CLÉMENT VIGUIER

PHD THESIS

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INTRODUCTION

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Objectives

1.1 Generic framework for modelling of plant communities

1.2 Effect of phenotypic plasticity on plant community dynamics

Individual level

Community response to drought event

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LITTERATURE REVIEW

2.1 Context: mountain grasslands and climate change

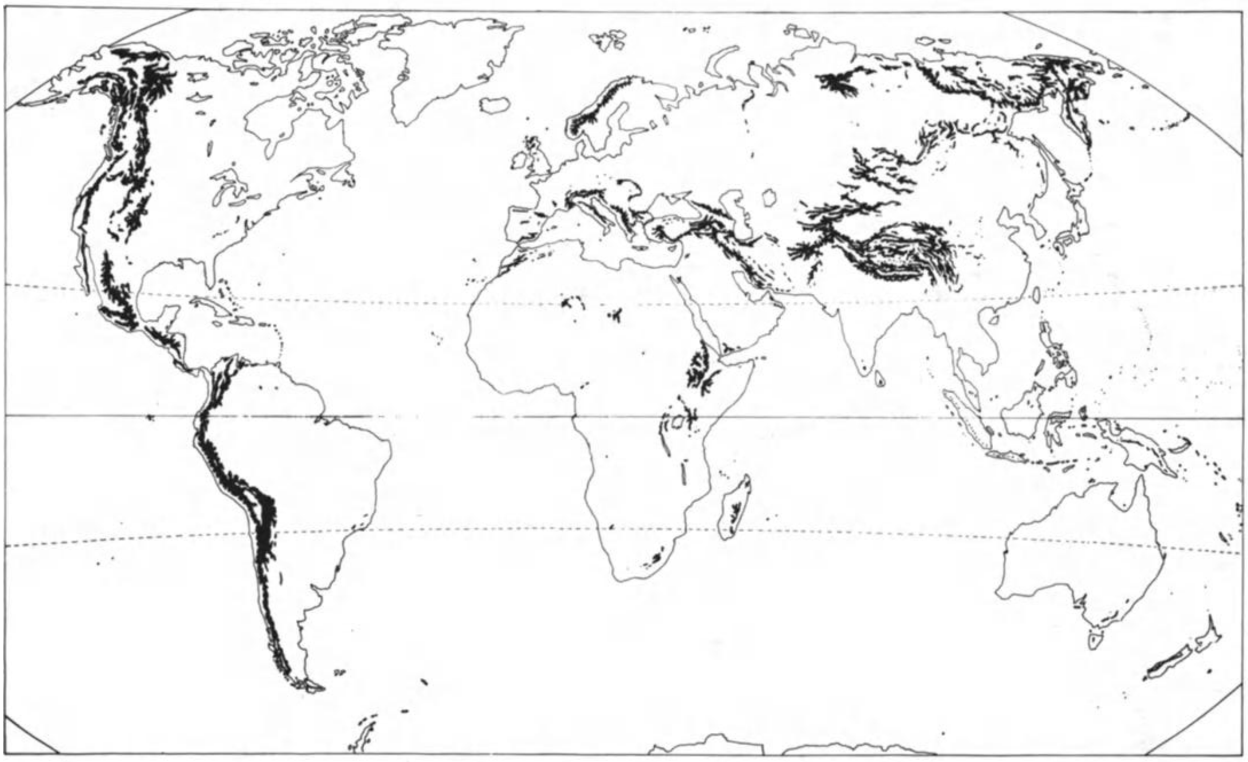

Figure 2.1: Distribution of alpine habitats

Climate change is probably the greatest challenge the humanity has to face this century. Expected drastic changes in both average climatic conditions and punctual climatic event frequencies and intensities will, and already have, an impact all around the globe on multiple aspects of our lives. From agricultural and economic, to social and political, but also scientific and technical, the problems for human societies are numerous and multidimensional.

Need to better understand and predict natural systems. Mountain grasslands are susceptible to be greatly impacted (even if certain think they might not). And in new ways as the rising temperature will certainly lead to migration to higher altitude, increasing the island characteristic of alpine habitats and reducing links between communities, and at the same time increasing the opportunity of invasion by lower altitude higher temperature species.

Detail a bit the characteristic of mountain grasslands, (snow, islands, grazing) the effect on species (snow-bed species, link to meta-community, diversity, species adaptation to frost etc... and how global change may affect that.

Because of that mountain grasslands are rich in species, but also vulnerable, that is why in parallel of predicting climate change, we also need to understand ecological mechanisms under this diversity and how they can be affected by global change [1]. A key part in community diversity and in adaptation of communities also lies in the diversity and adaptation of individuals, so we are interested in intra-specific diversity and phenotypic plasticity [2].

[1] section 2.2

[2] section2.3

2.2 Diversity and coexistence mechanisms

Diversity of natural systems have long been a subject of admiration but also a mystery to the scientific community. The extraordinary multitude of species and individuals living at the same time, in the same space, is hard to reproduce and to explain. This is particularly true in plankton communities where the resources are limited to few nutrients (nitrate, phosphates) and light. Early coexistence theories, like the competitive exclusion principle that predicts that the number of coexisting species at equilibrium can at most be equal to the number of limiting resources, fail to explain such variety. This gap between empirical observation of high diversity in different systems and at different scales, and the lack of theoretical explanation was called the *plankton paradox*. This paradox has now received multiples answers **NEED REFS**[3], but diversity and coexistence mechanisms are still investigated Falster et al. (2016). This illustrates our will to understand these mechanisms, but why are we still struggling with questions that animated ecologist decades ago? and why are we still interested by these questions? It is hard to answer the first interrogation, but the diversity of the interactions within such systems and the diversity and variability of external drivers shaping them are the main factors. That also explains partly the second question, and why scientists explore the genetic diversity of gut bacteria, or the phylogenetic diversity of phytoplankton in lakes, or the diversity of plants species from tropical forest of Brazil to snowy slopes of Alps. But besides the curiosity of scientists, studying the machinery behind the functioning the natural communities is essential if we want to understand and predict how they can evolve under the pressure of changing drivers, and how they can be managed. The following paragraphs attempt to explain the value of diversity, and so why we have to predict and manage it at best, and where is our current understanding of underlying mechanisms.

[3] discussed in later in subsection 2.2.2.

I may have been a bit far. Recentrate around mountain grasslands

2.2.1 Effects of diversity

Conservation
productivity
resistance ?
Ecosystem services and complementarity

2.2.2 Mechanisms for coexistence and strategies

main theories: niche, neutral, individual based. -> scale and dimension dependant.
chesson Chesson (2000)
Spatial and temporal variability
trade-off, strategy space, and variability.
in the end it's rarely direct interaction but capacity to respond to stress and interect interaction through resource pools.
chemical physical trade-off vs ecological trade-off.

STRATEGY SPACE AND TRADE-OFF
ABOUT TRADE-OFF

2.3 global change and community dynamics: theory and empirical results

2.3.1 Community dynamics: from individuals to group dynamics

Need to highligth how community dynamics emerge from individual response and interactions.

2.3.2 Intra-specific variability

frame of reference: deep traits vs shallow traits. definition of functional trait.
source of intra specific variability: genetic vs ontogeny vs plasticity (epigen)
effect on niche and interactions: effect on coexistence
-> plasticity a special form of ISV

2.3.3 Understanding phenotypic plasticity

adaptive intraspecific variation
cost and limits van kleunen, Dewitt and sultan
effect on coexistence and community

Molecular basis of phenotypic plasticity

Phenotypic plasticity lies both in the perception of external conditions through sensor organ and signaling pathways (auxin pathway, root stones for gravity ...), and the integration of this information to alter the development plan. This integration must be coordinated at the scale of the plant according to rules or objectives, question partly explore in this work, but ultimately is applied at the cell levels.
Because of the complexity and our partial understanding of these mechanisms, we will not attempt

to model them. However I hope that this little overview of molecular mechanisms at the scale of the cell will give the reader an idea of the processes behind the abstract concepts used in this manuscript.

BLABLABLA and figure

The diversity of mechanisms and scales (both spatial and temporal) these processes can act inside of plant gives an idea of the diversity of strategies a plant can deploy to face changes of its environment. Considering this complexity, only a small fraction can be explored in such model as MOUNTGRASS, but hopefully it will help make progress in our understanding of the role of these molecular mechanisms at the scale of the community.

2.4 Existing modelling solutions and approaches to question global change effect on vegetation community

Message: modelling coexistence is a challenge because 1) do not know/understand all mechanisms, 2) challenging to incorporate enough mechanisms, 3) costly computation and data wise. -> need for more generic and complete (multiple mechanisms approaches.

DGVMs
IBMs
Reaction norms
Source sink models
Functional-Structural plant models FSPMs ? vos 2009
Functional equilibrium. Somehow similar to the source sink in its philosophy, it allows optimisation of phenotype for multiple resources.

2.4.1 Modelling vegetation - traits and strategies

traits & strategies
existing models: a gap to fill
coexistence processes

II

MODELLING ALPINE GRASSLANDS: GENERICITY AND PLASTICITY

1

Mechanistic model for plant community dynamics centred around carbon allocation

Paper 1:

1.1 Introduction

1.2 Strategy space and allocation pools

Leaf economic spectrum + Shipley + Poorter

1.2.1 Allocation or anatomy: a choice to make

what is SLA and SRL: cost of exchange area: tissue density, tissue thickness. Poorter 2009, grace2017, Katabuchi 2017, de la riva 2016
THere is not only coordination -> part of RSR is explained by SRL:SLAFreschet et al. (2015a). Multiple source of information (memory) that affects these traits: composite traits that affect multiple fitness dimension -> memory not only for climate. -> but also coordination. More tight trade-off for root with smaller changes in SRL and more changes in RMF, the opposite for SLA. Need for a model that allow such asymmetry. Freschet et al. (2015b)

1.3 Model overview

PSEUDO-CODE AND ROUTINE ALLOCATION

mechanism and stochasticity
5 types of allocation

1.4 Plasticity: between species memory and individual experience

1.4.1 Concepts

MEMORY

Genetic memory (see Sonia Sultan book for references). Selection and evolutionary processes.

EQUILIBRIUM AND EFFICIENCY

OPTIMUM, STRATEGY AND MEMORY

There might be optimum. But not easy to compute, especially when you consider more complex cost and interactions. Depend on different efficiencies and equilibrium... Also, you may want to avoid efficient by risky strategies (if you wrong, or if there is a quick shift). Need for strategic traits to drive allocation more than memory.
Ok but what happen with optimisation allocation ? -> need the strategy to be tightly linked to memory. But that part has requirements: memory is a reliable source for strategy. Ultimately the resource availability is only one (ok, maybe two) dimension to phenotype optimisation. This strategy trait is necessary as other aspects of fitness are ignore (temperature implemented but not tested, grazzing vulnerability, frost damade, WUE, CO_2 etc...) If you multiply mechanisms affecting the fitness you complexify the fitness landscape and allow for multiple strategies to be explored. Otherwise you must aartifically constraint.

This is crucial to discuss this important aspect of strategic differenciation emerging for processes and how plant change strategy as the projection of environment evolves. Memory then plays more a role of sensitivity (with tau).
But for the moment the partial implementation of that through the artificial but meant to disappear default strategy is making analysis and assumptions difficult. Ok, but how do you treat it ?

equilibrium, resource use, resource availability, condition estimation

CONDITION ESTIMATION

Important role of condition estimation. Perception mechanisms. (cost). Difference between plasticity and acclimation and epigenetics.

1.4.2 Implementation

Why the use of a sampling method: complex effect of allocation and complex allocation system that is meant to be extended. Some results on the stability of phenotypes. How sampling method can drive the allocation.

1.4.3 comparison of different algorithms

full plasticity : freschet 2015 in poorter & Ryser 2015 the two sides of the performance/fitness: equilibrium and tissue efficiency
age vs biomass.

1.5 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 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.

1.6 Community dynamics parametrisation

Obj: demonstrate that the model is able to reproduce community dynamics (as it was designed for).
Find parameters that allows coexistence (suggest plasticity should allow a diversity of strategy). SLA and height data. Phytosociology for 10m quadrats.

2

Results: Model's properties and individuals response

(Related to the notions cited above, like performance decomposition)

2.1 Craft a trade-of and phenotypic map

Can memory be related to strategy and active/structural ratios in shoot and roots ?

2.2 Niche response

Obj1: understand how resource use mechanisms and allocation algorithms shape the environmental potential niche in the context of the model.
H1: strategy and memory affect niche in two ways if we suppose they are independent: shape and position. Strategy mostly affect shape (width and height) while memory (and so root:shoot ratio) affect mostly position.
H1': there is strong link between strategy and memory in the case of optimisation allocation that increase niche height and might reduce its width.
Obj2: understand the role of plasticity on the niche and if the effect in the same for all strategies/memories.
H2: the plasticity increase niche width but not height (as phenotype is optimum at the center of the niche where memory match the resource availability).

Stability and efficiency trade-off. Niche heigh and width and relationship with the strategy. How does plasticity affect that ? Does it increase the height and widen niches ? What does that mean for coexistence ?
Hopefully higher niche would go with unstable niche.

2.3 Transitivity and competition

1 vs 1 interactions
Is the resource competition transitive ? How does niche widening impact that, does plasticty change competition interaction. Is it related to the trait distance ? (don't think so)

3

THE EFFECT OF PHENOTYPIC PLASTICITY ON PLANT COMMUNITY DYNAMICS

Hypothesis on the cumulative effect on niche and interactions.

3.1 Individual resistance and resilience against drought events

Amplitude and length of the event :
- severity effect reduced by lower tau ?
- resistance versus resilience: H0: conservative strategy have higher resistance, H1 : low tau allows for re-equilibrium and increase resistance (low amplitude and long length. H2: high tau allow to avoid dead-end situation during short severe drought (high resilience)

3.2 Community response to drought event

coexistence effect vs resistance/resilience effect
uniform vs heterogenous (plasticity wise) community response H1:

III

SYNTHESIS & OUTLOOK

This section is meant to include thoughts and ideas on how to extend MountGrassbut 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 MountGrassor individual based vegetation modelling.

3.3 Notes

3.3.1 On modelling

Frustration: often look obvious, at least it's just logical, there is what we put in...

Modelling approach, when not for prediction, what is it about ?

- building understanding
- weight mechanisms
- test hypothesis

4

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.

4.1 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

5

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.

6

LAND-USE: A IMPORTANT DRIVER

6.1 Proto-model of management

Mapping, digestibility and selectivity (smoothing). Grazing and mowing. Height correction.

6.2 Individual and collective response

Response could be to grow thinner, more fragile leaves to go back on tracks (and take advantages of nutrients and lower competition) or grow bigger leaves and invest in predation resistance/avoidance.

6.3 Remaining questions

Calibration of herbivory pressure.

7

LOCAL ADAPTATION AND EPIGENETIC: BETWEEN SPECIES AND INDIVIDUAL MEMORY

8

Making it all fun

Making it fun to use, so that people use it. Making it pretty ?

8.1 Documentation and vignette

8.2 Fun and simple simulations

8.3 Theme and shiny ?

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IV

RAMBLING

9

EVOLUTION, PHYSIOLOGY AND JUSTIFICATION

10

ABOUT EFFICIENCY, EQUILIBRIUM AND OPTIMUM

Multidimension efficiency

11

THE DEAD END PLASTICITY

WHen resource is limited in amount, the exchange rate is always overestimated that leads to plant exaustion. It would matter if the condition does not change, both plant would probably die quickly, but it does if conditions change. -> discussion about being patient or reactive, and when to pay the price... This should feed the discussion about the interest of plasticity as implemented here as a strategic factor.
Arise from the instantaneous view of plasticity, that might not be selected. Reaction norm can give you plasticities that would not emerge from this system of rule, but could be selected in an evolutionary context.