CLÉMENT VIGUIER

PHD THESIS

Contents

I

INTRODUCTION

1

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

2

Litterature review

2.1 Context: mountain grasslands and climate change

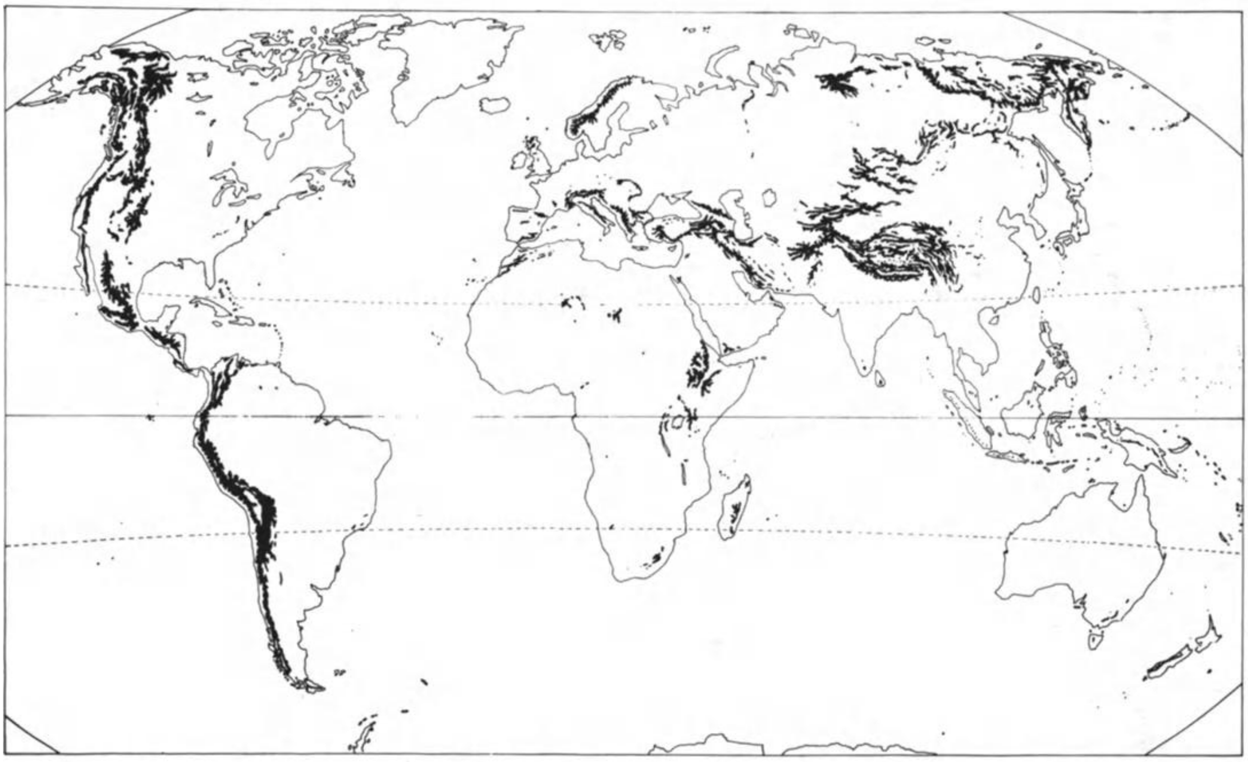

Figure 2.1: Distribution of alpine habitats

2.2 Diversity and coexistence mechanisms

Why interested in diversity? precious, main objective in conservation, plus services. Why coexistence mechanisms? Mechanism at plant level that allow diversity, understanding these will help us predict changes in diversity.

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 Intraspecific 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

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 artifically 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 makin.

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

The individual basis of plant coexistence in mountain grassland and the effect of phenotypic plasticity: investigation with the model ***MountGrass***

Elsevier[1]

Radarweg 29, Amsterdam

Clment Viguier[1,b], Global Customer Service[b,]*

[a]1600 John F Kennedy Boulevard, Philadelphia
[b]360 Park Avenue South, New York

Abstract

Keywords: `elsarticle.cls`, LaTeX, Elsevier, template
2010 MSC: 00-01, 99-00

---

1. Introduction

Global change has been subject of a large, and still growing, number of studies. Yet, because the complexitiy of ecological system coupled with the uncertainty around the future of climate and management, a lot of work is remaining to predict the state of natural and semi-natural systems in the future. Vegetation communities are of particular interest as they provide both economic value and ecosystem services. If a large part of plant community ecology is foccused on forests, the presumed vulnerability to global change of mountain grasslands has led scientists to study them. If their actual vulnerability is still discussed (phd of sandra, ecoveg 2015), mountain grasslands will certainly be exposed to increasing temperature and droughts, but also to changes in management practices with a reduction of grazing (ask greg, see ref in ceres baros first paper).

☆Fully documented templates are available in the elsarticle package on CTAN.
*Corresponding author
Email address: `support@elsevier.com` (Global Customer Service)
URL: `www.elsevier.com` (Clment Viguier)
[1]Since 1880.

To better understand and predict the effect of global change in these ecosystems of mountain grasslands, empiricall studies and experiments have been set. (see Jena, leca and Levine). These studies and others (Violle, albert, jung) highlight the importance of intra-specific variations in community ecology. Intra-specific variations represent around 20 and 30 percent of total variation in grasslands (see albert) and could greatly alter the species interactions and community response to abiotic factors. Considering intra-specific variations is important to better understand community dynamics (violle) and in models because they favour coexistence (Clark, Jung, Courbaud) and modify community responses (Jung). Such effects are succeptible to greatly influence the dynamic of communities facing global change by mitigating species level response, soften plant niches frontier, altering species competition. Another argument is the fact that intra-specific changes may alter directly the community response to a stress (Jung).

Moreover the role of long term evolutionary and ecological processes cannot be easilly assessed in such designs. Moreover, considering the multiplicity of climatic and management scenarios scales up the work to a limiting point.

To overcome these limitations and difficulties, modelling approaches has been developped (fate-h, samsara, taubert, lohier ...). They are either used for the retrospective studies long term dynamics from time series data, the prediction of community dynamics along different scenarios, or to interogate the underlying mecanisms of community dynamics (gemini). These models, to be able to account for changing condittions are all based on strong plant functioning processes at the scale of interest and are supported by field data through parametrisation.

Most of these models feature a fixed plant functioning where the dynamic of the community is mostly driven by, 1) the abiotic conditions, 2) the relative competitiveness of species/group specific parameters or direct competion coefficients. If 1) is essential in the context of climate change, the point 2) as main mechanism of plant interaction can be discussed as it relies on differences between species specific physiological parameters. Physiological or competition parameters are generally estimated by direct measures or derived from dta through calibration. Both methods give estimators in what we have good confidence, however they do not allow them to vary within the group (plant functional type, species or population) they have been defined for. The estimator produce good results and generally follow fundamental or ecological trade-offs. Yet, they do not allow for variations within the group for these parameters, as they are not strictly constraint by said trade-offs and could lead to Darwinian demons, or would require calibration of this variation space. More efforts must be done in the representation of the link between chemical, anatomical and morphological traits and physiological traits that drive plant growth and plant interactions. Defining such link would authorise variations within a group while maintaining strong trade-offs between physiological traits and allowing variation and search in the strategy space... (not clear).

We stressed the importance of considering intra-specific variations, ann highlight the necessity for a link between chemical and anatomical traits to functioning traits. Not clear what is genetic variation and selection/evolutionary processes or phenotypic plasticity. Phenotypic plasticity in models: theoretical: 2 species interactions, not at community model. (Heritability ?)

There is a need for community models capable of reproducing diverse plant communities. To investigate the effect of climate change it has to incorporate mechanism of response and individual level.
Such mechanism is called phenotypic plasticity

How is it really different from source-sink approaches ? Or functional equilibrium ? -¿ allocation based, trait variations, plasticity is a strategy. This last poinnt is important. It's related to the discussion around van kleunen ad Dewitt (not all species are plastic, sultan says most are) ¡- check that.

The need of mechanistic model integrating functional traits and carbon allocation ... [?] + probably general reviews on vegetation modelling

2. Methods

2.1. Model overview and concepts

Overview of MountGrass.

Plasticity in MountGrass: concepts and implementation. **Allocation** Why allocation and not just traits ? Allocation model provide structural constraint for plant strategies. Study ecology is studying the relative performance of individuals (and their impact on environmental conditions) in relationship with their strategies. Considering the amount of traits and strategies plants can develop, it is crucial to reduce the dimensionality of the strategic space (space define by all independent strategic axis plant can be found on). The most effective way to use laws of physics, chemistry and biology to eliminate impossible strategies (or combination of traits). Allocation based model take advantage of the "law of mass balance" ... to limit the number of possible allocation pattern, or strategies. This approach has the advantage of creating limited *continuous* strategy space that can be explored and reveal ecological relationships/constraint. The search for such relationships or trade-offs is a big challenge in empirical ecology (see [? ? ? ?] for plants) and ecological modelling (see [? ?]) as they reduce the complexity and help understand the main mechanisms that shape communities.
Introduce the idea of default strategy with this ratio of active vs structural tissues.

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.

Allocation algorithms

2.2. Calibration

Pot data. 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.

Individual calibration process. 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.

Strategy diversity filtering. 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[2].

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

Weather 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

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

1h) have been average daily and used to compute input variables for ***Mount-Grass*** .

2.3. Simulation setup

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

3. Results

3.1. Growth of diverse species

Individual calibration. . Calibration filtering results in the selection of n parameter sets over m preselected 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.

Acceptance rate without plasticity: Acceptance rate with RSR plasticity for equilibrium:

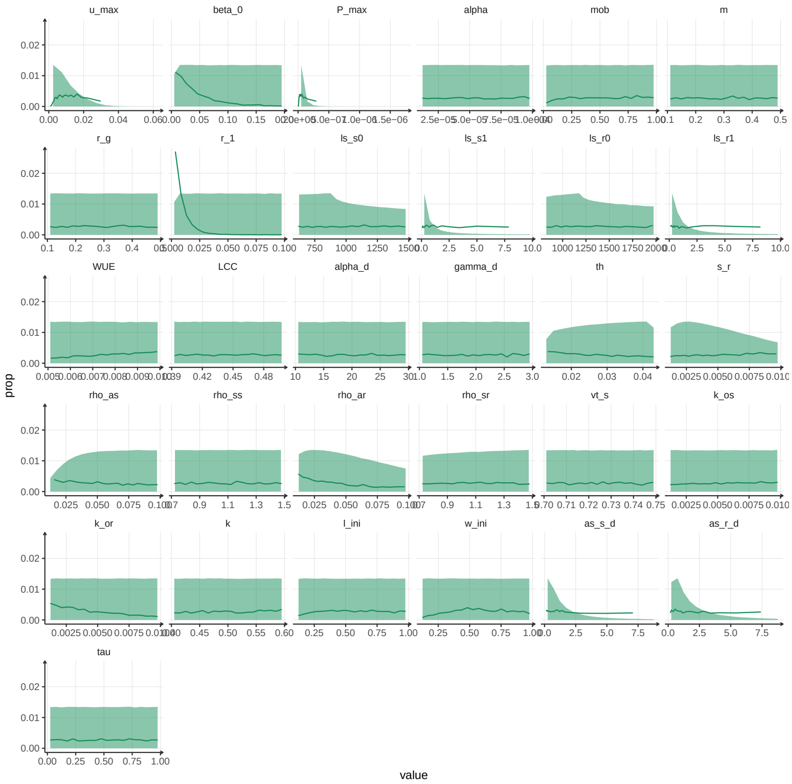

Figure 1: Acceptance rate per parameter for individual growth. No plasticity

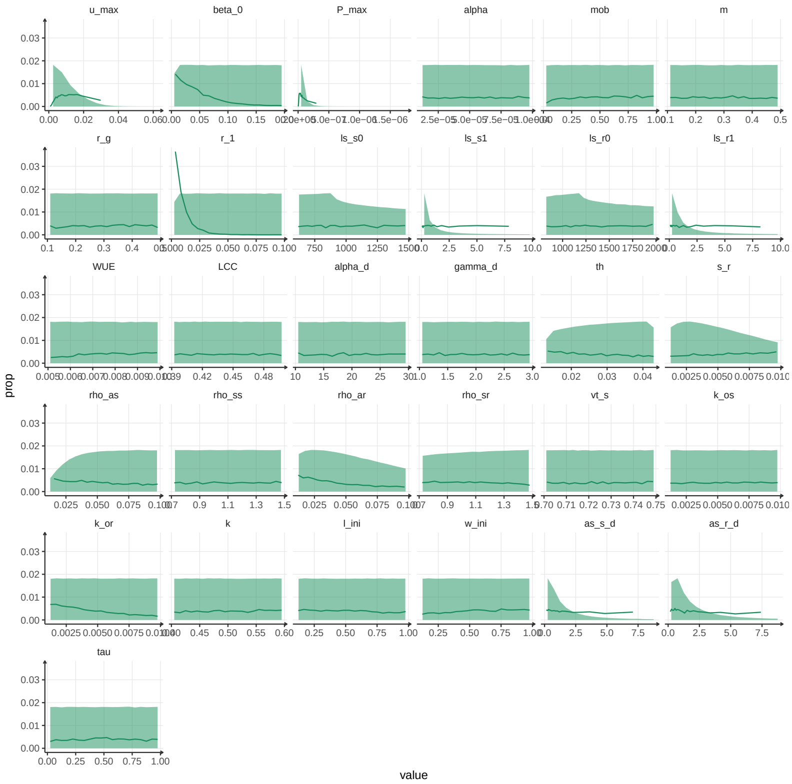

Figure 2: Acceptance rate per parameter for individual growth. RSR plasticity

	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

Change of relationship between parameters and acceptance rate -¿ none
accept = f(tau)

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.

Individual growth pattern and plasticity. Individual growth and allocation looks like that:
change in size of different pools (shoot, active, shoot str, stem ..., rep, storage).
Plus constant traits.

Different allocation algorithms change the growth but also the traits:
BMtot, RSR, SRL and SLA of the same plant with different algorithms, other things being equal.

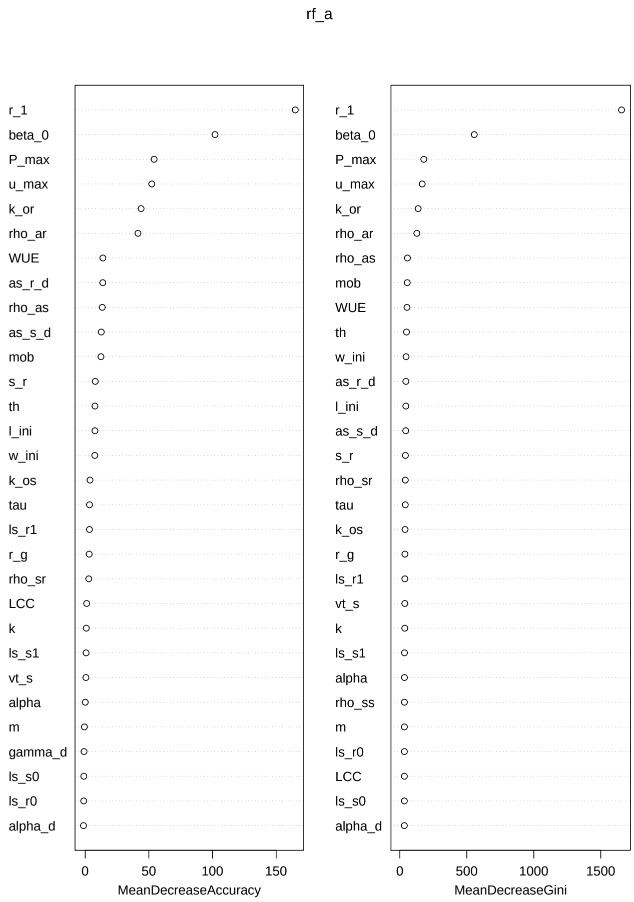

Figure 3: Importance of the random forest to explain filtering outcome (accepted or rejected) of a balanced sample of parameter set between all tested (all accepted parameters and an equivalent sample in rejected parameters). RSR plasticity.

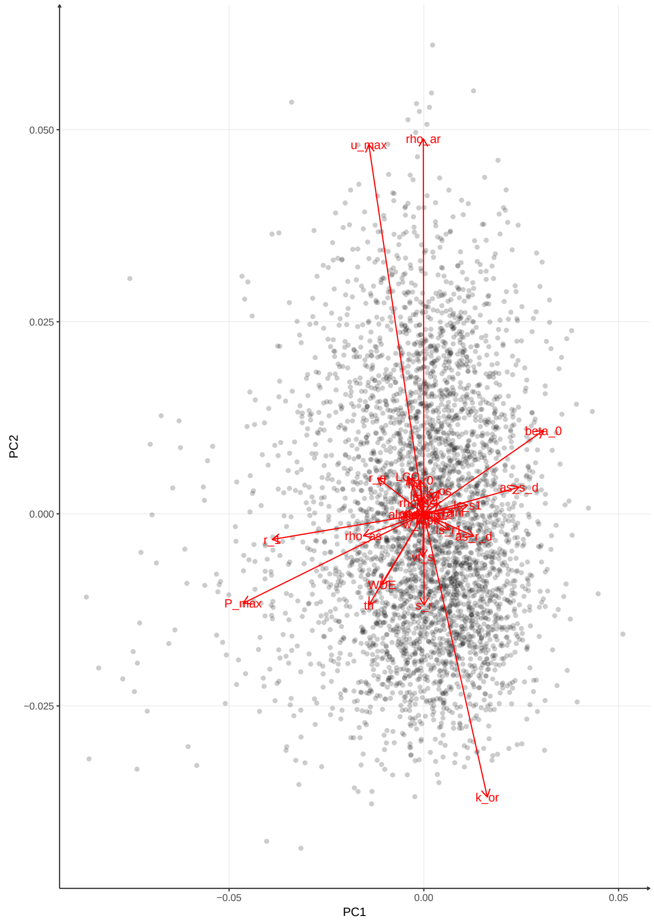

Figure 4: Accepted parameters set for plastic individual growth calibration filtering on the two main components of PCA.

	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

Active versus structural: the foundation of the niche. Niche results from the absolute (potential niche) or relative (realised niche) performance of individual plant along environmental gradient. Performance (if measured as living biomass at a given time) in ***MountGrass*** is a composite variable depending on: the absolute efficiency of the different organs (shoot and root), the relative proportion of these organs, and the equilibrium between shoot and root activity.
Theoretical performance trade-off: result from the mathematical expression of construction cost of tissue and their exchange rates.

figure and formulas

figure and formulas

Add conceptual graphics and arguments to explain the components of performance, and the problem of mismatch strategy and unbalance phenotype.

Simulations

Allocation matters: stability vs risk. Effect of algo on performance → why plasticity is important: not only good allocation is important, but also good measure

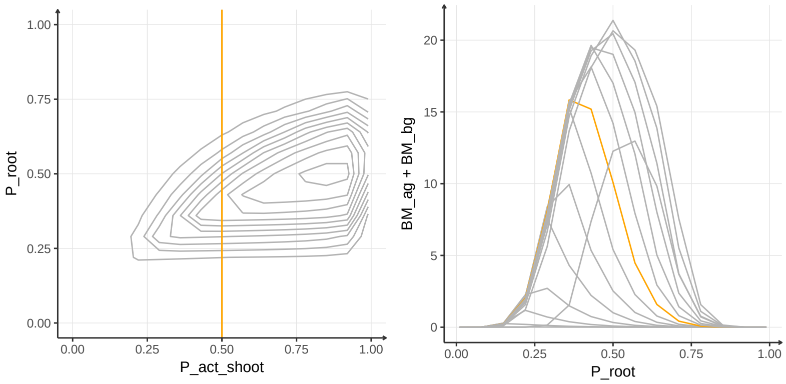

Figure 5: Performance landscape.

Landscape accessible with only RSR plasticity. Part of the landscape (espécailly) optimum is not accessible without trait plasticity.

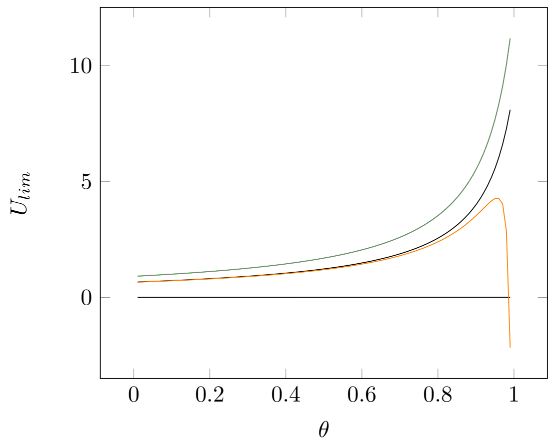

Figure 6: Organ efficiency

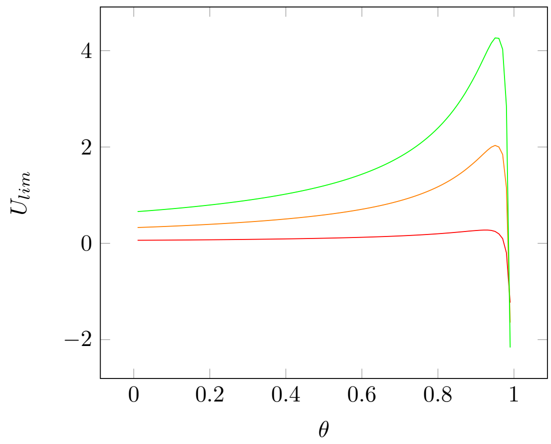

Figure 7: Organ efficiency

of conditions.

(there is some conceptual drawing to put in here: optimum landscape and how can allocation let you drive in that space.)

Freer allocation algorithms lead to convergence to phenotypes of higher performance. But these phenotype may also be of higher risk ! → need for good condition estimation.

Importance of having good estimation to have a good strat and good balance.

Plasticity: benefit ?. Niche experiment = previous analysis discussion. Test hypothesis through simulations for few selected (how ?) parameter sets.
Widden niche:

3.2. Community level

Coexisting species ? (look at seed bank to see the traits of coexisting (and persistent) species) How does plasticity may affect that ?

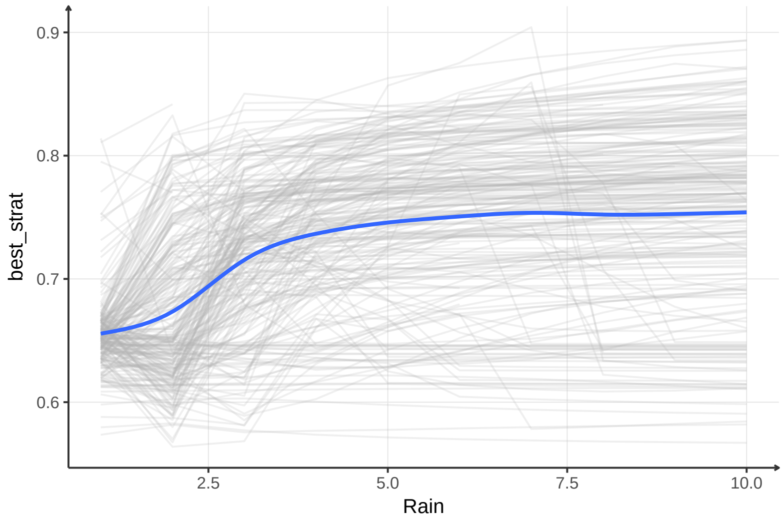

Figure 8: Best strategy for root along a precipitation gradient.

Growth of plants with different strategies (different RSR and active/structural ratio for roots) along a precipitation gradient have been simulated. The best strat is defined as the weighted mean of the active/structural ratio by the total fresh biomass after 100 days of simulation. Each grey line correspond to a parameter set, while the blue line is the fitted gam regression.

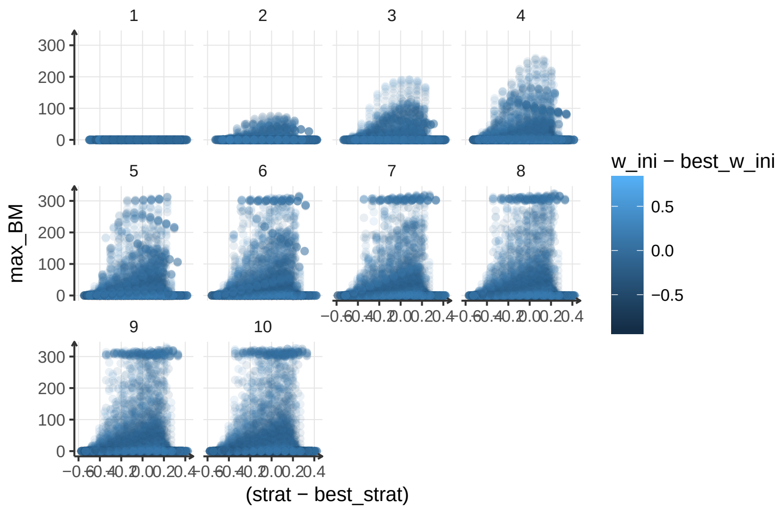

Figure 9: Biomass peak as function of distance to the optimum strategy (a/s ratio)

. Each panel correspond to a precipitation value (not indicated). There is a strong assymetry between more conservative strategies (left) that perform worse but are still viable even far from optimum (positive values far left) and exploitative strategies (right side) that perform well but only if close to the equilibrium. (could it be interesting to show the relationship between strategy and performance variability ?)

4. Discussion

Individual calibration. Individual calibration allowed to filter parameters related to individual growth with only few parameters being sensitive.

individual growth. Link memory and phenotype.

Link allocation algo and plasticity to the different components of performance. Because the performance depends on multiple aspects of plant allocation in relation with external conditions, it is difficult to isolate each aspect and compute their relative importance or response to certain variables ¿ this is complex to study. Hope this model will help bring more light on plasticity and plant strategies interactions.

5. Conclusion

using fundamental ”deep” traits and memory: able to reproduce a diversity of resource use strategies. Possibility to

This framework is compatible with phenotypic plasticity

plasticity change the niche shape (and probably interactions) and may have an impact on community dynamics.

References

[1] I. Marchaux, J. Chave, An individual-based forest model to jointly simulate carbon and tree diversity in Amazonia: description and applications, Ecol Monogr 87 (4) (2017) 632–664. doi:10.1002/ecm.1271.
URL http://onlinelibrary.wiley.com/doi/10.1002/ecm.1271/abstract

[2] P. B. Reich, I. J. Wright, J. CavenderBares, J. M. Craine, J. Oleksyn, M. Westoby, M. B. Walters, The Evolution of Plant Functional Variation: Traits, Spectra, and Strategies, International Journal of Plant Sciences

164 (S3) (2003) S143–S164. doi:10.1086/374368.
URL http://www.jstor.org/stable/10.1086/374368

[3] I. J. Wright, P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M.-L. Navas, . Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, R. Villar, The worldwide leaf economics spectrum, Nature 428 (6985) (2004) 821–827. doi:10.1038/nature02403.
URL http://www.nature.com/nature/journal/v428/n6985/abs/nature02403.html

[4] S. Diaz, J. Hodgson, K. Thompson, M. Cabido, J. Cornelissen, A. Jalili, G. Montserrat-Mart, J. Grime, F. Zarrinkamar, Y. Asri, S. Band, S. Basconcelo, P. Castro-Dez, G. Funes, B. Hamzehee, M. Khoshnevi, N. Prez-Harguindeguy, M. Prez-Rontom, F. Shirvany, F. Vendramini, S. Yazdani, R. Abbas-Azimi, A. Bogaard, S. Boustani, M. Charles, M. Dehghan, L. de Torres-Espuny, V. Falczuk, J. Guerrero-Campo, A. Hynd, G. Jones, E. Kowsary, F. Kazemi-Saeed, M. Maestro-Martnez, A. Romo-Dez, S. Shaw, B. Siavash, P. Villar-Salvador, M. Zak, The plant traits that drive ecosystems: Evidence from three continents, Journal of Vegetation Science 15 (3) (2004) 295–304. doi:10.1111/j.1654-1103.2004.tb02266.x.
URL http://onlinelibrary.wiley.com/doi/10.1111/j.1654-1103.2004.tb02266.x/abstract

[5] S. Daz, J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth, I. Colin Prentice, E. Garnier, G. Bnisch, M. Westoby, H. Poorter, P. B. Reich, A. T. Moles, J. Dickie, A. N. Gillison, A. E. Zanne, J. Chave, S. Joseph Wright, S. N. Sheremetev, H. Jactel, C. Baraloto, B. Cerabolini, S. Pierce, B. Shipley, D. Kirkup, F. Casanoves, J. S. Joswig, A. Gnther, V. Falczuk, N. Rger, M. D. Mahecha, L. D. Gorn, The global spectrum of plant form and function, Nature 529 (7585) (2016)

167–171. doi:10.1038/nature16489.
URL http://www.nature.com/nature/journal/v529/n7585/full/nature16489.html

[6] B. Reineking, M. Veste, C. Wissel, A. Huth, Environmental variability and allocation trade-offs maintain species diversity in a process-based model of succulent plant communities, Ecological Modelling 199 (4) (2006) 486–504. doi:10.1016/j.ecolmodel.2006.03.038.
URL http://www.sciencedirect.com/science/article/pii/S0304380006002924

[7] D. S. Falster, R. G. FitzJohn, . Brnnstrm, U. Dieckmann, M. Westoby, plant: A package for modelling forest trait ecology and evolution, Methods Ecol Evol 7 (2) (2016) 136–146. doi:10.1111/2041-210X.12525.
URL http://onlinelibrary.wiley.com/doi/10.1111/2041-210X.12525/abstract

Appendices

6. *MountGrass* description

7. State variables, traits and parameters

7.1. State variables

7.2. Species specific traits

7.3. Parameters

8. Simulations

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

mechanism and stochasticity
5 types of allocation

PSEUDO-CODE AND ROUTINE ALLOCATION

1.4 Plasticity: between species memory and individual experience

1.4.1 Concepts

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

Memory

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, CO2 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 ?

Bibliography

Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. Annual Review of Ecology and Systematics *31*, 343–366.

Freschet, G. T., Kichenin, E. and Wardle, D. A. (2015a). Explaining within-community variation in plant biomass allocation: a balance between organ biomass and morphology above vs below ground? J Veg Sci , n/a–n/a.

Freschet, G. T., Swart, E. M. and Cornelissen, J. H. C. (2015b). Integrated plant phenotypic responses to contrasting above- and below-ground resources: key roles of specific leaf area and root mass fraction. New Phytol *206*, 1247–1260.

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.