses and relative impact should follow general rules of plant physiology but also integrates specific behaviour based on the species resource use strategy and individual characteristics. Therefore the model should allow to follow distinct individuals from different groups (e.g. species) in a spatially explicit environment where they compete for resources.

Moreover, since we focus on the community levels, coexistence mechanisms are important and we should include a certain number of these if we want to maintain diversity to observed levels. These mechanisms include: multiple resources competition (water and light), spatial and temporal heterogeneity of resource levels, strategic trade-off between species, perturbation mechanisms (frost, management), link to meta-population, etc...

The model is built to try to satisfy conditions to reproduce and explore mountain grassland community dynamics. In the current version of the model (`MountGrass2.0`), a generalist approach has been privileged, and focus on some coexistence maintenance mechanisms and integration of phenotypic plasticity framework. In this state the model has to be seen as a toy model with good generalisation potential. The link between to ecosystem services are not included, but we can easily imagine to compute them from the community trait distribution. All processes and mechanism are detailed below.

4.1.2 State variables

In mountain grasslands individuals (tillers) generally do not grow big and interact only with close neighbours and form little patches. And thus it is possible to represent rich community at a fairly small scale ($\approx$ dm or m), but the spatial resolution should be relatively fine ($\approx$ cm) to capture inter-individual interactions. Because the model is intended to explore climate change impact on mountain grasslands, it can runs on multiple growth seasons separated by snow covered periods, but must also integrates the intra-seasonal variations at daily scale. Mountain weather (mostly temperature) is known for its large hourly
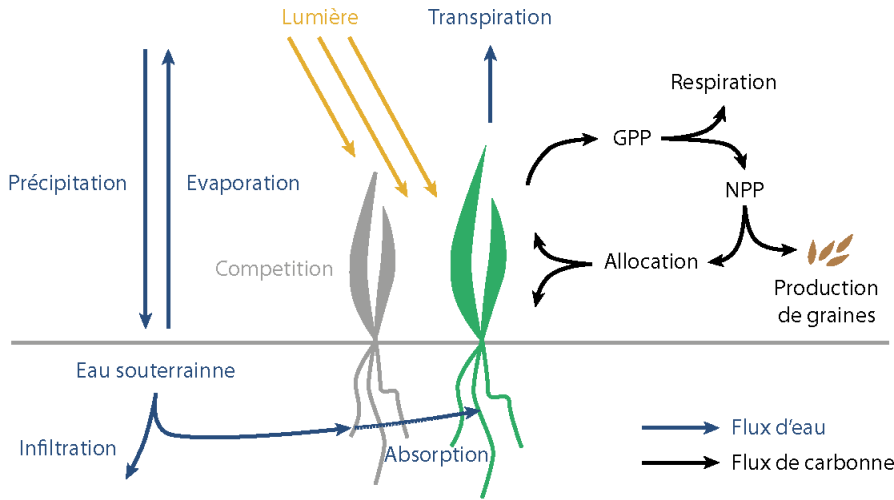
SCALES

variations, it would however require too much computational power to consider such variations. In addition to this argument, we believe that even-though they imply physiological flexibility and specific strategies for plants experiencing these conditions, they will not have a huge impact on overall community dynamics changes caused by the climate change. That why hourly variations will not be considered, and physiological processes are estimated at the daily time scale.

PLANTS

The plants are described in the model by state variables described in table 4.1. The best way to understand how plant are represented is to imagine two homogeneous cylinders on top of each others, the shoot cylinder varying in radius and height representing the light acquisition (and shading) zone, and the root cylinder varying only in diameter (because of shallow soil in mountain ecosystems) representing the water acquisition zone. These cylinders are centred on cells of the torus simulation plan.

Figure 4.2: Plant geometry and growth axis.

In addition to classic variables (age, position, height, diameter, shoot and root biomasses) the plants are described by traits, that can be species specific or non-specific, others are variable (SLA, SRL) and depend on particular traits that are unique to this model: the **ratio between active tissue and structural tissue** (in shoot and root) (variables $\frac{act}{str}_{ag}$ and $\frac{act}{str}_{bg}$ in table 4.1). This couple of traits come from the evidences that numerous trade-off observed in leaves can be explained (at least partially) by this allocation trade-off between active tissue producing organic matter, but increasing respiration, and structural tissue that increase tissue lifespan.

SPECIES

Plants are characterised by state variables that describe them individually, but they also share common characteristics with individuals of the same group, (we will refer as *species* to talk about this group in the rest of the document even-though it could be a group at an other scale (i.e. population, clones). These species are the groups present in the meta-population and that can invade the simulated ecosystem. There are described by multiple traits characterising the strategy of the species (table 4.2).
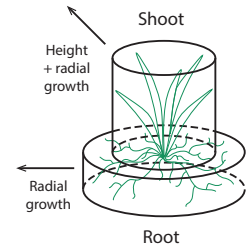
Variable	Description	Unit
x	x position on the grid	cells
y	y position on the grid	cells
age	age	days
sp	species	-
BM_{ag}	above-ground biomass	g
$BM_{ag,sen}$	senescent above-ground biomass	g
SLA_{sen}	senescent above-ground biomass	$cm^2.g^{-1}$
BM_{bg}	below-ground biomass	g
stem	stem biomass	g
$\frac{act}{str}{}_{ag}$	above-ground active on structural biomass ratio	g/g
$\frac{act}{str}{}_{bg}$	below-ground active on structural biomass ratio	g/g
h	height	cm
r	shoot radius	cm
r_r	root radius	cm
$light_{exp}$	above-ground potential resource availability	gH2O.leaf area
$water_{exp}$	below-ground potential resource availability	gH2O.root area

Table 4.1: State variables of individual plants

Trait	Range (close range)	unit	trade-off or strategy
seed mass	(0.00001 - 0.001)	g	seed ouput vs seedling productivity
maturity	-	green biomass	flowering time vs reproduction potential
fract_dev	0-1 (0.05-0.6)	-	blooming vs persistence
fract_rep	0-1 (0-1)	-	reproduction vs persistence
geometric constant (k_g)	(0.1 - 20)	-	competition sensitivity vs self-shading
plasticity stability	0-1 (0.8-1)	-	genetic information vs experience
initial water resource	(0.001 - 0.05)	$gH_2O.cm^{-2}$	water resource niche
initial light resource	(0.001 - 0.05)	$gH_2O.cm^{-2}$	light (in H_2 equivalent) resource niche
$\frac{act}{str}{}_{ag,d}$	(0.03 - 0.3)	$g.g^{-1}$	active vs structural tissue
$\frac{act}{str}{}_{gg,d}$	(0.03 - 0.3)	$g.g^{-1}$	active vs structural tissue
mean temp.	(0 - 5)	°C	early vs late germination
germination rate	0-1 (0.5 - 1)	-	good season bet-hedging
thickness	(0.012 - 0.05)	cm	WUE vs light efficiency (not in this version)

Table 4.2: Species traits

The seed-bank is the transition state between the different seasons. Individuals may persist thanks to stored resources, but they can also reproduce by the production of new individuals. Lot of grasses use clonal reproduction, in addition or replacement of sexual reproduction. This type of reproduction is characterised by a persistent link between the newly produced individuals and the parent one that allow the two to communicate and exchange resources. Such dynamics are complex and costly to represent as the link between ramets must be stored and strategies defined for the resource distribution (see Oborny 2012) for more details on clonal growth modelling). To avoid too much complexity, it is possible to approximate the representation of clones to big seeds with little dispersion around the parent plant[1]. For this reason, reproduction mechanism is reduce to sexual reproduction mechanism with production of "seeds". Seeds are stored in the seed-bank and only defined by their species and positions.

Soil is an important aspect of the model as it drives (with the precipitations) the water competition between individuals. It is however limited, as in numerous vegetation models, to a grid characterised by: its capacity to retain water, and its depth. Only the first component (water retention capacity) is spatially variable and is described by the critical water content (minimum soil water content), the saturation water content (maximum water content, the water non absorbed leaves the system we assume the same root depth for all species), and the current water content (temporally variable, depending on competition, precipitation and evaporation, between the critical and the saturation water content) only dynamic variable among the three.

SEED-BANK

[1] This would take advantage of dispersion kernels. Not implemented in current version. Dispersion is uniformly random within the simulation plan

SOIL

Figure 4.3: Soil section.

4.1.3 Process overview and scheduling

As mentioned the model runs at daily step to capture individual responses to conditions and over multiple seasons to capture long temporal dynamics. Some processes occur (or are evaluated) at the daily time-step, some at the season time-step. The following ordered list presents the different processes and the scheduling over days and season of one simulation.

One season can be divided in the following parts:

- *germination*: marks the beginning of the season when the ground is no more snow-covered;

- *growing season*: consists in daily processes like competition, production of organic matter (OM), allocation, and death lottery;

- *reproduction-invasion-persistence*: marks the end of the season when the first persistent snow-fall occurs. OM invested in reproductive tissues turns into seeds that are sampled to create the seed-bank. Seeds from the meta-population may integrate the seed-bank. Persistent perennial loose most of their biomass but storage (and eventually stem) and regrow from stored organic mass at the begining of the following season.

The *growing season* part consists in all processes evaluated every day of the growing season. These processes are:

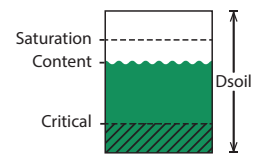- *light competition*: the individual potential photosynthetic activity is computed based on average daily light and shoot properties;

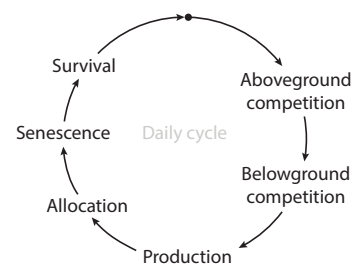Figure 4.4: Seasons cycle in *MountGrass* .

Figure 4.5: Processes in order during the daily cycle.

- *water competition*: evaporation and the individual water update (and potential water uptake) are computed based on potential transpiration, water availability and potential evaporation;

- *production*: respiration and production are computed to give the net productivity in OM;

- *senescence*: based on lifespan a part of tissue is no longer active.

- *death*: death of individuals based on their age and their desiccation stage (number of consecutive days with negative growth).

- *allocation*: allocation of produced OM to the different carbon pools of the plant.

- *grazing/cutting*: (optional) grazing or cutting of plants to a certain height. The grazing can be selective.[1]

4.2 Design concepts

4.2.1 Design concepts

This part clarifies the rules that drives the dynamics of the model.

The purpose of the model being to understand the rules that drive the community responses, we tried make the community dynamics emerge from the underlying processes of plant growth, resource use and reproduction. That means that population dynamics is at least partially emergent from the surviving and reproducing individuals. *Partially* emergent because it depends on the invasion rules applied to the system. The traits and biomass distribution that describe the community are completely emergent from the individual traits exposed by the individuals and their relative biomass and abundance.

Plants have in theory many options to adjust their phenotype and increase their fitness in response to changes in environmental conditions (resource availability, temperature, ...). High diversity of mountain grasslands suggests that multiple strategies coexist and that individuals do not change to converge toward a unique strategy. These strategies are set up at the species level by the species specific traits (see table 4.2). Therefore, individuals may only adapt morphological traits but not strategic traits (unless there is an epigenetic mechanism added). These morphological traits are: the relative biomass of shoot and root, relative proportion of active and structural tissues in each leaves, and roots (controlling respectively the SLA and SRL and the overall resource acquisition cost)[2]. Geometry traits (distribution of leaves and roots within space) are not considered plastic as grasses have far less control on their geometry than forbs or trees. Root distribution plasticity has been shown to greatly improve the individual and community productivity (Gemini article), but to keep the model (and implementation) simple we will ignore root distribution plasticity and foraging strategies to focus on allocation problems instead of spatial distribution questions. Shallow soils and relative small rooting zone are also arguments to ignore spatial distribution plasticity for roots.

In the model the realised fitness can be estimated as the capacity of plants to maintain themselves or their descendants through time. It emerges from the productivity, allocation to storage or reproductive carbon pools, and survival.

[1] remarks in grey are features or components implemented in the model but not used and-or calibrated.
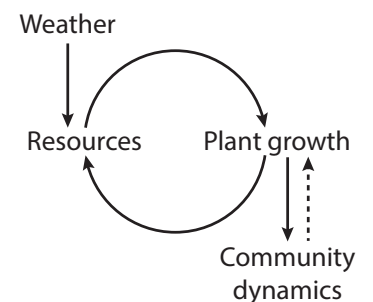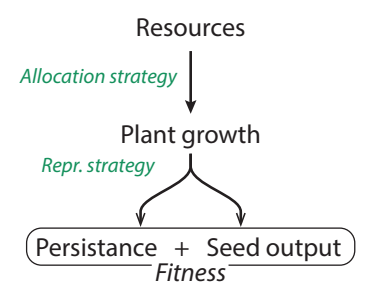
EMERGENCE

Figure 4.6: Population dynamics emerging from plant growth and weather.

ADAPTATION

[2] and optionally the proportion of stored OM dedicated to frost resistance and not to growth

FITNESS

Assessing fitness as the average number of persistent individuals is however a bit hazardous in simulations limited in time and to a relatively small spatial scale. Plus, plants cannot easily make prediction of such variable to adjust their phenotype. They need a proxy function for fitness that integrate measures of external conditions to evaluate the best strategy to develop. As said above, this strategy should be a composite between the species strategy and individual adjustment specific to the individual experience of the environment. Plant fitness is estimated by individual plant thanks to a gain function integrating current phenotype, species strategy and projection of future conditions. This gain function can take multiple forms and be more or less constraint. In the context of the model, the function should include a measure of productivity that relies on the principle of functional equilibrium - that is the allocation of organic matter to maintain the balance between the shoot activity (transpiration) and root activity (water uptake). This equilibrium can be achieved by changes in shoot:root ratio only, or also changes in active over structural tissues ratio. Further details about the gain function are discussed in the dedicated paragraphs (4.3.3). More complex form of functional equilibrium incorporating nutrients (like nitrogen) could be added to the framework of this model.

Adaptation or plasticity mechanisms imply that agents have an insight of what will be the future. In `MountGrass` we consider that plants have two main sources of information. The first source of information is the genetic information. Indeed, the evolutionary process of genotype selection has led to the selection of genotypes adapted to the local conditions. This selection relationship can be seen as a link between environmental conditions and genetic information. Because plants cannot fully predict future environmental conditions, they grow following (at least partially) the plan contained in genetic information that match conditions where previous generations grew in. This is an internal *a priori* information about the external conditions. If the conditions where the seed grow change from the conditions its genotype has been selected for, the genetic information does not fit the environmental conditions is not sufficient enough to build a working phenotype. In this case, if the plant has a plasticity capacity, it can integrate the second source of information, in the form of the experienced conditions, to its "a priori" and forge a new estimation of what conditions will be. One question emerges to this idea is: how to create an image of future conditions and how to balance the genetic *a priori* information with the experienced information ? This balance can be described by a term of "reactivity" that describe the relative weight of genetic and experienced information. A reactive species will give a higher weight to experienced condition information, whereas an stable species will give a higher weight to genetic information.

PREDICTION

The way the two source of information are brought together and used to define the plant phenotype is at the core of plant strategy and is the main feature of the model `MountGrass` .

4.3 Details

Further details on daily mechanisms are described in the following paragraphs.
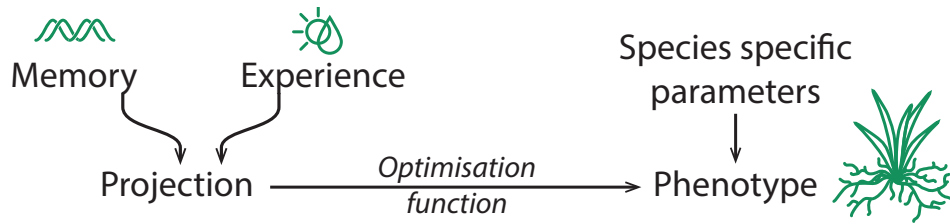
4.3.1 Initialisation

The model doesn't need particular initialisation if the state of the community species pool, the seedbank and the soil are given as inputs. Otherwise, a set of *E(n/s)* individuals are created from a set of *s* species (randomly generated if not given) and randomly positioned on the soil grid, where *s* and *n* are respectively the number of species and the approximate number of individuals within the grid. Soil grid is also randomly generated within default ranges for critical and saturation water contents then slightly smooth, and homogeneously filled ($filling = \frac{w_{cont} - w_{crit}}{w_{sat} - w_{crit}}$).

4.3.2 Inputs

MountGrass needs system state information (individuals, species, seed-bank and soil) and climate data. If the state of the system is not completely given, then the complete state is generated in the initialisation. The daily climate data at must contain the following fields:

- *date*;
- *radiance*, in $Watt.m^2$;
- *precipitation*, in mm;
- *mean temperature*, in K;
- *mean day temperature*, in K;
- *min temperature*, in K;
- *max temperature*, in K;
- *relative humidity* in %;

Vapour pressure deficit is then computed from temperature and relative humidity.

The climate data must explicitly differentiate the seasons (delimited by the first day of the year without snow and by the first day of the second semester with snow).

4.3.3 Submodels

Individuals from the seed-bank randomly germinate according to their species specific germination rate. Germination consist of investing a percentage (*mob* parameter) of the seed mass into shoot and root biomass according to default

GERMINATION

traits. This is coupled with a round of random seed death following uniform law of parameter $seed_{surv}$. Living non germinating seeds stay in the seed-bank until the next season.

Daily processes

Light competition is central in all vegetation model as it constraints the photosynthetic activity and so plant growth. To avoid costly calculation of ray propagation we assume vertical homogeneous top radiation. Relief and orientation effects is taken into account in the computation of irradiance data.

Light competition sub-model allows calculation of individual potential photosynthesis activity and light at soil surface for evaporation calculation.

Competition for light is calculated independently for each pixel, potential photosynthetic activity is then aggregated at the individual level. Each pixel can be seen as a column of homogeneous layers containing at least one individual (top layer). For each layer the light transmission is computed based on leaf density.

$$I(h) = I_0 e^{-LAI(h)} \tag{4.1}$$

where $LAI(h)$ is the cumulative LAI at the bottom of layer l (between h and $h + \Delta_h$) defined as the homogeneous layer delimited by the top of consecutive individuals in the same pixel. The LAI is calculated like this:

$$LAI(h) = LAI(h + \Delta_h) + \Delta_h.pix\_width^2 \sum_{i\ in\ l} d_i.coverage_{i,p} \tag{4.2}$$

where d_i is the individual leaf area density corrected by the coverage ($0 < coverage =< 1$) of the pixel p by the plant i, $\Delta_h = (h_l - h_{l-1})$ is the height of the layer l.

Following Thornley and Johnson, the potential photosynthetic leaf activity is calculated as:

$$P_{leaf}(h) = \frac{\alpha.I_{leaf}(h).P_{max}}{\alpha I_{leaf}(h) + P_{max}} \tag{4.3}$$

where $I_{leaf}(h)$ is the light absorbed by the leaf at height h, α the initial slope of the light response curve and Pm_i the maximum photosynthetic rate per unit of area and unit of time. I_{leaf} is the radiance at the leaf surface, derived by correcting the radiance at the top of the layer following the equation used in Taubert with the extinction and transmission coefficients k and m:

$$Ileaf(h) = \frac{k}{1 - m} I(h) \tag{4.4}$$

The equation (4.3) can be integrated over the leaf surface by mixing it with equations (4.1) and (4.2) to give the total potential photosynthesis for layer l in pixel p:

$$P_{leaf}(p, l) = d_i.coverage_{i,p}.\Delta_h(l) \int_{h_{bottom}}^{h_{top}} P_{leaf}(h) \tag{4.5}$$

the total leaf potential photosynthesis is then calculated as follow:

$$PS_{pot} = \sum_{p\ in\ shoot} \sum_{l\ in\ pixel} P_{leaf}(p, l) \tag{4.6}$$

Potential photosynthesis must then be converted to potential transpiration to define the water demand. The conversion from photosynthesis to transpiration
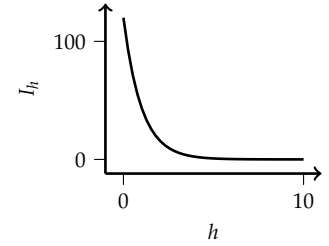

Figure 4.10: Net gain function and its first derivative.
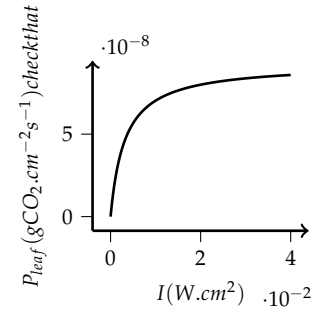Looks like there is some kind of mismatch here.

Figure 4.11: Photosynthetic saturation function

is done by dividing the potential photosynthesis by the water use efficiency (WUE). The potential activity of leaves are also dependent on the regulation of stomata so the transpiration can be written:

$$transp = \frac{PS_{pot} \cdot g_{red}}{WUE} \qquad (4.7)$$

Photosynthesis depends on gazes exchanges at the leaf surface. These fluxes result from relative concentration in carbon dioxide and water, and from the stomatal conductance. Stomatal conductance is reduced and limits productivity when vapour pressure deficit is too high [1]. A linear relationship describe this relationship:

$$g_{red} = 1 + VPD_{g\_red} \qquad (4.8)$$

[1] g_{red} is set to 1 for current version to avoid potential problems between allocation and regulation

Potential evaporation is calculated for each pixel depending on the light at soil surface:

EVAPORATION

$$\beta = 0.25 * (1 - cos(\frac{\theta}{\theta_{sat}} * \pi))^2 \qquad if\, water_{cont} \leq water_{sat} \quad (4.9)$$

$$\beta = 1 \qquad otherwise \quad (4.10)$$

$$PET = 0.0023.\sqrt{(T_{max} - T_{min})} * (T_{mean} + 17.8) \qquad (4.11)$$

$$evap = PET.\beta.I_{surface}.daylength \qquad (4.12)$$
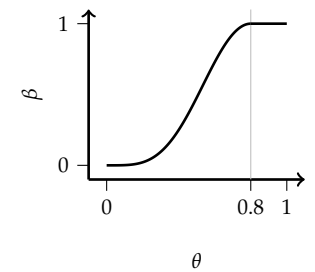
Figure 4.12: Evaporation limitation function.

Water competition is also computed at the pixel level. To determine the water uptake, first the individual water demand is computed as the minimum between the transpiration and the potential water uptake. Transpiration demand per pixel is easily calculated by dividing the total potential transpiration by the volume in the pixel $V_{i,p}$ over the overall root volume V_i. Water potential uptake is the product of root area in the pixel and root water uptake rate reduced by the water availability reduction factor U_{lim}, leading to the water demand for individual i in pixel p:

WATER COMPETITION

$$transp_i(p) = transp.\frac{V_{i,p}}{V_i} \qquad (4.13)$$

$$Wpot_i(p) = Root_{area}(p).U_{max}.U_{lim} \qquad (4.14)$$

$$Wdem_i(p) = min(transp_i(p), Wpot_i(p)) \qquad (4.15)$$

$$(4.16)$$

where, the limitation function U_{lim} is defined as in [2]:

$$U_{lim} = exp\left(\beta_\theta\left(\frac{1}{\theta_s - \theta_{crit}} - \frac{1}{\theta - \theta_{crit}}\right)\right) \qquad if\, \theta < \theta_{crit} \quad (4.17)$$

$$= 0 \qquad otherwise \quad (4.18)$$

The total water demand per pixel is then the sum of all individual water demand of the pixel and potential evaporation. If the total water demand exceeds the total water availability (W_{av} product of water content and soil volume in the
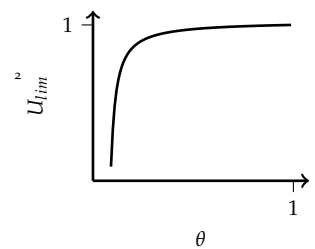

Figure 4.13: Water uptake limitation response function to soil saturation

pixel) then the available water is distributed proportionally to the individual demand.

$$Wup_i = Wdem_i.\frac{Wdem_{total}}{min(Wdem_{total}, W_{av})} \tag{4.19}$$

The potential water uptake ($Wpup$), non limited by the transpiration is calculated the same way but considering $Wdem_i = Wpot_i$ in equation (4.19).

Because the water competition is computed at the pixel level, there is no compensation between two pixels containing respectively not enough and too much water.

No radial flow of water between pixel is implemented in the model. This simplification leads inevitably to edge effects, but allows simpler implementation and is partially covered by the effect of the pixel size. Indeed, increasing pixel size would have similar effect in the pixels at the border of the rooting zone than radial flow because it would increase the potential water pool plant has access to.

Once potential and realised transpiration and water uptake are computed, plant productivity can be calculated.

Following previous vegetation models, the respiration is decomposed in growth respiration and maintenance respiration. The first is function of trait values, biomass and temperature:

PRODUCTION, AND RESPIRATION

$$R_m = \left(R_{act}.\left(Act_{ag} + Act_{bg}\right)\right).daylength.T_{effect} \tag{4.20}$$

where R_{act} is the respiration rate of active tissues, and Act_{ag} and Act_{bg} are the active biomass pools in shoot and root.

Net Primary production (in CO_2 equivalent) can then be calculated the difference of GPP and respiration, then converted in OM production thanks to tissue carbon content (under the assumption of fixed carbon content for leaf and roots between species):

$$NPP_{carbon} = (1 - R_g).(WUE.min(w_up, trans_p) - R_m) - BM_{total} * Pl_cost \tag{4.21}$$

$$NPP_{OM} = NPP_{carbon}.(12/44)/TCC \tag{4.22}$$

Here R_g is a fixed parameter but is set to 0 if the difference between gross productivity ($GPP = WUE.min(w_up, trans_p) - R_m$) and maintenance respiration is negative. Pl_{cost} is the plasticity cost as calculated in the dedicated paragraph below.

Temperature has a effect of plant activity, this effect can be modelled by a bell shape function around an optimum value of 20 °C. See Lohier for details.

TEMPERATURE EFFECT

The projection of environmental conditions is central in any implementaion of phenotype plasticity. Differences between the current perception of environment and the projections lead to adjustment of phenotype to increase fitness. In the model `MountGrass` this projection results from hte averaging of two key concept: memory and perception. The latter is relatively simple to understand and corresponds to the perceived resource availability computed as the mean potential exchange rate per unit of area (total leaf or root area) and per hour(the hourly measure is used instead of daily measure to simulate the ability of plant to perceive the photoperiod. This is an easy way of taking into account one aspect of

CONDITION ESTIMATION

seasonality without complicating the model. However, it also reduce the range of memory and its impact to determine the phenotype, as an additional information would be needed to define the optimum phenotype: the day length).:

$$light_{exp} = \frac{transp}{exhangearea_{ag}} \tag{4.23}$$

$$water_{exp} = \frac{Wpup}{exchangearea_{bg}} \tag{4.24}$$

$$\tag{4.25}$$

The former is related to the species (or group) history and result from processes of selection and acclimation. It is the default projection of resource availability when the plant is not plastic.

$$light_{est}(t+1) = (1-\tau).light_{exp}(t) + \tau.light_{memory}.daylenght(t+1) \tag{4.26}$$

$$water_{est}(t+1) = (1-\tau).water_{exp}(t) + \tau.water_{memory}.daylenght(t+1) \tag{4.27}$$

Because these are supposed to be expected conditions for the future, other formulation can be used instead of an average that is likely to introduce a lag in estimations. For example the following equation allow for a more stable projection that better fits the slower process of plant physiology adjustments:

$$light_{est}(t+1) = ((1-\tau_{react}).light_{exp}(t) + \tau_{react}.light_{est}(t))((1-\tau_{amp}) + \tau_{amp}.light_{memory}).daylenght(t+1) \tag{4.28}$$

with τ_{amp} and τ_{react} being respectively amplitude and reactivity where only τ_{amp} is used in the first equation. Such solution could limit sensitivity and phenotypic instability.

The estimation of external conditions as expressed here is then used to select the best allocation scheme during the allocation process. Limited here to levels of two resources (light and water), this estimation equation could be extended to other mechanisms such as herbivory risk, frost risk, humidity impact on water pressure deficit.

Allocation is primordial in plant development and ontogeny. The following paragraph detail the implementation of the plastic allocation in `MountGrass` .

ALLOCATION

Maturity: For most of plants the development cycle is divided in two phases of different durations: the vegetative phase when plant growths organs to gather resources and product OM, and the reproductive phase when plant take advantage of these organs to accumulate carbon and invest them in reproduction mechanisms. Plants are considered mature (they switch from vegetative to reproductive phase) in `MountGrass` when the phenologic variable has reach a species specific threshold. The phenologic variable can be either the age, the height, the biomass, degree.days, in the current version total living biomass is used as trigger for reproductive phase.

Allocation to supporting tissues: Even-though grasses do not grow tall vegetative parts like trees, some grow vertically and they are exposed to stronger winds than most of forest. Therefore they need structural supports[1]. Not all grasses grow stem, but they'll have stronger central vein in their leaves to structurally support the weight of leaves. In addition shoots and roots also need

[1] This supporting tissue mechanic is also needed to avoid exponential growth rate.

supporting tissues for water transport, for this reason the minimal mechanical support needed is calculated as a function of total living biomass:

$$support = \alpha.(BM_{ag} + BM_{bg})^{\gamma} \qquad (4.29)$$

where α and γ are allometry coefficients.

At each time step we must determine what fraction of new OM will be allocated to tissues growth while the remaining will support these need tissues. This leads to an optimisation problem numerically solved by the function `uniroot`.
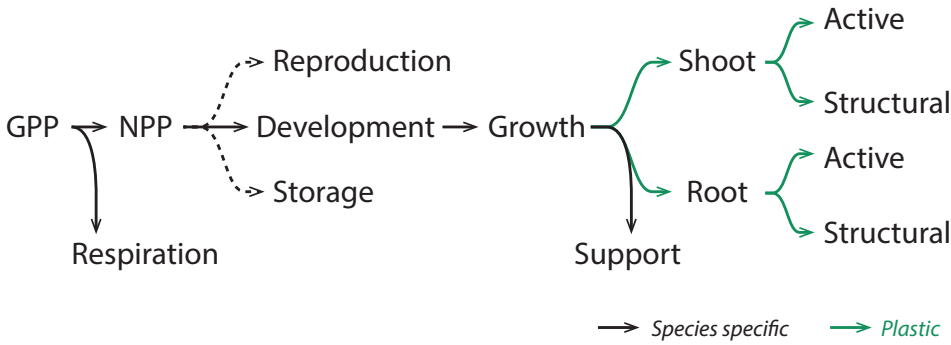

Figure 4.14: Allocation of produced organic matter to different processes and pools.

Allocation to organs: Allocation of produced organic matter is central in vegetation as it shapes the plant and define the strength of the different organs. There are multiple ways to model the distribution of produced organic matter between the plant organs. We believe that such mechanism has great impact on individual development and response to external conditions, and so on community dynamics. To explore the role of this mechanism, multiple options are implemented. The different allocation algorithms are summarised in table 4.3.

There are two major components in the allocation algorithm:

- the objective function;

- the plastic dimensions.

The *objective function*: it is the function that give an fitness estimation or gain metrics for any given phenotype. This function is used to compute the optimum phenotype (phenotype at which the function is evaluated at the maximum value), or rank alternative phenotypes[1].

The *plastic dimensions*: they are the dimensions along which the individual can move. The space defined by these dimensions is the phenotypic space within which each individual plant can look for an alternative phenotype. They do not necessarily fully define a phenotype since some dimensions of the individual's phenotype can be fixed [2].

The objective of this step of the model is to solve the objective function with the unknown variables being the plastic dimensions (RSR, SLA and SRL). In case of simple equations an analytical solution could be used to find an optimum [3]. However, because the analytical solutions are already non trivial and the model is likely to evolve, a numeric solving method is adopted. **Need to detail the random algorithm.**

---

[1] in this case, if not all possible phenotypes are tested, the solution might be only a local optimum. This is the case in *MountGrass* .

[2] either by shared parameters of species specific ones.

[3] under the condition that such optimum exists. The design of the model should ensure that.
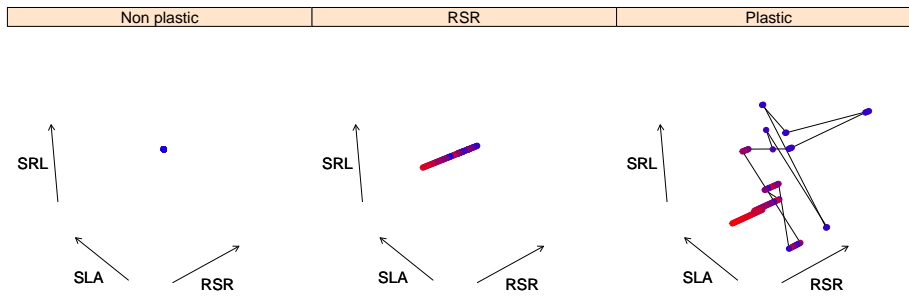
Figure 4.15: Trajectories of a plant in the trait space depending on the plastic dimensions explored.

Also make a note on multiple optimum and the choice for a 'gradient descent" type of algorithm. Also sensitivity at eraly stages

Algorithm	Objective	variable RSR	variable SLA-SRL	stochastic
No plasticty	—	○	○	○
Equilibrium	functional eq.	●	●	●
Eq-Fixed	functional eq.	●	○	●
Optimisation	instantaneous gain	●	●	●
Optim-Fixed	instantaneous gain	●	○	●

Table 4.3: Allocation algorithms implemented in `MountGrass`

No plasticity allocation: this allocation is very similar to classic vegetation model where the biomass is allocated to the different carbon pools according to species specific parameters. But `MountGrass` differs from other models by the order of the different steps of growth. In this model, the senescence comes between the allocation step and the resource competition-production steps [1]. The partitioning coefficient are directly computed from species default trait to maintain the phenotype after senescence.

[1] see plastic allocation algorithm for explanation

Fixed trait allocation: The fixed allocation supposes the allocation on OM to maintain trait values to fixed species specific values. The shoot:root ratio may however change to maintain functional equilibrium. The shoot root ratio is derived from the following equation of the functional equilibrium:

$$SLA.BM_{ag}.light_{est} = SRL.BM_{bg}.water_{est} \tag{4.30}$$

$$\frac{BM_{ab}}{BM_{bg}} = \frac{SRL}{SLA}.\frac{water_{est}}{light_{est}} \tag{4.31}$$

where $light_{est}$ and $water_{est}$ are the estimated resource availabilities.

Plastic trait allocation: Another approach to allocation is to try to optimize phenotype based on a fitness proxy. This proxy can be the sum of NPP, tissue turn-over loss and plasticity cost. But in a complex model like `MountGrass` , plant performance is function of multiple aspects:

- individual organ efficiency;

- relative mass of each organ;

- balance between organ water exchange activities.

And this could be extended to herbivory or frost risks. To take into account all these components, and take advantage of having all processes already made explicit by the implementation in the model, the daily processes of senescence and production are recalculated according to the **estimation of conditions** and the plant phenotype. This function is used to rank different alternative phenotypes (algorithm detailed below).

Plastic trait equilibrium: An alternative approach can be easily derived from the previous one and extend the principle of the first: the functional equilibrium with plastic traits. This approach consists in using the same algorithm as before but rank phenotypes with a function negatively correlated to the difference between estimated shoot and root activity. Such mechanism would nonetheless require the algorithm to look for close solutions within the allocation space to avoid convergence or drift from species strategy. Having non zero cost of plasticity in this approach should limit the drifting of the plant phenotype.

Fixed trait optimisation: This algorithm takes the idea of the optimisation algorithm but limits the plastic traits to the RSR ratio. If we can expect similar response than the fixed trait equilibrium if we suppose that the equilibrium is the main aspect of plant performance, global efficiency being considered in this case the result may vary.

Alternative phenotypes are computed from the actual phenotype and random uniform distribution of available organic matter to the main active and structural carbon pools of the plant.[1] ... This algorithm has the advantage of being relatively cheap compare to other optimization functions, however its performances are variables and it is very sensitive to the number of samples used. As a consequence there is a trade-off between model stability and performance as a function of number of samples (*i.e.* alternative phenotypes) considered.
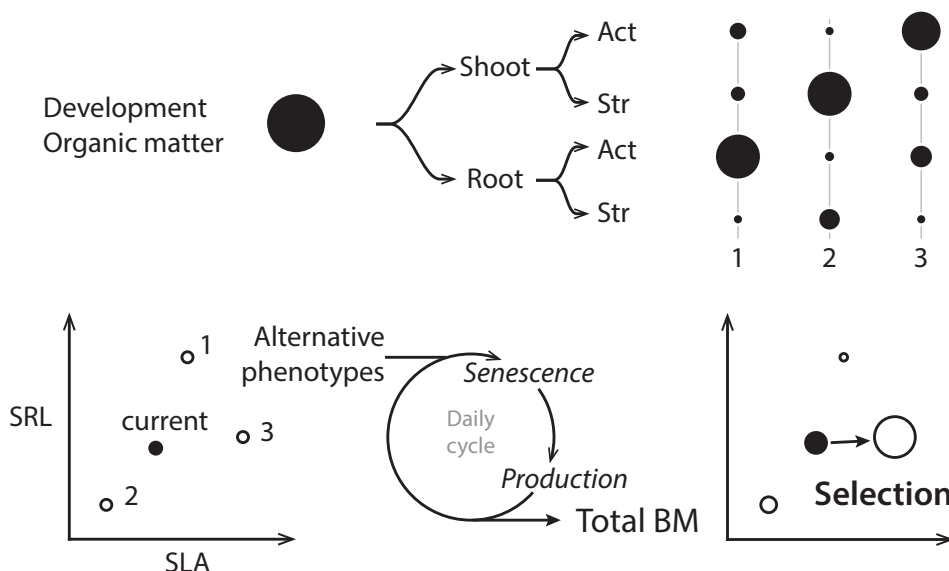
Figure 4.16: Algorithm for the evaluation and selection of randomly generated alternative phenotypes.

The limits and costs of plasticity has long been discussed in related litterature. If *MountGrass* is intended to be used to examine ecological costs and limits, it has to include physiological aspects of plasticity limits. There are two physiological processes involved in the mechanism of altering a phenotype based on changes

PLASTICITY COST

in external conditions: sensing and signalling. 'Sensing' relates to the capacity of the individual to perceive environmental conditions. This is related to capacity of the individual to perceive the environment and should therefore be considered constant over time. To take into account the cost of precise sensing, the first component of the plastcitiy cost is proportional to τ.

The other component is related to the capacity of the plant to transmit this knowledge of conditions to change the development plan toward a new phenotype. This cost is proportional to the carbon based distance (calculated as the difference between proportion of active tissues) between the default phenotype and the alternative (during allocation algorithm) or current phenotype.[1]

Plasticity cost is the sum of both component and is proportional to the total biomass since most of tissues should have the appropriated cell machinery and are affected b plasticity.

[1] We could imagine cost based not on the default, but previous phenotype, but it would have lead to large phenotypic shifting and convergence.

$$pc_{maintenance} = (1 - tau) * pc_m \qquad (4.32)$$

$$pc_{plasticity} = d_{traits} * pc_p \qquad (4.33)$$

where d_{traits} is the euclidean distance between default phenotype and the alternative phenotype in the space defined by the proportion in active tissue for shoot and for roots.

Plasticity in trait suggests that trait values are modified in time. Because plants are described by single values (e.g. one SLA value for all leaves), this values must be updated after the plastic allocation. This values could be updated as average of old tissue value weighted by old biomass and new tissue value weighted by the freshly produced biomass. This however would work only if active on structural tissues ratio were linearly link to others traits. This is not the case, it is then simpler to consider that organs have uniform active and structural distribution. This hypothesis suggests that whenever the allocation scheme change, old tissue reallocate their own biomass to follow the new scheme. Nevertheless, to avoid full plasticity allowed by this hypothesis, the changes in trait carbon pool sizes is limited by the produced biomass available for plant development.

ollowing the following survival probabilities:

From this, supposing homogeneous distribution of active and structural tissues within an organ allow to directly link the size of the carbon pools to average traits by the following relationships:

TRAIT UPDATE

Figure 4.17: Specific Leaf Area as a function of the proportion in active tissues in shoot

$$SLA = \frac{1}{(th.p_{act_{shoot}}.\rho_{as} + th.(1 - p_{act_{shoot}}).\rho_{ss}).V_t} \qquad (4.34)$$

$$SRL = \frac{1}{(s_r.p_{act_{shoot}}.\rho_{ar} + s_r.(1 - p_{act_{shoot}}).\rho_{sr}} \qquad (4.35)$$

Senescence is the process of ageing of tissues. This process usually occurs at the scale of an individual organ (e.g. a leaf), however `MountGrass` does not consider organs independently because it would be complex and computationally expensive to follow multiple leaves and roots for all individuals. So the process is considered homogeneous over all tissues. To emulate the senescence process senescence is calculated from the tissues lifespan, giving :
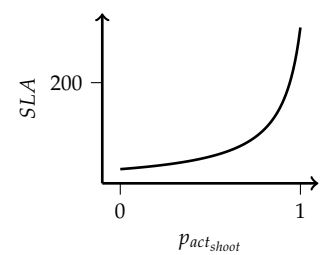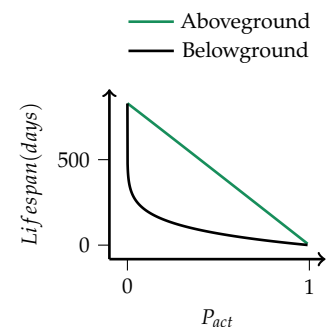
SENESCENCE

Figure 4.18: Lifespan of organs as a function of proportion of active tis-

$$sen_{leaf} = \frac{1}{LLS} \qquad (4.36)$$

$$sen_{root} = \frac{1}{RLS} \qquad (4.37)$$

Because `MountGrass` does not contain any mechanism preventing plant from growing only active tissues[1], it is necessary for this cost function to make this strategy unreliable. The is then expressed as follow:

[1] it was intended to make the WUE negatively correlated to the amount of structural tissue per area.

$$LLS = LSs_{s0} * (1 - p_{act_{shoot}}^{LSs_1}) \qquad (4.38)$$

$$RLS = LSr_{s0} * (1 - p_{act_{root}}^{LSr_1}) \qquad (4.39)$$

where LLS and RLS are respectively the leaf and the root lifespans calculated as negative log-linear relationships with proportion of active tissue.

Root senescent tissues disappear from the system. Information about senescent aboveground biomass is stored, but senescent biomass effect of light competition is ignored in this version because as it is implemented senescent tissues appear early in plant development and have large negative effect on light absorption.

To the natural senescence and artificial cost of having only active tissue, an additional component can be added to the turn-over rate: the negative NPP. In case of negative NPP the biomass will be taken from the already allocated following the shoot root ratio. This can lead to a lower overall productivity (negative growth during unproductive periods) but also changes in the equilibrium if tissue have different efficiencies.

Death is modelled as in Reineking [2]. Age and desiccation (negative NPP) are the two reasons why a plant can die. The two death mechanism are simulated by independent random lotteries following the following survival probabilities:

$$P_d = exp\left(-\left[\left(\frac{des}{\alpha_d}\right)^{\gamma_d} - \left(\frac{max(des-1,0)}{\alpha_d}\right)^{\gamma_d}\right]\right) \qquad if\, NPP \leq 0 \qquad (4.40)$$

$$= 1 \qquad\qquad otherwise \qquad (4.41)$$

$$P_a = exp\left(-\left[\left(\frac{age+1}{\alpha_a}\right)^{\gamma_a} - \left(\frac{age}{\alpha_a}\right)^{\gamma_a}\right]\right) \qquad (4.42)$$

Figure 4.19: Age related survival probability function

State of dead individuals is store until the end of the season when seed are stored in the seed bank. Seeds of dead individual then join other seeds.

Sexual & clonal reproduction: reproduction is handled at the end of the season. To limit the number of parameters reproduction is limited to the division of the invested biomass in reproduction by the species specific seed biomass into a round number of seeds (the number of seed per plant could also be a differentiation axis). Clonal reproduction is not explicitly represented but can be mimic with bigger seeds and by adding a dispersion process around the parents. The seeds then are added to a potential seed-bank. This potential seed-bank is sampled, after eventual invasion, and merged with the existing seed-bank.
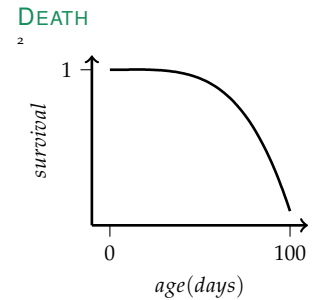
Persistence Some grasses are perennial and persist over the cold season. This is allowed in the model by investment in storage tissues instead of reproductive tissues. At the end of the season, marked by the first snowfall, these plants (with non-null storage biomass) loose their living and supporting biomass, but will regrow from a large pool of store organic matter.

Explore management effect on the community is one of the aim of the `MountGrass` model. The management of mountain grassland will be explore only of the aspect of biomass removal, as productivity changes can be explore by changing the parameters value as the nutrients are not explicitly modelled. The management sub-model is not detailed here but it is based on the mapping of biomass and target trait (e.g. fraction of structural biomass as proxy for digestibility). Both cutting and grazing can be modelled but require management plan in the form of calendar of management operation and a cutting height or harvest objective.

GRAZING/CUTTING

4.4 Limitations and problems

4.4.1 Link to the real world and data

The generalized framework introduced in `MountGrass` allows to create a rich community in a high number of dimension strategy space, it however comes with downsides.

One of the first problem is that some parameters (not explicitly detailed here) are hard to access (e.g. tissue density of active, or structural, tissue). It makes the calibration long as the incertitude for some parameters is very high. This is problematic when calibration is made difficult by a large execution time (see subsection below).

Another issue with such model is that the high dimensionality of the species strategy space allows a lot of different strategies that are not viable. This could be overcome by selection mechanism over multiple plots, but again require a lot of simulation. Moreover, there are dependencies between viable strategies and parameter values that makes it hard to restrict meta-community to viable species to set-up calibration runs.

It is possible to extract summary statistics from the model output and compare them to information from collected data making calibration and community analysis easy. However going from the data to feed the model is harder, indeed without a great knowledge of a species it is hard to define its representation within the model framework. To do so would require the knowledge of the plasticity capacity to set the reactivity, anatomical traits to define default ratios of active over structural tissues, and climatic niche to define the *a priori* estimation of external conditions. Without making direct association with real species, it is possible and interesting to try to reproduce some strategies and explore their response to various conditions.

4.4.2 Technical problems

The model is implemented in R with some limiting function using RCPP to speed up the process. Simulations are fairly slow compare to theoretical C++ equivalent

code. The main problem is in the choice of the data structure. Indeed agents are stored in data.frames that are often modified with the `mutate` function, that makes the implementation much easier and the code readable, but slow down the execution due to constant condition checking on operations. This makes calibration routine methods almost impossible to use as they demand a very number of runs to be efficient.

The slowness of the model also limit to simple algorithms for the research of favourable positions in the allocation space.

IV

Individual performance: strategy and plasticity

1 Results: Model's properties and individuals response

1.1 Parameter filtering and sensitivity analysis

Obj: give confidence in the model, demonstrate is able to reproduce simple growth pattern.

Obj2: have a beter idea of plasticity effect on growth. growth plastic and non plastic parameter filtering: can we distinguish species thanks to species specific parameters instead of shared parameters.

does plasticity make it easier ?

Impact of plasticity related parameters.

1.1.1 Method

Pot data consists in total biomass and root shoot ration (RSR) data of ... species grown in pots by Peterson and al. (peterson). This old dataset has the advantages of being grass species grown in a described steady environment with two conditions of watering with measures of essential components of growth: biomass and RSR. The inputs used to simulated these experriment are detailed in appendix.

Bayessian calibration could not be used for the model considering the number of parameters and the simulation time. A filtering process has been implemented in R. Parameters are sampled following the LHS method (from `lhs` package) within parameter ranges (desccribed in table ...) defined from the litterature, and constraints dicted by desired behaviours from the model. When necessary the sample is log transformed. Because of strong relationship between exchange rate parameters and cost of exchagne area, exchanges rates parameters are expressed on a mass basis for sampling then transform to an area basis for the model. Phtosynthetic activity is defined relatively to the water uptake activity and water use efficiency (WUE) to avoid extreme root shoot ratios.

Once generated a first filtering is applied to save simulation time and avoid unrealistic trait values (see table for ranges extracted from LES data in alpine biome) that are not tested against calibartion data.

Once the parameters transformed and filtered, simulations matching growth conditions in Peterson experiments.

Generated data from finished simulations (i.e. plant lives until the end and do not exceed model's internal size limits) are then compared to experiment data

species by species. Parameters of logistic distribution are computed from species means and standards deviantions for RSR and total biomass. The use of this distribution form is justified by the intrinsic form of RSR measure and the need to reject negative values for total biomass. A parameter set is accepted for one species if it within a 95% range of the calculated distribution for both RSR and total biomass in wet and dry conditions.

1.1.2 Results

. Calibration filtering results in the selection of n parameter sets over m prese- $\quad$ INDIVIDUAL CALIBRATION
lected parameters sets. Accepted sets are distributed among the 11 species of the dataset like presented in the table. Species A, B and C are the most numerous. sensitivity analysis. The models about seems to be sensitive to the following parameters: r_1, β_0, P_{max}, u_{max}, k_{or}, ρ_{ar}. The four first parameters are related to global resource availability and directly related to growth rate, while the second and the last three and related to the below-ground resource foraging and exchange rate.
Total biomass is particularly sensitive to exchange rate parameters, but also tissue construction cost. (not shown)

Plasticity does not change the acceptance rate in any form (only slight increased from 0.26% to 0.38%). Despite non overlapping (around respectively and third and a quarter of accepted parameter sets are shared between non plastic and plastic calibration) the distribution of not shared parameter sets are very similar and does not show any clear pattern.

Figure 1.1: Acceptance rate per parameter for individual growth. No plasticity
Figure 1.2: Acceptance rate per parameter for individual growth. RSR plasticity

Acceptance rate without plasticity: Acceptance rate with RSR plasticity

	species	nb accepted	rate
1	Silene acaulis	227	0.02
2	Trifolium dasyphyllum	271	0.03
3	Geum rossii	51	0.01
4	Thlaspi alpestre	342	0.03
5	Deschampsia caespitosa	0	0.00
6	Eriogonum umbellatum	500	0.05
7	Townsendia scapigera	593	0.06
8	Astragalus whitneyi	1570	0.16
9	Lupinus lobbii	678	0.07
10	Erigeron peregrinus	1	0.00
11	Oxyria digyna	0	0.00

for equilibrium:
Change of relationship between parameters and acceptance rate -> none
accept = f(tau)

	species	nb accepted	rate
1	Silene acaulis	396	0.04
2	Trifolium dasyphyllum	317	0.03
3	Geum rossii	72	0.01
4	Thlaspi alpestre	360	0.04
5	Deschampsia caespitosa	0	0.00
6	Eriogonum umbellatum	805	0.08
7	Townsendia scapigera	930	0.09
8	Astragalus whitneyi	2424	0.24
9	Lupinus lobbii	868	0.09
10	Erigeron peregrinus	0	0.00
11	Oxyria digyna	0	0.00

PCA reveal that sensitive parameters are also the dominant variables in the main components of the component analysis of the accepted parameter sets. Species cannot be distinguished on the two main component space, neither on 1 or 2D species specific parameters space (l_ini, w_ini, w_ini vs l_ini, as_s_d, as_r_d, as_r_d vs as_s_d) despite small variations in distribution shapes between species.

Figure 1.3: Importance of the random forest to explain filtering outcome (accepted or rejected) of a balanced sample of parameter sets between plastic tested (all accepted parameters and an equivalent sample component parameters). RSR plasticity.

Figure 1.4: Acceptance rate for plastic (all accepted parameters and an equivalent sample component parameters). RSR plasticity.

Rerun acceptance rate for non plastic simulations with growth only.

1.1.3 Discussion

Growth is reproduced, but only for one species, not full strategy space.

Sensitivity of different variable to the parameters make sense and align with the two criterion of selection (that work with the independence of trade-off).

Root shoot ratio changes were not captured by the model. The structure of the plasticity mechanisms does not work with the given watering cycle. Needs to add one parameter for reactivity.

1.2 Individual level behaviour and properties

1.2.1 Method

To further reduce the number of parameter sets considered, we proceeded in an additional filtering step. Because the first filtering was conduced for only one strategy over the whole 4D strategy space (l_ini, w_ini, as_s_d, as_r_d) it is necessary to verify that other strategies do not lead to potential Darwinian demon. This should be limited by the choice of priors, while at the same time promoted by the selection of parameters increasing growth to counter balance potential unfitted strategies[1].

All common parameters for pot simulations. i.e. weather, soil, default species parameters.

ACCEPTANCE RATE

SENSITIVITY
ROOT SHOOT RATIO AND PLASTICITY
GROWTH AND STRATEGY SPACE

STRATEGY DIVERSITY FILTERING

[1] Better do that beforehand than after... But I guess it's too late now.
SIMULATION SETUP

1.2.2 Results

1.2.3 Discussion

Allocation rules are extremely important as they reduce the phenotypic space explore. Without even considering plasticity. Need a good understanding of the performance within the phneotypic landscape. Plus there is a need for alignment between starting phenotype and endpoint. Will also affect how plasticity is driven.

ALLOCATION RULES, PLASTIC-ITY AND PERFORMANCE

Allocation trade-off allow for strategies from the fast-slow spectrum to arise, independently for shoot and root, in coherent framework. Potential effect of other strategy axis can be analysed alongside this trade-off, even if they affect composite traits like SLA or SRL.

FAST SLOW STRATEGY AND AL-LOCATION TRADE-OFF

Memory is a strong enough driver to control plant organ strategy. The effect of overall activity should be studied too and considered if memory is used to determine the default phenotype.)

MEMORY AND PHENOTYPES

1.3 Performance landscape, plasticity and response to a gradient

1.3.1 Method

1.3.2 Results

1.3.3 Discussion

Somehow I need to talk about the cost of being wrong. Can be observe in the delta heatmap on delta strat and delta w-ini: in this case there is less impact of being wrong of memory if you're good with strategy, because your not in different conditions...

CONVERGENCE TO SUBSPACE

The phenotypic plasticity implemented in `MountGrass` improve the relative performance of multiple strategies by concentrating the plant toward a subspace of higher performance for most of plants. Convergence to a smaller subspace can be assimilated to reduction in phenotypic diversity, but it reduce performance heterogeneity and should favour local plant diversity. Meta-community diversity is however reduces by the reduction of potential axis for niche differentiation. Plasticity costs and limits should play major role in the balance between these mechanisms. Community level simulations are needed to further understand the cumulative role of competition, spatial and temporal variability and plasticity costs on phenotypic plasticity influence on plant community dynamics.

Phenotypic plasticity

IMPROVEMENT IN VARIABLE CONDITIONS

HETEROGENEITY OF RE-SPONSE

Kichenin (different response to gradient) Doesn't work in this framework: Not so sure about that: depending on your initial memory plants show directional changes toward one phenotype. Yeah, but they should have converged for other conditions too... So, it doesn't work. Might be explained by:

- different conditions: because heterogeneity and habitat selection, or changes in competition hierarchy;

- different ways to tackle changes on one dimensions;

- different weights between mechanisms impacting composite traits, because of the different traits.

V
Community dynamics

1 COMMUNITY LEVEL CALIBRATION

1.1 Method

New random parameters sets (with no species specific parameters) for population dynamics and competition specific parameters (see table ...). Sequence of around 60 year for each site. Parameters were selected by...

FIELD CALIBRATION

Field data has been collected between years 201 .. and 201 by Claire Deleglise and al. ().

FIELD DATA

Weather data has be computed by the MeteoFrance model SAFRAN by ... using GPS coordinates and slope, azimuth and horizon computed from a "MNT". These parameters were also used by the model CROCUS to compute snow accumulation and melting. These high frequency data (resolution under 1h) have been average daily and used to compute input variables for `MountGrass` .

WEATHER DATA

1.2 Results

2 PLASTICITY: A WINNING STRATEGY ?

3 PLASTICITY MECHANISM OF COEXISTENCE

VI

Synthesis & Outlook

1 SYNTHESIS

Point out the novelty, acheived work

1.1 Phenotypic plasticity...

1.2 The limit of the species.

In this work, but also because of the improvement of molecular biology, and the deeper and deeper dive ecology is doing within individual, the limits of species are fuzzy (started with trait and the introduction of continuity). At some point, there will be a need for a way to go back from the a space of numerous continuous dimensions to the species. Also, understanding species as evolving 3D objects, where the different aspects of intra-specific variations play different shaping roles.

2 Outlook

Further reading, thinking and rambling about what's developped in the papers.

3 Extensions

This section is meant to include thoughts and ideas on how to extend `MountGrass` but that could not be included in the first versions of the model for various reasons. Despite not being included, these extensions are interesting from a scientific or technical point of view, and I hope these notes can be useful to anyone interested in `MountGrass` or individual based vegetation modelling.

3.1 Include nitrogen: source of trade-off

As seen previously in chapter , the emergence of trade-off in growth strategy in the actual framework actually rely on a strong genetic constraint over plant plasticity. Indeed, without plasticity cost and low reactivity there would be a high rate of phenotypic convergence of individuals from different species. This is explained by the existence of optimum carbon partitioning (for a given size) in a stable environment. The coexistence of different resource use strategies (exploitative vs conservative) is allowed only through temporal variations and non equilibrium state. This is quite common since a lot of models will predict rapid dominance of one entity in case of equilibrium (need references here).
Multiple questions arise from this observation: are the conclusions of this work still interesting in the understanding of the coexistence mechanisms? (I hope I did convince you in the dedicated part of this document, see .. for more details), is it possible to see coexistence of multiple strategies in a temporally stable environment? how can we produce trade-off by including only one more resource?

In the following paragraphs I try to answer these questions with theoretical arguments and suggestions on how to integrate them in `MountGrass` .

3.2 Stable coexistence: the need for a resource dependent tissue efficiency

Coexistence mechanisms are listed and detailed in the introduction of this thesis (see chapter **??**). Here I focus on the efficiency of tissues... Nitrogen based, why coexistence ? different phenotype correspond to different limiting resources and for different resource availabilities, different phenotype will optimize the return cost of tissues.Nitrogen also allow the model to have an extra dimension into strategy: WUE (local scale) versus NUE (global scale) (element of reflexion in Maire's thesis).
Its also can be related to

3.3 Specific resistance carbon pools: diversify strategies (and memory)

Original idea was to have specific carbon pools for different function, and weight the relative allocation based on gain projections.

3.3.1 Resistance carbon pools

3.4 Local adaptation and epigenetic: between species and individual memory