

CLÉMENT VIGUIER

MOUNTAIN GRASSLANDS
DYNAMICS: INTEGRATING
PHENOTYPIC PLASTICITY
IN A NEW AGENT-BASED
MODEL

ABSTRACT

Mountain grasslands provide numerous ecosystem services that need fine understanding and characterisation to be assessed and predicted. The vulnerability to climate change and the complexity of mechanisms driving alpine community dynamics require the development of new tools to predict the dynamics of these communities facing new conditions. Moreover, individual variation has large effects on community responses to external condition changes, as shown by multiple empirical studies but often overlooked in modelling approaches. In addition to these effects, intra-specific variability has contrasting potential impacts on coexistence mechanisms that need to be disentangled.

To answer both the need for a dynamic model of species rich communities and the integration of individual level , the model *MountGrass* was developed. It is designed around two main components: (1) a closed strategy space allowing a efficient representation of high species diversity, and (2) a plastic allocation mechanism integrating trade-offs between active and structural tissues, as well as between shoot and root tissues. In a first result part, after a parameter filtering step, the combined effects of allocation rules, species strategy and phenotypic plasticity on individual plants are studied. In a second part, the effect of plasticity is then studied at the scale of the community.

This work demonstrates the importance of phenotypic plasticity both at the individual scale and its role for community dynamics. While further work is needed to fully capture plasticity mechanisms, the model provides sound starting point to further explore the role of intra-specific variability in coexistence mechanisms, the resistance and resilience to drought events, or the detection of regime shift in this type of systems.

ACKNOWLEDGEMENTS

I LOVE YOU ALL, BUT I LOVE YOU MORE MOM.

CONTENTS

I Introduction	VII
1 Context	1
1.1 Global change: how to describe the future of alpine ecosystems?	1
1.2 The need for new mechanistic models	5
2 Aims, Objectives, and Overview	8
2.1 Aims: understanding and prediction	9
2.2 Objectives: a new agent-based model for plant community dynamics	9
2.3 Thesis overview	10
II Background: community dynamics, traits and phenotypic plasticity	13
1 Understanding community dynamics and properties: drivers and theories	17
1.1 Community assembly and coexistence	17
1.2 The complexity of diversity	21
2 How to represent plant community	22
2.1 The continuity of functional ecology	23
2.2 How trade-offs make strategy space	25
2.3 How traits link to ecosystem properties	28
2.4 Modelling diverse plant community	31
3 The importance of phenotypic plasticity as a specific case intra-specific variability	33
3.1 Intra-specific variability change the rules	33
3.2 Phenotypic plasticity: a specific case of intra-specific variability	36
3.3 Toward an integrative framework of plant strategy and phenotypic plasticity	41
3.4 How phenotypic plasticity affect ecosystem properties and dynamics	43
III Modelling alpine grasslands with MountGrass, a generic framework integrating phenotypic plasticity	49
1 Alpine environment: conditions, resources, and perturbations	55

1.1	The scales of alpine grasslands	55
1.2	Resources: light and water	56
1.3	Perturbations: frost, grazing, and mowing	56
2	Multi-dimensional strategy space, carbon pools, and trade-offs	57
2.1	Multi-dimensional strategy space and allocation pools	57
2.2	Craft a trade-off: active and structural tissues	60
3	Modelling phenotypic plasticity	61
3.1	Plasticity as a strategy: between species memory and individual experience	62
3.2	Driving rules of allocation	64
4	ODD description of the model <i>MountGrass</i>	66
4.1	Model overview	66
4.2	Design concepts	70
4.3	Details	72
4.4	Limitations and problems	82
IV	Individual performance: strategy and plasticity	85
1	Model properties and individual responses	87
1.1	Parametrisation and sensitivity analysis	87
1.2	Individual level behaviour and properties	97
2	Individual performance, plasticity and variable conditions	101
2.1	Individual performance: between strategy, memory and plasticity	102
2.2	Plasticity and variability of conditions	113
2.3	From model behaviour to competition and coexistence in the real world	122
V	Community dynamics	125
1	Community level simulations: non plastic community	127
1.1	Parameter filtering	127
1.2	Non plastic communities	128
2	Plasticity: impact on species fitness and diversity	128
2.1	Plasticity and diversity	128
VI	Synthesis & Outlook	133
1	Synthesis	135
1.1	Modelling diverse community	135
1.2	Effect of plasticity of mountain grasslands properties	135
1.3	On plasticity modelling	135
1.4	The limit of the species.	136
2	Outlook	137
2.1	Competition and feedback	137

2.2 Extend to climate change effects	138
3 Extensions	139
3.1 Ecology of plasticity: plasticity as a trait	139
3.2 Include nitrogen: source of trade-off	139
3.3 For more interaction	140
Glossary	143
4 Index	143

I

INTRODUCTION

II

BACKGROUND: COMMUNITY DYNAMICS, TRAITS AND PHENOTYPIC PLASTICITY

III

MODELLING ALPINE GRASSLANDS WITH MOUNT- GRASS, A GENERIC FRAMEWORK INTEGRATING PHE- NOTYPIC PLASTICITY

IV

INDIVIDUAL PERFORMANCE: STRATEGY AND PLASTICITY

The chapter contains the main results from simulations experiments at the individual scale. It provides insight on the impact of plastic allocation algorithm on individual growth and potential effects on community properties.

The first part is dedicated to the parameter filtering and the study on individual growth in a stable environment. The second part examines response of individual root strategies to two gradients of water availability: (1) with constant influx but differences in means simulating spatial heterogeneity, (2) with shared mean influx, but contrasting rate of reduction of precipitation simulating the reduction of available resource during the growing season.

1 MODEL PROPERTIES AND INDIVIDUAL RESPONSES

The first part of the chapter is dedicated to the parameter filtering process, the sensitivity analysis and basic model behaviour.

1.1 Parametrisation and sensitivity analysis

Calibration, or **parametrisation**, is an essential step in the development of an agent-based model. ABMs are often characterised by multiple processes, and though parameters, at individual levels. The results of these processes (depending of parameter values) from numerous individuals combine to produce the group or community behaviour. Because there are interactions between the processes and between the agents, the overall behaviour of the group (often the subject of interest) is sensitive to these parameters. For the same reasons, an incredible variety of results could be produced with ABMs if the parameters were not chosen in order to produce sensible responses to simulated conditions. The aim of the calibration is to determine, from the *a priori* knowledge of the processes and parameters, and the comparison with data, the best values for the model parameters. This step often goes along with a sensitivity analysis that determine the relative sensitivity of variables of interest to specific parameters.

Because of their nature, ABMs often model processes for which the parameters are either unknown, or hard to access (because at the individual scale). In such cases, advance calibration techniques like pattern oriented modelling(hartig; Grimm et al. 2005) can be developed. However, such method require a high number of simulations and relatively precise simulation parameters. Because the implementation in R makes the model relatively slow, and because available datasets, despite being very interesting lack information on sensitive parameters, a less robust but less expensive approach is chosen: **parameter filtering** at the individual scale. The focus of the part of this work on the individual growth, and the will for more individual-centric approach also support this choice.

For similar reasons of computational cost, the **sensitivity analysis** is realised *a posteriori* on calibration runs.

1.1.1 Method

Pot data consists in total biomass and root shoot ration (RSR) data of 11 species grown in pots by Peterson and Billings (Peterson and Billings 1982). This 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.

POT DATA

Simulated plant grow in square pots 9 cm wide and 12 cm deep. The soil is characterised by the following parameters: critical soil water content: $0.1m^3.m^{-3}$, and saturation water content: $0.1m^3.m^{-3}$. Simulation time of 111 days of 15 hours is divided between the growing phase of ... days, followed by the treatment phase when plant are water (soil saturation) either once a week or once a day. The light level and water influx are simulated with water event of ... mm and lighting of ... Watts per square meter. Plants have default geometry parameters and reproduction is ignored and I assume plants do not stop their growth.

POT SIMULATION

The whole filtering process has been implemented in R. Model parameters are sampled following the LHS method (from `lhs` package) within parameter ranges (described in table ??) defined both thanks to the literature and constraints dictated by desired behaviours from the model. When necessary the sample is log transformed. Because of strong relationship between exchange rate parameters and cost of exchange area, exchanges rates parameters are expressed on a mass basis for sampling then transformed into an area basis for the model. To avoid extreme RSR ratios, the ratio between the mass based exchange rate parameters is limited between 0.1 and 10.

PARAMETER FILTERING PROCESS

As explained in previous chapter, species specific parameters are required to model plant growth. These parameters are sampled at the same time that the parameters of the model, according to ranges detailed in table 4.2.

Once the parameters generated, a first filtering is applied to save simulation time and avoid unrealistic trait values. Compute initial trait values considered out of range (see table for ranges extracted from LES data (Wright et al. 2004) in alpine biome) are excluded.

These two steps lead to the creation of a list of n independent parameter sets that are then used for individual pot simulations following Peterson and Billings experiment sett-up.

Results 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 deviations 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.

The parameter filtering procedure is applied on the three main allocation algorithms: *non plastic*, *fixed-equilibrium* and *plastic-optimisation*.

Relative importance of variables in the selection process is investigated with the packages `randomForest`. A random forest analysis (depth = 5, number of trees = 300) is performed on a balance dataset composed by all selected parameter sets and a random sample of rejected sets of equal size. Importance is assessed on the results of the random forest.

SENSITIVITY ANALYSIS

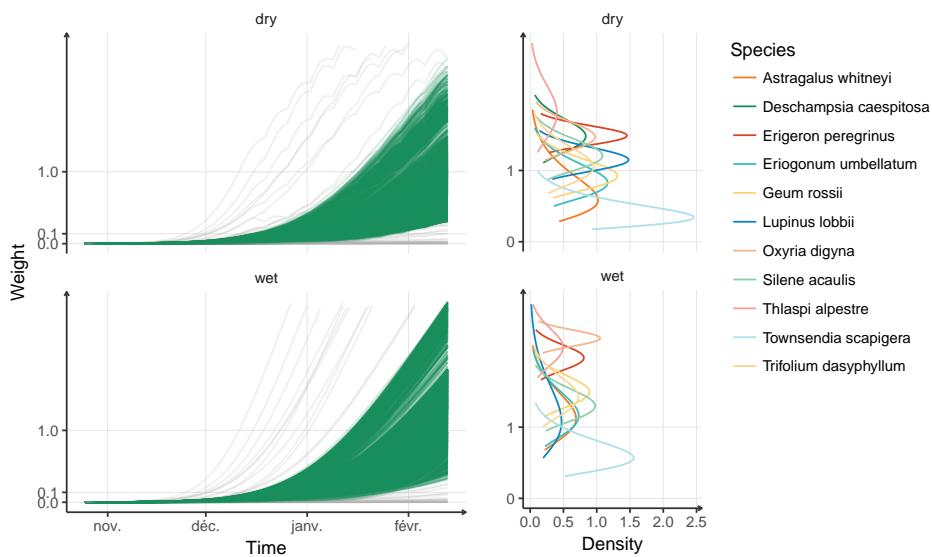


Figure 1.1: Comparison of simulated weights with distribution of weights of real alpine species for contrasting conditions.

1.1.2 Results

Parameter filtering process resulted in the selection of a low number of parameter sets (below 0.2%) for each allocation algorithms (table 1.1.2). This number is below the sum of accepted parameter sets per species because a parameter set can match to multiple species. Not all species contribute to the same extend to the filtering process. *Astragalus whitneyi* accounts for a high percentage of accepted parameter sets, while no parameter set could match 2 species (*Oxyria dignya* and *Deschampsia caespitosa*). The former is characterised by wide distribution in both conditions for the two variables of interest (weight and RSR), while the latter show relatively tight distribution with little overlap between the conditions for the both variables (see figure 1.1 for comparison between simulations and data for total weight).

SELECTION RATE

Table 1.1: Acceptance rate per species for the 3 main allocation algorithms. Because some parameter sets match multiple species, the total number and rate of accepted parameter sets is lower than the sum of accepted parameter sets per species. All rates are given in %.

species	non plastic		fixed-eq		plastic	
	n (2M)	rate	n (2M)	rate	n (200,000)	rate
Silene acaulis	227	0.02	396	0.04	55	0.03
Trifolium dasypodium	271	0.03	317	0.03	45	0.02
Geum rossii	51	0.01	72	0.01	12	0.01
Thlaspi alpestre	342	0.03	360	0.04	59	0.03
Deschampsia caespitosa	-	-	-	-	-	-
Eriogonum umbellatum	500	0.05	805	0.08	118	0.06
Townsendia scapigera	593	0.06	930	0.09	107	0.05
Astragalus whitneyi	1570	0.016	2424	0.24	318	0.16
Lupinus lobbii	678	0.07	868	0.09	123	0.06
Erigeron peregrinus	1	<0.01	-	-	-	-
Oxyria digyna	-	-	-	-	-	-
Total	4233	0.43	6172	0.62	837	0.42
Accepted	924	0.09	1416	0.14	200	0.10

Despite the low selection rate, a difference can be noted between the *fixed-equilibrium* algorithm and the two other algorithms with a accepted rate of 0.14 % against 0.09% and 0.10% (table 1.1.2). This difference cannot be explained by a significantly better selection rate for specific species, but rather higher rates for all species.

Most of parameter sets are not shared between the algorithms (*i.e.* around respectively and third and a quarter of accepted parameter sets are shared between *non plastic* allocation and *fixed-equilibrium* allocation calibrations), despite that the distribution of parameter values that are not shared are very similar and do not show any clear pattern (data not shown).

Out of the 31 parameters, 6 show graphical response of selection rate (see figure 1.2), and only u_{max} and P_{max} present a possible optimum different from limit values. The relative importance of the parameters is better explored in sensitivity analysis.

A total of 12 parameters show relative influence on selection rate for at least one of the algorithm. These parameters are divided between model parameters and species parameters. Species parameters show influence only for the *non plastic* allocation algorithm. Model parameters express relatively similar importance for all three algorithms. The respiration rate of active tissues (r_{-1}) is the most sensitive parameters (see figures 1.2 and 1.1.2). Other sensitive parameters are related to water availability (β_0), organ exchange rates (P_{max} and u_{max}) and soil coverage by roots (ρ_{ar} and k_{or}).

SENSITIVITY ANALYSIS

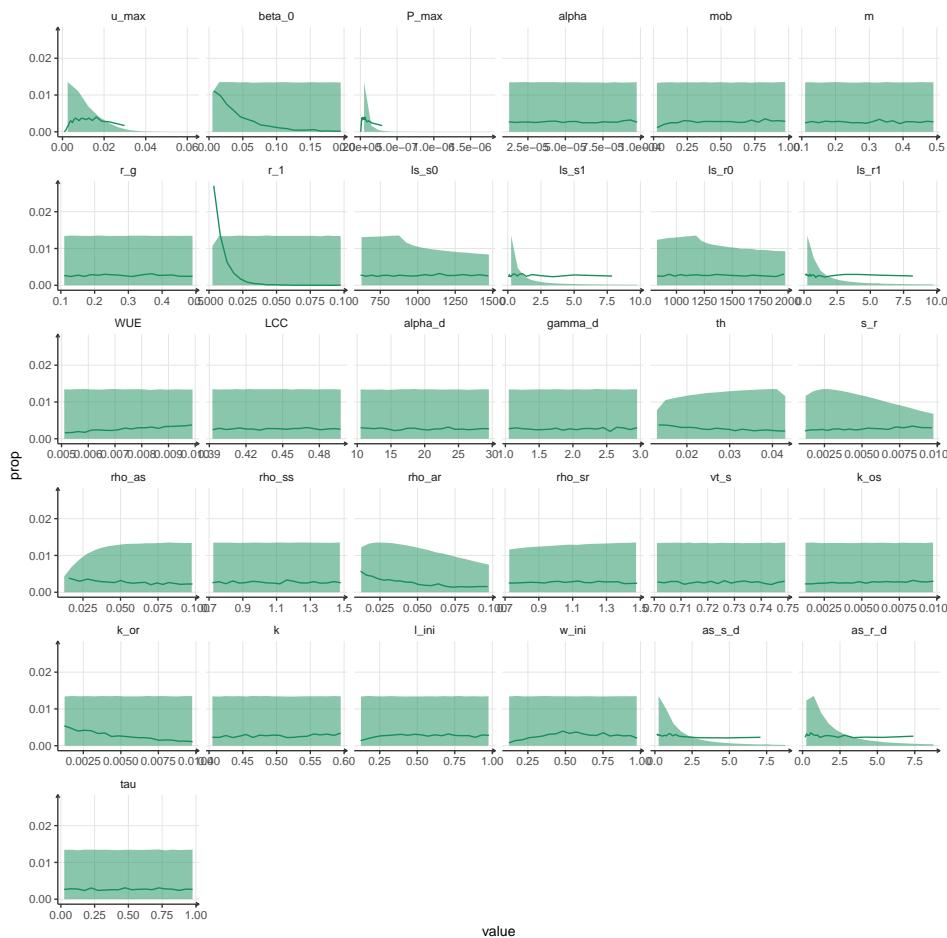


Figure 1.2: Selection rate per parameter for individual growth. Non plastic.

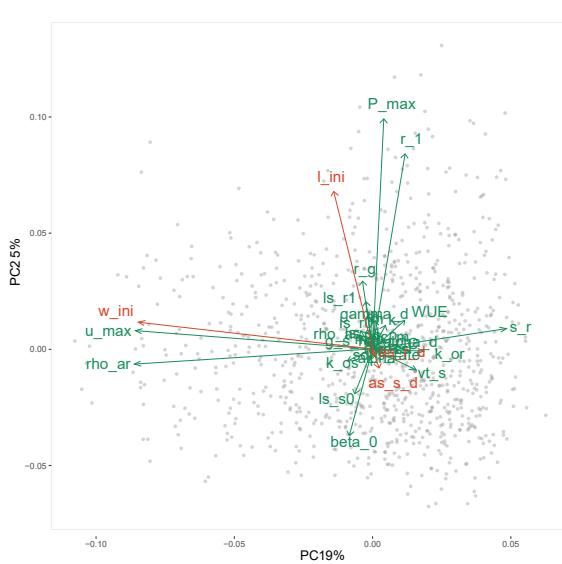


Figure 1.4: Representation of the PCA of parameter sets selected in parameter filtering process on the first principal components. *Non plastic*.

Relative mean decrease accuracy

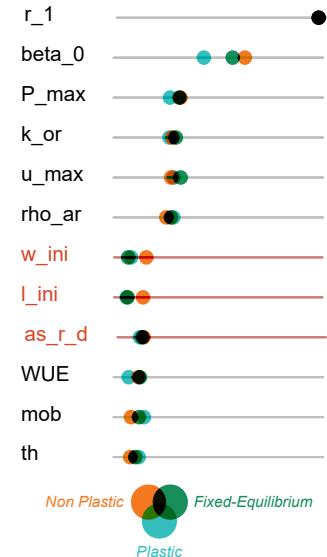


Figure 1.3: Relative importance of main parameters for selection under the three main allocation algorithms: (*non plastic*, *fixed-equilibrium* & *plastic*).

The PCA performed for *non plastic* algorithm only on parameter values reveals that important parameters are also the dominant variables that shapes the selected subspace. The two first axis explain only 14% of variance. The first one is related to the root activity and efficiency (u_{max} , l_{ini} , ρ_{ar} and s_r), the second is in line with global efficiency and resource availability.

The parameter filtering process is based on individual species, ... Species cannot be distinguished on these two main component space, neither on species specific parameters space (l_{ini} , w_{ini} , w_{ini} & l_{ini} , as_{s_d} , as_{r_d} , as_{r_d} & as_{s_d}) despite small variations in distribution shapes and ranges between species (data not shown).

For each algorithm the response of the two filtering variables (weight and RSR) are plotted against the most important variables in figures 1.5 and ??.

VARIABLE RESPONSES

Total biomass is particularly sensitive to tissue respiration cost (r_1), but also maximum exchange rate parameters. There is a notable difference in growth maxima between the two conditions in favour of wet conditions, in line with observed data. This difference is observed for the three algorithm that differ mainly by the amplitude of the biomass ranges (need data). Growth response curves are similar for all allocation algorithm. Growth is only weakly related to species specific parameters. Total biomass under *Plastic-optimisation* algorithm seems to be more sensitive to variables influencing the exchange area per unit of biomass.

The species specific parameters τ controlling the balance between genetic and environmental control does not emerge as a influencing parameter at the global scale for any of the two flexible allocation rules.

Root:Shoot Ratio (or RMF in figure 1.6) strongly responds to species specific parameters under *non plastic* allocation because the memory parameters (l_{ini} and w_{ini}) are the means plants control their RSR. For other allocation rules, species specific parameters have little control over RSR. Surprisingly, the photosynthetic capacity has stronger influence on the ratio than the root maximum exchange rate.

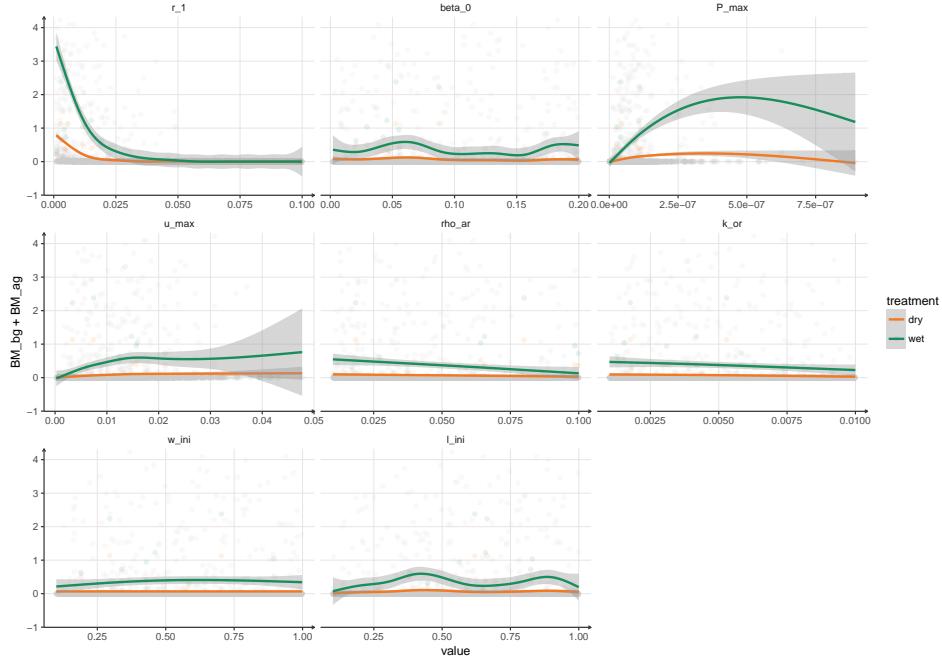


Figure 1.5: Main parameters effect on the total plant biomass. Non plastic. One dot represents a parameter set. Not all parameter set are represented as the y axis is limited around the smooth function (loess). Coloured points represent selected parameter sets in the two treatments (**dry** and **wet**).

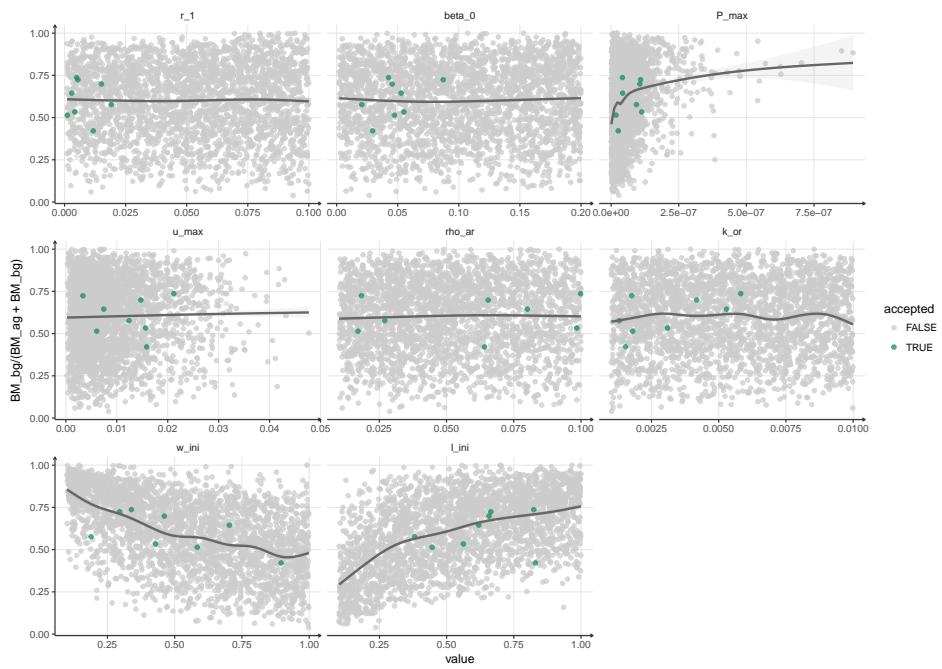


Figure 1.6: Main parameters effect on the total plant Root Mass Fraction (RMF). Non plastic

Little to no difference in RSR is expected for *non plastic* allocation rule since allocation promoted a fixed phenotype, but both *fixed-equilibrium* and *plastic-optimisation* allocation rules allow for changes in RSR. Nevertheless, no stable change in RSR is observed in any of the simulations. Fluctuations are present but consist in stable oscillations between two fixed values (see figure 1.7), synchronized with water variations. These rapid adaptations of the relative proportion of roots denote a high flexibility of plant phenotypes in *MountGrass*.

ROOT SHOOT RATIO AND PLASTICITY

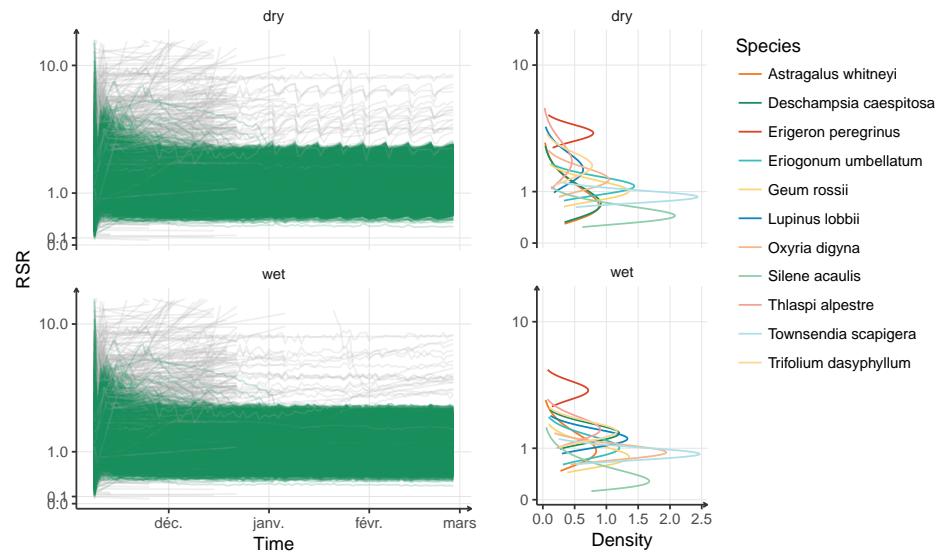


Figure 1.7: Comparison of simulated values of RSR with real species RSR in two contrasting conditions. Because there is no plasticity or ontogeny, the simulated plant do not express any changes in RSR.*Fixed-equilibrium*.

1.1.3 Discussion

The relative low selection rates for all allocation rules highlight the complexity of fitting such complex model to empirical data, despite the relative simplicity of the data. This difficulty seems to lie in two factors: the high number of parameters and the lack of stable changes in RSR. This last point is further discussed in the following paragraphs. Nevertheless, plant growth is reproduced in two contrasting conditions for multiple species, and while plastic algorithms have a greater potential for growth (more high growth rate), this is not systematic and the absence of clear pattern for the most influencing parameters, such as maximum exchange rates and respiration rates, indicates that such high growth depends on a combination of parameter values. I believe that the shape of gain and cost functions along the functional trade-off between active and structural tissues plays a determining role in the growth. A trade-off function with a wider viable range is more likely to be selected as more strategies would grow (therefore reducing the relative sensitivity to species-specific parameters). Considering the exponential shape of the turn-over function (one of the main cost with respiration), the width and height of the trade-off (or net gain function) is probably more strongly linked to the gain functions (exchange rates) and linear cost function (respiration), explaining little effect of parameters related to lifespan (already preselected otherwise). There is a strong dependency between viable strategies (and as a consequence functional potential diversity) and the main trade-off between resource acquisition and efficiency.

GROWTH AND STRATEGY SPACE

Filtering the parameter sets based on all species instead of individually would have been ideal to quantify this link and better calibrate the model. However, such approach would have required many more simulations, when the parameter filtering method was chosen for its low computational cost. Moreover, considering the number of species-specific parameters, fitting the strategy subspace (at least default active tissue allocation parameters, the memory of resources and stability) of 11 species to the data in combination with more than 20 models parameters is near impossible. Ones should have had first determined the relative positions of the species within the said strategy space before any global calibration routine. Nonetheless, species-specific parameters have an influence on model main variables. Memory parameter affected the RSR in the context of *non plastic* allocation rule (see figures 1.7 and ??, while the default proportion of active tissues in roots was an influencing parameter in all algorithms (figure 1.1.2, `as_r_d`). Therefore, they should be analyzed in further simulations within the same set of model parameters.

Change in modelling paradigm. The Bayesian paradigm where the information is contained in data and revealed by the structure of the model. Go for simulation experiment approaches where the model is used as a simulation tool and results as new data. The emerging patterns inform us on the impact of the modelled mechanisms (even if they do not totally match the data). Model as an understanding tool.

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

If the parameter filtering step did not result in the selection of optimum values for all parameters, it provides information on the main mechanisms influence plant growth. Indeed, the relatively high importance of parameters related to water shows the importance of the resource on the model behaviour. Both water availability (water absorption limitation, exchange rate) and root mass and construction parameters are important to match the empirical data. Considering that the calibration relies on experiment data of drought events, it is no surprise that parameters related to water economy show strong influence on the selection rate and model behaviour. In the context where the model has been developed, water shortage is expected to an important factor in community dynamics. In this perspective, the ability of *MountGrass* to reproduce the difference in productivity in both conditions, and the relative sensitivity to water related parameters is an advantage. The link between water resource, species strategy, plant performance and phenotypic plasticity is explored more in details in the following section.

THE ROLE OF WATER

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).

As mentioned earlier in this discussion, the model is not able to produce any shift in RSR in different water treatment. It is not a surprise for *non plastic* algorithm, but the filter was still applied on this criterion to allow the comparison with plastic algorithm and to be able to measure the improvement in selection rate. However, even plastic algorithms do not show strong enough response to water treatment in term of RSR. A strong and good (in the sense it would have matched the data) is larger in amplitude and more stable in time. Such processes

MORE COMPLEX PLASTICITY?

generally amplify with time, *i.e.* when the number of drought event increases, the response (allocation to roots) increases (relative to default phenotype). Unlike natural systems, plants in *MountGrass* fluctuates between two "states", or phenotypes associates to the dry and wet conditions. The RSR post drought event is reached after the first week without water. This can be explained by two main mechanisms that are related but have contrasting implications. The quickness in response to the changing conditions is allowed by relatively high assimilation rate. If the net growth rate is controlled by the total weight condition during the filtering process, the assimilation rate is not and can be compensated with relatively high turn-over rate. Net growth rate being equal, species with higher assimilation rate will have higher phenotypic flexibility (higher fraction of biomass to invest in carbon pool of choice) than species with lower assimilation rate. This flexibility, similar to reallocation, allows changes in RSR, but not the accumulation of biomass in roots. Unfortunately, both the constant turn-over rate implemented in the model, and the selection toward "wide and high" gain functions limit control on this aspect.

Moreover, the fact that plants are more productive during periods where they may not want to invest in roots strengthen this effect. Indeed, a plant would drift to higher RSR if it was more productive when pursuing the high RSR phenotype than when pursuing the low RSR phenotype. This last point mentions the "will" of the plant, in the context of *MountGrass* this target phenotype is encoded in the projection of external conditions. Because this projection is daily based by design, the accumulation of drought stress is not translated in the internal projection variables of the plant (like it can be with the accumulation of phyto-hormones (**need ref**)). This limitation highlights a big difference between simulated plants in *MountGrass* and natural plants. While solutions to overcome this problem can easily be imagined(see equation 4.28 in 4.3.3), they would require more parameters and introduce more complexity to the analysis. This model provides a first approach to phenotypic plasticity in grassland models and the formulation of the projection, key element of the phenotypic plasticity, is certainly a starting point for further development. Nevertheless, the differences in response to the parameters between the three allocation rules, despite shared plant functioning, demonstrate the importance of plasticity itself. And simplification of the processes should not be a reason to not explore its effects. The fact that the parameter tau has a relatively small impact on selection rates also support the need to better understand all strategic axis before focusing on the effect of projection. While there are many ways of simulating the phenotypic plasticity, the parsimony is privileged. This simple representation is enough to understand the effects of active plastic allocation in association with the other strategic differences between species.

Bayesian paradigm where the information is contained in data and revealed by the structure of the model. Go for simulation experiment approaches where the model is used as a simulation tool and results as new data. The emerging patterns inform us on the impact of the modelled mechanisms (even if they do not totally match the data). Model as an understanding tool.

MODELLING PARADIGM

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

Calibration and sensitivity analysis give information on the main processes of plant growth, but the general effects of the allocation rules on plant growth are not fully identified. In addition, because the parameter filtering processes was limited to individual plants, and the response of species specific parameters dependent on other parameters of the model, the effects of these species specific parameters should further be investigated. The objective of this part is to set better understanding on the role of **allocation rules** and **species memory** on plant development as basis for interpretation of plasticity effects in following chapters.

The challenge of the framework presented in paragraph 2.2.1 under *plastic-optimisation* is to control the phenotype with the values of the memory. The risk of this approach is to have too tight estimation function of the fitness (or driving function) and to see the convergence of all species (with different memory values) toward the same phenotype (same allocation of active and structural tissues in roots and shoot). The extend to which different species memory lead to different phenotypes under full genetic control (non influence of external conditions) is explored through simulation experiment under *plastic optimisation* allocation algorithm.

1.2.1 Method

The effect of allocation rule on phenotypic development is investigated thanks to pot simulations (see Methods in 1.1) of 100 days in 3 watering treatment: 2mm, 8m and 16mm per day. To avoid drift in the phenotype due to allocation algorithm (see paragraph 2.2.1 on phenotypic determination), simulations where run a first time, then rerun with default specific traits matching traits at the end of the first simulation set. All four algorithms are simulated. To reduce the number of simulations 100 parameter sets are selected randomly within the accepted parameter sets for the *non plastic algorithm*.

ALLOCATION ALGORITHMS

Memory of external conditions plays a determining role in phenotypic development under *plastic-optimisation* allocation rules. The effect of the memory alone (environmental cues ignored by setting tau to 1) on the default emerging phenotype is explored for diverse memories (9 values on the two axis from 0.1 to 1 later scaled to the maximum area exchange rates for model parameter set considered, or 81 values) for each accepted parameter set. The effect of the memory values on the final position of plants in the phenotypic space are visualised by fitting loess curves between memory values and individual trait values.

MEMORY & PHENOTYPE

1.2.2 Results

think of a "showtime" visualisation that shows how growth and traits are impacted by allocation rules and tau.

ALLOCATION RULES

Have the proportion of tissues changing over time

Show the respiration, assimilation and turn-over rates.

Isn't it possible to show these along memory or active/str ratio axis ?

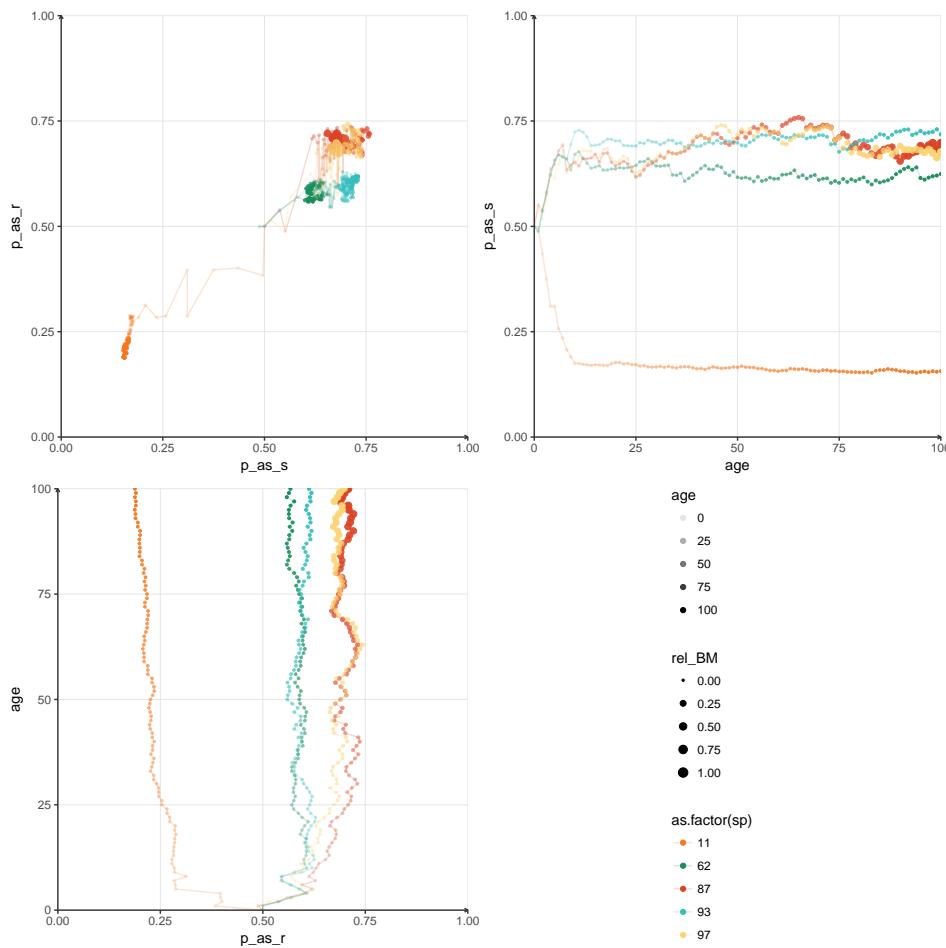


Figure 1.8: Trajectories along time in the strategy space of 5 plants with different memories. After 10 days, all plants have converged toward the estimated optimum.

The kinetic of the phenotypic shift is first visualised for one parameter set on the two main phenotypic axis (proportion of active tissues in roots: PAR and proportion of active tissues in shoot: PAS). From the same starting point the five species show distinct rapid shift toward segregated subspace of the 2D strategy space. The equilibrium point is reached in approximately 10 days for all 5 species. Despite constant memory, variations are visible on both tissue allocation traits of roots and shoot. These variations lead to partial overlap but the five species are distinct on the 2D space.

MEMORY AND PHENOTYPE

The memory of resource availability is a strong enough driver to alter the default phenotype of a species. The effect of the two components of the memory (memory of water availability and memory of light availability) on the three main traits is explored through local regressions. The proportion of active tissues in roots increases to a plateau with increase in water availability memory (figure 1.9). This response pattern is consistent between all parameter sets, but the starting points and slopes may differ. The same pattern is observed between light availability memory and proportion of active tissues in roots (data not shown). The allocation convergence in the root is also influenced by the increase in light availability memory. An increase in the latter leads to a smooth increase in the former (see figure 1.10) with less drastic response than the water. This response

is mirrored in shoot allocation response to increase in water availability memory (data not shown). Both organs react in symmetric ways to increases in resource availability. The RSR has a negative log response to water availability memory (positive in the case of light availability memory).

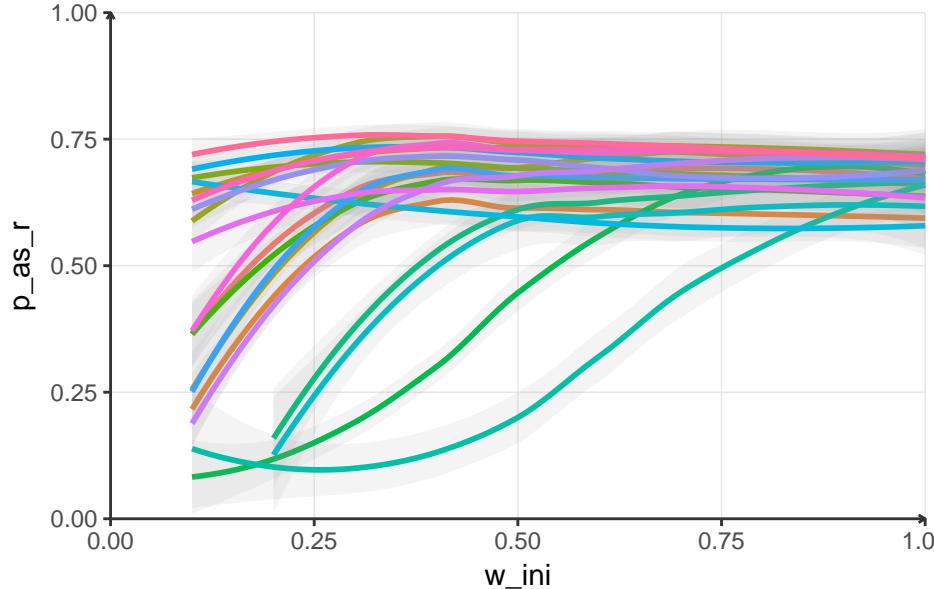


Figure 1.9: Effect of memory of water availability on proportion of active tissues in roots. *Plastic-optimisation*. Each line correspond to a local regression fitted for all memory combinations for a given parameter set. Water availability memory is given in percentage of maximum exchange rate, absolute values may change between parameter sets.

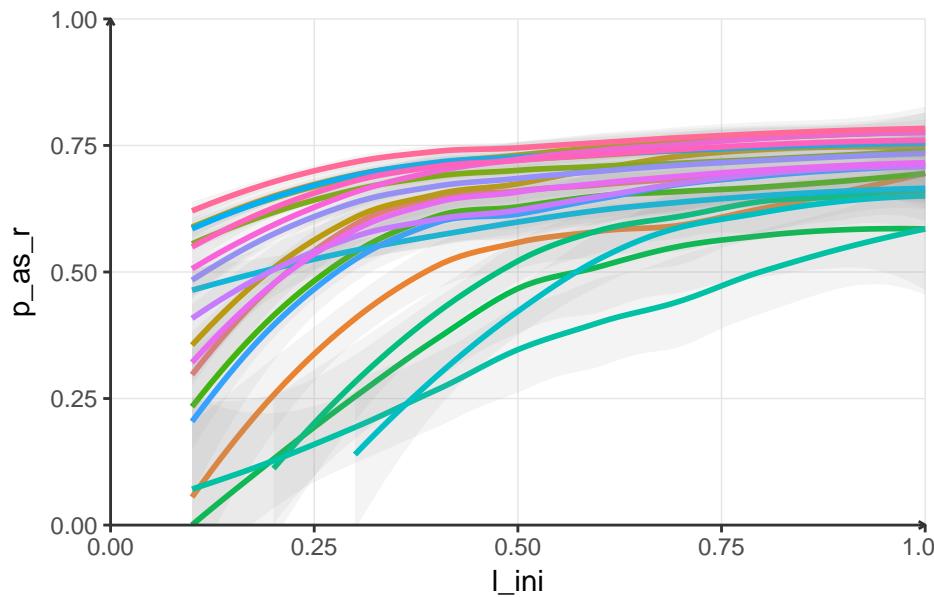


Figure 1.10: Effect of memory of water availability on proportion of active tissues in shoot. *Plastic-optimisation*. Each line correspond to a local regression fitted for all memory combinations for a given parameter set. Light availability memory is given in percentage of maximum exchange rate, absolute values may change between parameter sets.

The combine effect of the two axis of plant resource availability memory is observed by plotting the phenotypes (on the 2D space of active tissue allocation) of four contrasting memories for all parameter sets (figure 1.11). There is clear clustering of the four memory profiles, with some overlaps due to the fact that multiple parameter sets are plotted at the same time. The memory of low availability (●) has a much larger distribution area than others, suggesting the relative instability of this profile within the "estimated net gain landscape". Memory of

low availability for both resource drives plant toward very conservative strategies (need some values here) than other strategy. High expected availability of at least one resource increases allocation to active tissues to both organs. This confirms the positive effect of complementary resource (light for roots and water for shoot) of active tissue allocation in organs (see figure 1.10). Because of this, there is no highly unbalance phenotypes with high contrast between organ specific allocation emerging from the *plastic-optimisation* allocation in *MountGrass*. There is general coordination, but the balance between resource availability memories still impacts the position on the 2D, illustrated by the absence of overlap between low light - high water (●) and high light - low water (○) phenotypes. In case of high resource availability and coordination, high investment in active tissues for both organ is achieved(●) and high light - high water), but the range of values is similar than for unbalanced memories(●) and high light - low water (○).

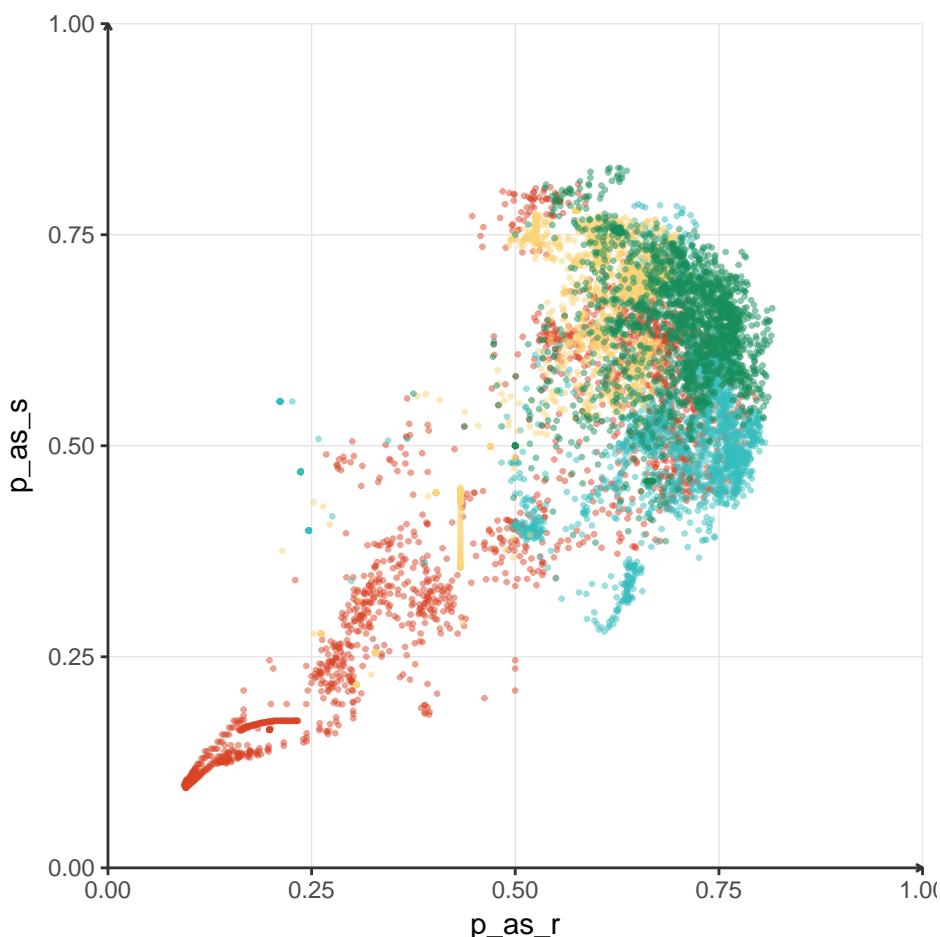


Figure 1.11: Impact of species memory on final phenotype in case of fully plastic allocation. *Plastic-optimisation*. Each point corresponds to a plant phenotype for a memory syndrome for a given parameter set. Colours denote the memory syndromes.

- low light - low water,
- HIGH light - low water,
- low light - HIGH water,
- HIGH light - HIGH water.

1.2.3 Discussion

rapid convergence.

[ALLOCATION RULES](#)

Cost and gains

Diversity of phenotypes

Crossed and symmetric influence: the respective efficiencies cannot be analysed independently.

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 phenotypic landscape. Plus there is a need for alignment between starting phenotype and endpoint. Will also affect how plasticity is driven.

... nothing here yet, the idea was to show that the "strategy" of the species conduce to slow and fast archetypes. Should be able to show that with some memory simulations.

FAST-SLOW STRATEGIES

But not equal distribution along the axis probably.

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.

The symmetry and the curves shapes suggest that resource related organ is more sensitive and that "apparent" increase in resource availability promote more exploitative strategy. - what mechanism ?

MEMORY AND PHENOTYPES

It seems that there is greater concentration around high values of active tissues. This is consequence of net gain curves. Is this verified in other allocation rules ? Or is this an artefact ?

The role of memory highlight the expected problem of matching default phenotype with memory: little ontogeny effect (due to high growth and turn-over rates) and problem with distance based plasticity cost (would require a moving cost, instead of fixed reference cost).

For each parameter set the alpha shape of the volume could be drawn to have an idea on how parameters impact potential functional diversity. But no time here to test that.

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.)

Role of allocation rule and changes in traits, traits affect strategy and performance, memory lead to different phenotype/strategies (based on gain function), there is coordination, effect of complementary resource. Need to better understand allocation rule and optimum strategy, and convergence and diversity.

I REALLY NEED TO EXTEND THE CONCLUSIONS AND GO BEYOND MY OWN WORK. REFER MORE TO OTHER PEOPLE WORK !!!

2 INDIVIDUAL PERFORMANCE, PLASTICITY AND VARIABLE CONDITIONS

The previous section highlighted the ability of the model to model growth, but also the importance of species specific parameters. While the plasticity mechanism did not replicate to a full extend (stable and higher amplitude) the phenotypic changes between the different conditions, there were some changes both in traits and in growth, leading to a higher selection rate. Considering the importance of species specific parameters and their potential impact on growth, these differences between plastic and non plastic allocation rules should be investigated in an extended manner. The specific roles of strategy and memory on the multiple components of plant growth need to be disentangled to draw better hypotheses on the role of phenotypic plastic on plant performance and coexistence. The role of resource availability on these mechanisms also needs to be interrogated. The effect of plasticity on coexistence can also be approached with respect to relative performances and contraction of the strategy space.

This chapter tends to answer these questions with simulations of individual plants with diverse strategies and under multiple allocation rules. To simplify the approach and focus on the interaction between species strategies and allocation algorithm, the plasticity will be model as discrete mechanism ($\tau = 0$ for all plastic allocation algorithms).

2.1 Individual performance: between strategy, memory and plasticity

This first subsection focuses on the link between the phenotype and the plant performance. The plasticity and allocation mechanisms can affect both the link between phenotype and performance and the distribution of the existing phenotypes.

2.1.1 Method

Because little differences are found between accepted parameter sets for the three main algorithms, parameter sets selected for the *non plastic* algorithm are used for all algorithm. To reduce the number of simulations but have a measure of the genericity of the observed patterns, 20 parameter sets are selected among the accepted parameter sets for the *non plastic* allocation algorithm. As mentioned in the previous section, the parameter sets have been selected for only one species-specific and therefore an additional step was used to filter out the parameter sets that could lead to high biomass values. For each parameter set, simulations of diverse phenotypes run for 100 days of 15 hours with favourable temperature conditions (20 °C) along resource availability gradient. The parameter sets are selected based on the maximum biomass of all simulated plants. One parameter set is randomly selected for each of the 20 brackets between 0 and 2 grams of total biomass.

PARAMETER SETS

To better understand what make a plant perform in the model, a multitude of phenotype needed to be tested. Tested phenotypes are distributed regularly along the three axis of the strategy space (proportion of active tissues in root, proportion of active tissues in shoot, proportion of roots) between extreme values (respectively (0.1, 0.99), (0.1, 0.99) and (0.1, 0.9)) for a total of 3375 combinations (15^3). Because the RSR is defined by the memory, and in this set of simulation experiments the RSR is defined before, the species memory needs to be computed afterwards. There is an infinite number of couple of memory values that can match a given RSR. Also, the projection of conditions is sensitive to both memory and experienced conditions, therefore the choice of memory can affect the relative sensitivity of species to changes in external conditions and alter the model behaviour. Because the role of memory is not the focus here, and because there is much more focus on the role of the plasticity as a mechanism (as opposed as a strategy with various values of tau), the parameter tau is set to 0. This ensures that only the starting phenotype and the experienced conditions play a role in plant performance.

STRATEGY SPACE SAMPLING

For each phenotype a pot simulation is ran for 100 days of 15 hours under 4 millimetres rainfall and 120 Watt per square metres and per hour with the 4 main allocation algorithms (*non plastic*, *fixed-equilibrium*, *fixed-optimisation* and *plastic-optimisation*). Two resource levels are tested for each simulations. The low resource availability conditions correspond to a reduction by a factor 4 of resource influx, but the day length was conserved.

SIMULATION SET-UP

To visualise the performance landscape (plant performance relative to biggest plant as function of its phenotype) the performance of best phenotypes are projected against the 3 plans that compose the phenotypic space. Such projections are preferred to 3D alternatives as they work better with static visualisation and when most of the space is occupied. Alternative axis are defined to facilitate the interpretation and description of the performance landscape: the organ strategy plane(PAR-PAS plane) can be transformed into strategy balance (difference between PAS and PAR) and "speed" (in sense of Reich (Reich 2014))(mean allocation to active tissues).

PROJECTIONS

To study the potential effect of resource availability and or allocation mechanism on the link between strategy and performance, an aggregated measure is designed: the **gravity center** of the phenotypic space is defined as the average phenotype weighted by the relative performance of each phenotype. It can be defined with respect to the initial strategy, or to take into account the plasticity, to the final position in the phenotypic space. Shift of this gravity center within the projection space inform of translation of the performance landscape.

Biomass measures are relative to best performing non plastic plant (to remove the general parameter set effect on growth) and compare (within each condition) the effect of allocation algorithm.

NORMALISATION

2.1.2 Results

The effect of species specific parameter on growth are first studied with the analysis of the performance landscape drawn by the growth of plants uniformly distributed in the strategy space.

PERFORMANCE LANDSCAPE

On the tissue allocation plan (proportion of active tissues in leaves and roots)

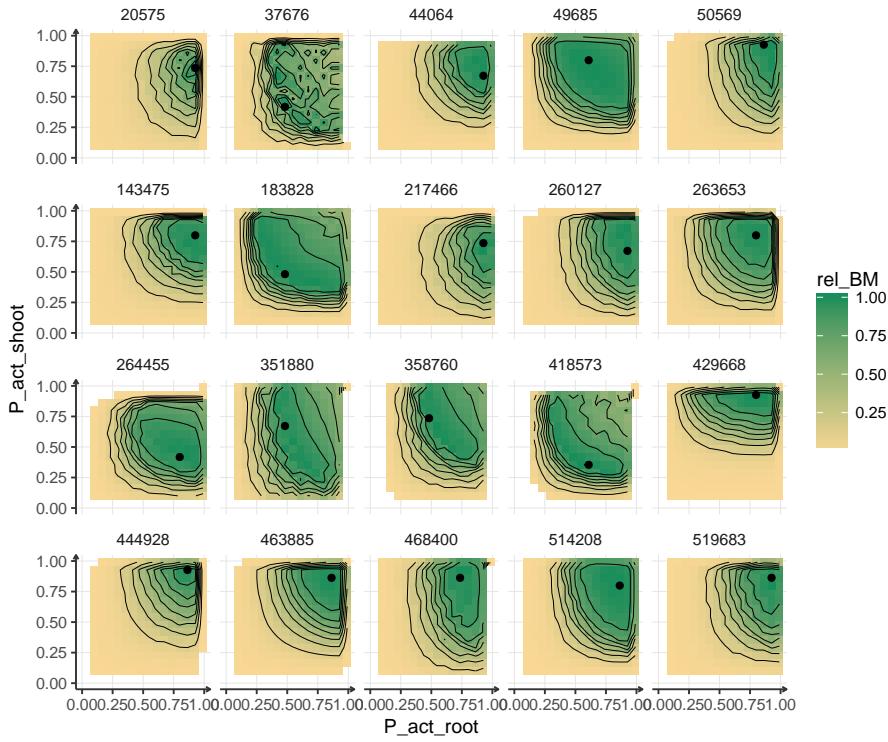


Figure 2.1: Projection of best phenotypes (varying RMF) on the 2D PAR-PAS plane for each parameter set. Points identify the optimums. *Non plastic.*

(see figure 2.1), the best performing phenotypes present a bean shape. This shape covers a good fraction of the space, in the center and sometimes top-right corner (high active tissue allocation) of the 2D space, while other corners are ignored. Too low values for any of the organs lead to a limited growth. For certain parameter sets, the top-right corner, corresponding to high resource acquisition strategies, has lower growth values than the center. They have lower growth values than phenotypes with similar values for one of the organ and lower value for the other organ.

Projection of the best phenotypes over the three planes also gives information on the importance of the ignored variable on each plane. If the contrast between the growth projected phenotypes is high, at least on the main dimension is crucial for the growth. If the contrast is lower when the variable is ignored (*i.e.* the best value is used) then the projected variable is likely to be important. The projection on PAR-RMF and PAS-RMF (see figure ??) planes show higher contrast between phenotypes relatively to PAR-PAS plane, therefore the RMF is a more sensitive variable than the allocation factors to active tissues in organs.

Introducing resource availability variations and plasticity can impact the shape of the performance landscape.

OPTIMUM SHIFTING

A shift of gravity centres can be observed between the two resource levels in all allocation algorithms (see figure 2.2, the four panels). *Non plastic* and *fixed* algorithm show similar trends with an increase of proportion in active tissues in both organs. This change toward more exploitative tissues is consistent and is observable for all parameter sets but one. The *plastic-optimisation* algorithm show drastically different responses of gravity center of phenotypes. There is little change in shoot proportion of active tissues, but a consistent reduction of

active tissues in root system, and a reduction of root mass fraction (data not shown). These two responses indicates a net reduction of root activity in favour of shoot activity. Two things must be taken into consideration while looking at these results: (1) the gravity center is computed from final position into the phenotypic space, not the starting position, (2) because *plastic-optimisation* algorithm allows changes in traits that are represented (PAR and PAS), shifts along these axis can be driven by the plasticity mechanisms and not necessarily only performance differences. Similar representation of the gravity center computed from the initial phenotype (not shown) shows similar response for the three first algorithms, and no apparent shift for the *plastic-optimisation* plasticity.

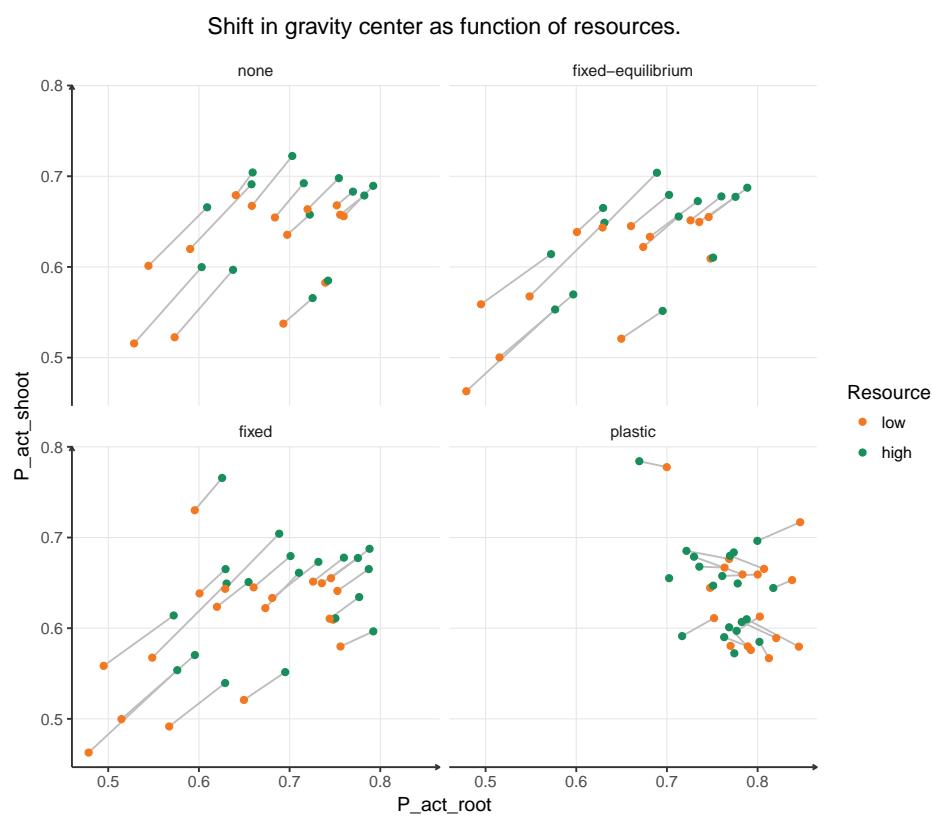


Figure 2.2: Shift on the 2D phenotypic space of the center of gravity as function of resource availability. The center of gravity is defined as the average phenotype weighted by the relative biomass, and characterises the performance landscape. *Non plastic*.

Non plastic and *fixed* plasticities respond the same way to a shift in resource availability. However, we can note that the gravity centres have lower proportion of active tissues for *fixed* allocation algorithm compared to the *non plastic* one.

Plastic allocation lead to an improvement in mean biomass of all individuals for all three plastic allocation algorithms (see figure 2.3). The *fixed-equilibrium* plants are 2.5 times bigger in average than *non plastic* plants (in low resource conditions,

PRODUCTIVITY CHANGES

and up to 7 times bigger for *plastic-optimisation* plant. These ratios are relatively similar for high resource availability.

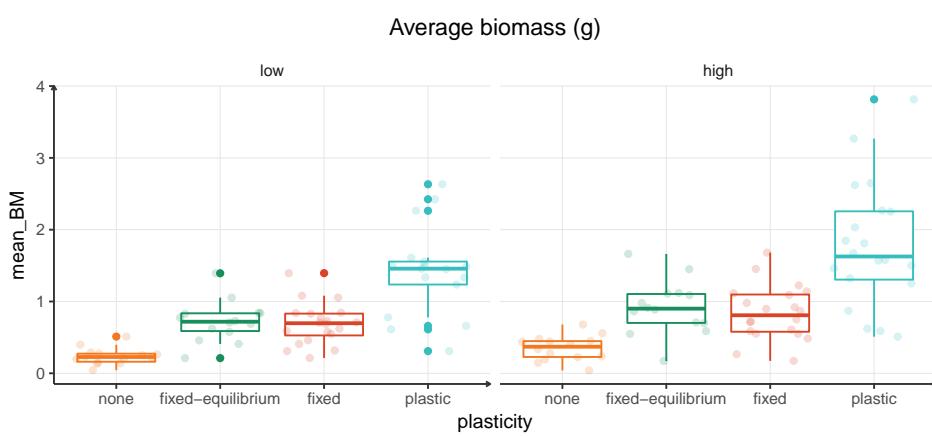


Figure 2.3: Mean relative biomass as a function of allocation algorithm and resource level.

However, the maximum biomass is only marginally improved with an increase of 6% for *fixed-equilibrium* and 8% for *fixed-optimisation* in low resource condition (see figure 2.4). These percentages drop to less than 1% in high resource availability conditions. The *plastic-optimisation* algorithm even lead to a decrease in the maximum biomass averaging 10% and 13% respectively in low and high resource availability conditions.

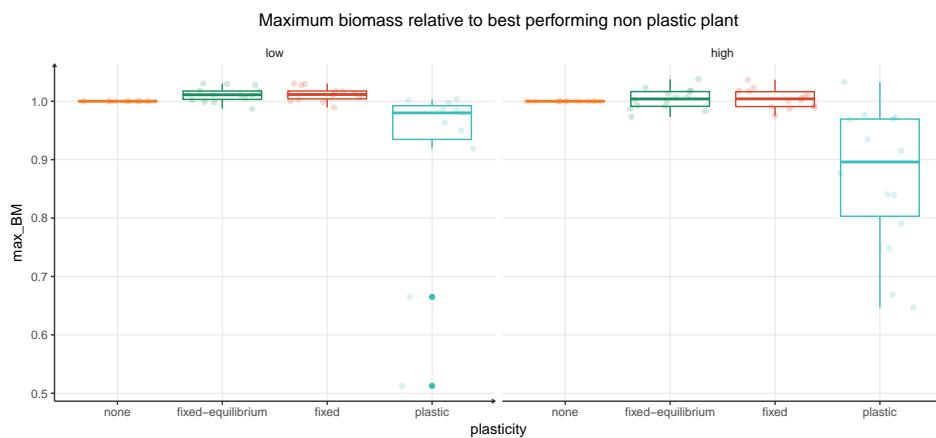


Figure 2.4: Maximum biomass relative to the *non plastic* simulations, as a function of allocation algorithm and resource level.

The effect of plasticity on the potential diversity is estimated by looking at the species that reach the range of 90% to 100% of the maximum biomass within the specific conditions (for each parameter set, algorithm and condition separately).

NEED AN UPDATE OF RESULTS, BUT SAME TRENDS

The number of species within this range is extremely low in *non plastic* allocation algorithm simulations, with 1.4% and 2.1% respectively for low and high resource conditions. This percentage is greatly improved by plastic allocation algorithm and reach in average 9% to 15% of species in *fixed-equilibrium* and *fixed-optimisation* algorithm, while it can reach up to 100 % for *plastic-optimisation* algorithm, with a mean proportion of species with a top performance around

PHENOTYPIC CONVERGENCE

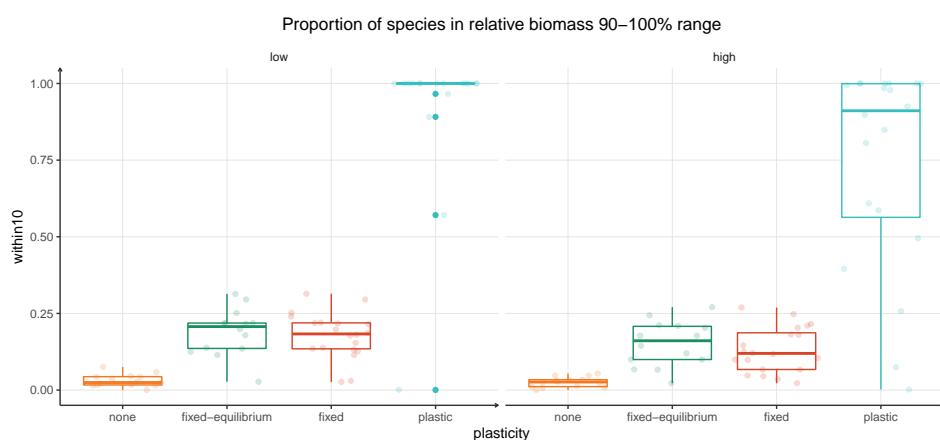


Figure 2.5: Number of species within the range of 90% to 100% of the maximum biomass, as a function of allocation algorithm and resource level.

72% in low availability condition, and up to 82% in high resource availability condition.

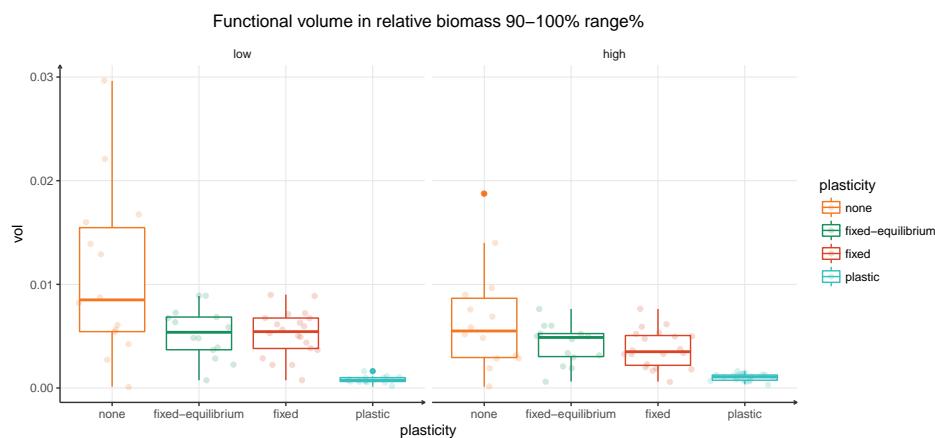


Figure 2.6: Functional volume occupied by the species within the range of 90% to 100% of the maximum biomass, as a function of allocation algorithm and resource level.

The functional diversity, estimated with the approximate volume of the top phenotypes, follows a opposite trend, with the highest value for the *non plastic* allocation algorithm. *Fixed* algorithms present half the functional volume of the *non plastic* algorithm, and the *plastic-optimisation* algorithm has extremely low values five times lower than the *non plastic* ones.

2.1.3 Discussion

The study of the performance landscape puts in light the different components of **plant performance**. To understand how plasticity can play a role, it is important to understand what make a phenotype a good phenotype. On one hand, the extend of strategies (plan PAR-PAS in figure 2.1) with high relative growth (green area) is high when the best RMF is considered, while this is greatly reduced on plans that integrates RMF variability (see figure 2.7). This result suggest the high importance on this axis for the plants performance. This can be explained by a stronger effect of this dimension on the exchange area through changes in organ masses, instead of organ densities (affected by PAR and PAS). The RMF fraction

COMPONENTS OF PERFORMANCE

impacts the plant performance in two ways: by changing the **equilibrium** between shoot and root exchange activities, and by changing the global carbon loss rate (respiration and tissue turn-over) if the organ differ on this aspect. These two components may have opposed directions, as the limiting organ may also be the least efficient, and therefore the RMF could be greatly constrained if the two aspects have similar importance. The effect on the equilibrium is likely be more important as a wide range of RMF values can be observed for numerous datasets (data not shown), and plant with uncoordinated (low-PAS & high-PAR, or high-PAS & low-PAR, see figure 2.7) organs still present high biomass values, suggesting that the respiration and turn-over loss are less important than a balanced resource acquisition.

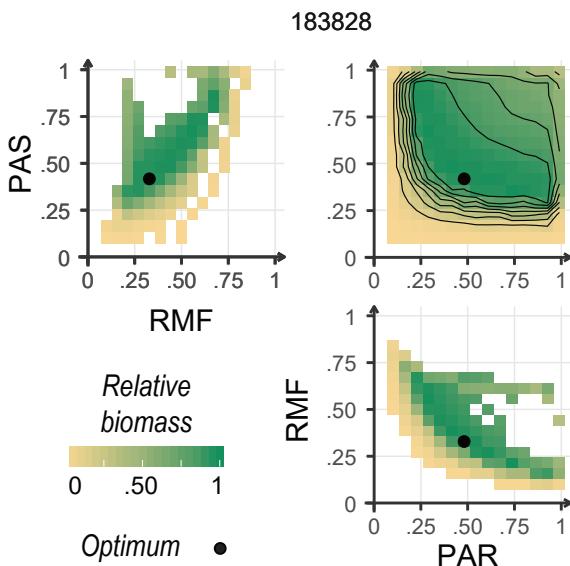


Figure 2.7: Projection for the parameter set 183828 of best phenotypes (according to the variable that is ignored) on 2D plans of the phenotypic space. The dots represent the optimum phenotype. White space indicates the absence of phenotypes able to survive until the end of the simulation (100 days). RMF: root mass fraction, PAR: proportion of active tissues in roots, PAS: proportion of active tissues in shoot.

On the other hand the organ specific strategies are also important as low values for any of the organs (leaves or roots) lead to very low growth. Extreme high values can also be limiting, suggesting the existence of an optimum of the proportion of active tissue for the tissue efficient. This **optimum tissue efficiency** results from trade-off between active and structural tissues, driven by the relative importance of carbon gain (increased exchange area with active tissues) and carbon loss (increased respiration and turn-over with proportion of active tissues) that depends on models parameters and resource availability (that change the exchange rate).

However, meeting these tissues specific optima might not be sufficient, as the bean shape of the best phenotypes suggests, another component is relevant. Low values of proportion of active tissue in one organ can be compensated by a high allocation of active tissues in the other organ that allows a higher allocation in the low exchange rate organ. This confirms the importance of the equilibrium over the tissue specific strategies. But the shape also reveals a last component of the plant performances. The fact that species with high values of proportion of active tissues in both organs have lower biomass, is certainly due to a limitation of both resources (equilibrium is assumed), reducing the overall efficiency.

From this visualisation of plant biomass as a function of the phenotypes, three main components play a role. The **equilibrium**, mostly driven by the changes in RMF is essential to the plant growth. This is explained by a re-

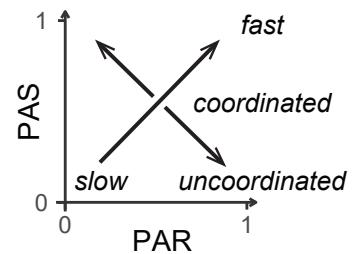


Figure 2.8: Alternative axes to describe the plant phenotypes on the plan PAR-PAR (PAR: proportion of active tissues in roots, PAS: proportion of active tissues in shoot). The slow-fast axis refers to the proportion of active tissues (close to the fast-slow strategies of Reich 2014), while the orthogonal axis show how coordinated the plant is (see Freschet, Swart, and Cornelissen 2015 for similar concept).

duction of the exchange rate of the non limiting organ that greatly reduces its organ specific efficiency (see figure ??). This **organ tissue efficiency**, driven by its effective exchange rate, respiration and turn-over, is also an important component of plant performance. Low values of allocation of active tissues greatly reduces this efficiency, but it can be compensated by bigger organs. However, such mechanisms can affect the overall efficiency defined as the average mean of organ realised efficiencies (taking into account resource limitations) weighted by the organ masses. Finally, the **speed** of the plant, or the overall resource acquisition rate, admits an optimum that is between an over-capacity leading to a co-limitation of resource on both organ reducing their individual efficiencies, and the under-capacity, leading to a sub-optimum use of resources and letting space for competition.

The phenotypic plasticity allows species to move within this performance landscape along certain axis. It is often perceived with a species-centric perspective, that is to say, that plasticity is seen as variations in the species mean phenotype. However, in the context of community ecology, it is also interesting to try to see how it not only affect individual species but shape the community distribution in the strategy space. The plasticity relies on changes of default phenotypes toward "better" strategies in the context of the given conditions, therefore it implies that if it exists an optimum subspace (one strategy or an ensemble of strategies) species will converge toward this subspace, distorting the functional space. Environmental variations and plant interactions aside, in a constant environment the **performance landscape** is fixed. As a consequence, the plasticity benefits to the plant in a static manner, that is to say, it is only a tool to reach a better phenotype where the plant stays in if conditions do not change. This can be related to spatial heterogeneity that would lead individuals from the same species to adopt different phenotype to acclimate to the particular conditions of their spatial situation. It is opposed to the perception of a more dynamic phenotypic plasticity as a tool for a given individual to cope with temporal variations in environmental conditions. These two aspects are further discussed in the following section, while the effects of the contraction of the phenotypic space are discussed now.

CONVERGENCE TO SUBSPACE

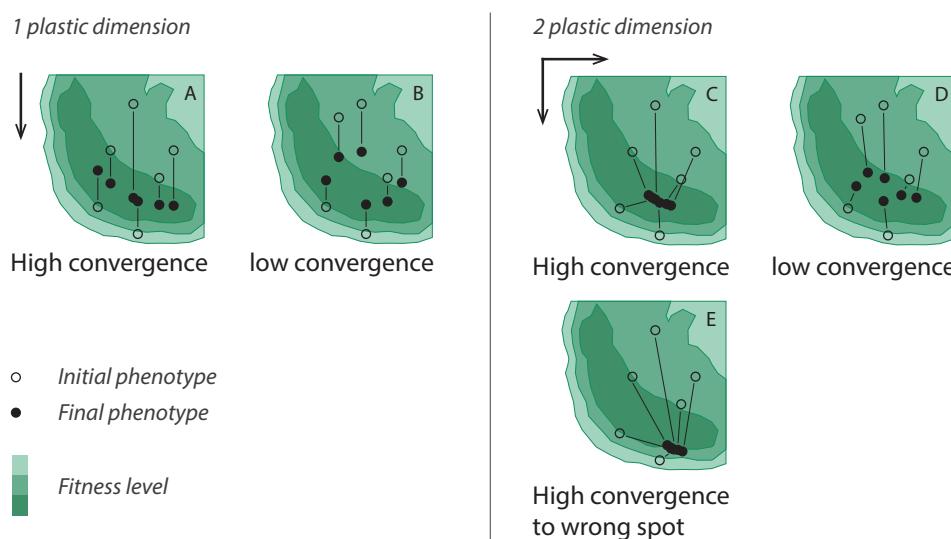


Figure 2.9: Convergence patterns on a 2D phenotypic fitness landscape, with 1 plastic dimension (A & B) or 2 plastic dimensions (C, D & E). Plasticity can lead to high convergence (A, C and E) with potentially high fitness evenness, especially in space with numerous plastic dimensions (A & E), this is problematic especially if the point of convergence is not the optimum (E). Limits to high convergence are necessary to allow realistic functional diversity with plasticity (B & D).

As just mentioned, the plasticity can be seen at the scale of the species assembly¹ as a contraction of the phenotypic space of the species assembly. This contraction has two main effects: the reduction of potential functional diversity and a reduction of growth rate differences. There is here an emerging trade-off between the **species diversity**, supported by lower fitness differences, and **functional diversity**, reduced by the contraction of the phenotypic space. However, if the plasticity reduces greatly the potential functional diversity (volume of the whole phenotypic space without considering filtering based on relative fitness), the realised diversity (expressed as the functional diversity of the species within the 90%-100% maximum biomass range) is less impacted because a large parts of the phenotypic space have low growth rate in the given conditions. Nevertheless, there is a reduction of the diversity of expressed phenotypes. Indeed, in this scenario of "extreme" plasticity ($\tau = 0$) the convergence is important on plastic dimensions while partial convergence would be enough to have good fitness (see conceptual figure 2.9). Lower convergence on plastic dimension should lead to less compact phenotypic subspace while keeping relative fitness evenness. In the case of *fixed-equilibrium* and *fixed-optimisation* allocation mechanisms, this reduction of diversity is lower because only one axis is plastic.

Reduction of the phenotypic convergence can be achieved by other allocation mechanisms, differences in projection (different τ values leading to different projections) and plasticity costs. In heterogeneous system, this convergence is expected to be lower as heterogeneity will lead to different projections.

The convergence of the phenotypes to a sub-space of lower performance lead to an increase in the mean biomass (see figure 2.4). However, the maximum biomass is only marginally improved in *fixed* plastic allocation simulations, and reduced in *plastic optimisation* allocation simulations. This two contrasted results, show different effects of plasticity. The light increase can be due to either a dynamic gain or a static gain. The **dynamic gain** can emerge because the plant growth affects the resource availability, changing the optimum phenotype, and allowing plastic plants to follow these changes during time. It could also result from a **static gain** because the phenotypic plasticity allows a better resolution in tested phenotypes (the plastic axis are continuous while the phenotypic space sampling was discrete). The role of plasticity and dynamic gain is explored in the following sections with temporal resource heterogeneity.

The reduction of the maximum biomass highlights the difficulty to find the optimum phenotype. Because, the growth mechanisms are reproduced in an exact manner in the plasticity algorithm, this mismatch is certainly due to a difficulty to project the future of resource availability. Because of that, it is possible that the gain in maximum biomass, mentioned above, due to static or dynamic gain is greater than it appears. The particular case of mis-projection in *plastic-optimisation* simulations is discussed in the following paragraph.

Plastic-optimisation algorithm is characterised by a high convergence of the species within the phenotypic space, high mean biomass but maximum biomass lower than best *non plastic* phenotype, and high potential species diversity. The convergence is expected and explained by the fact that all three traits are plastic and all species (for a given resource level) experience similar conditions leading to the computation of the same optimum. The absence of plasticity cost limiting the convergence leads to a phenotype concentration toward this optimum. This

¹ here I draw a distinction between species assembly that refers to all present species, and community that refers to the interacting individuals of the present species. However, some interpretations can be translated to communities.

LIMITED DYNAMIC GAIN

PLASTIC EXHAUSTION

convergence explains both the high potential species diversity, as all species have very similar growth rate, and the relatively high mean biomass because only few species did not survive or had very little growth rate.

The fact that this plasticity does not translates into higher maximum biomass is surprising, especially considering the fact that RMF plasticity improves maximum biomass (see figure 2.3). Lag in adaptation is often identified as a limit of plasticity (DeWitt, Sih, and Wilson 1998; Van Kleunen and Fischer 2005), nevertheless, in a constant resource influx experiment, and considering the high phenotypic flexibility of plants in *MountGrass*, this explanation is unlikely. Another problem highlighted with plasticity is its adaptiveness. Evolutionary speaking, it is hard to imagine the emergence and maintenance of a plasticity mechanism (in a given context) if it is no adaptive. Yet, such process could be maladaptive in a new context. Because plasticity is not emerging, but imposed by the simulation set up, its adaptiveness can be interrogated. Here adaptiveness do not refer to a reduction of fitness due to plasticity, but to the capacity of the plastic mechanism to define an optimum (or at least better) phenotype. Plasticity as implemented in model has no explicit bias and all mechanisms involved in plant growth are simulated by the allocation algorithm. The sampling of phenotypes is random and could be source of uncertainty, but it is uniform and no consistent drift is likely to emerge from the noise introduced by such sampling. The last aspect of plasticity that can affect the adaptiveness of plasticity is the estimation of conditions. The estimation of conditions is based on resource levels experienced by the plant and by definition are exact, therefore the problem lies in the projection of these conditions and how they translate into resource uptake.

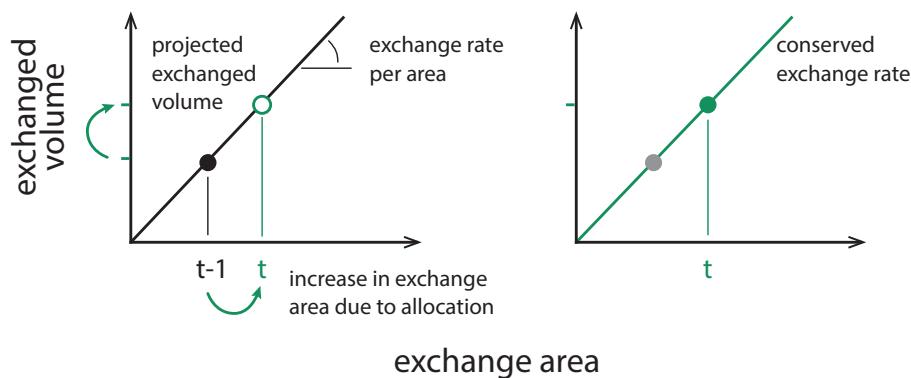


Figure 2.10: Projection of the water volume exchange after increase in exchange area at equilibrium and with no limitation.

In *MountGrass* the resource availability is coded as an uptake rate per day and per unit of exchange area, and is computed as the resource uptake divided by the exchange area. This resource availability is supposed constant, and plants make the assumption that increasing their exchange area leads to a proportional increase in resource volume exchanged (see figure 2.10).

However, in the case where a plant already absorbs all the available resource, then this assumption is not respected, and the uptake rate per area is lower than expected (see figure 2.11 right panel, realised exchanged volume does not match the projection because it cannot exceed the total volume of available water). This gap between perception and actual resource availability occurs because the plant is not able to perceive that the limitation cannot be compensated by a higher investment in the limiting organ. This behaviour explain a very high

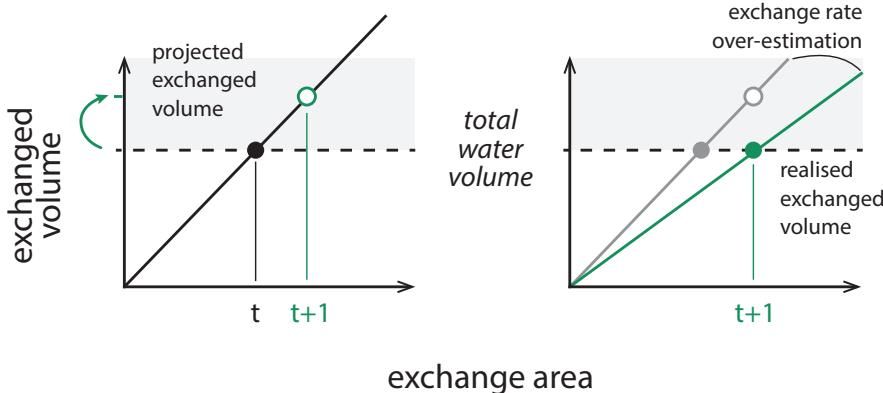


Figure 2.11: Projection of the water volume exchange after increase in exchange area when total available water volume is limiting. The water volume exchanged cannot exceed the total available water volume, leading to a systematic over-estimation of water availability and offset between shoot and root activity.

investment toward root and root active tissues in low resource conditions under *plastic-optimisation* allocation (figure 2.2). This gap¹ is the cause of the **plastic exhaustion** phenomenon. Indeed, this constant over-estimation leads to constant discrepancy between the estimated optimum phenotype and the actual phenotype, and a larger allocation to root active tissues. This effect is particularly noticeable in the context of pot simulations where the water pool is limited. The absence of plasticity costs also favours such extreme behaviour.

Despite this particular seemingly non-adaptive behaviour, the *plastic-optimisation* algorithm is still interesting to study in community simulations. First, the presence of plasticity cost should limit such extreme behaviours. Second, in a context of competition in a larger environment, this aggressive search behaviour is likely to be an advantage against individual with less aggressive, or stable strategy. Finally, this mechanism emerges in constant influx conditions that allow growth, but its emergence should be reduced in variable environment where water shortage leads to reduced growth.

Plastic-optimisation simulations expose this phenomenon with large effects, but it is probably present for simulations with other plastic allocations but with smaller effects. The difference in magnitude can be explained by a less effective growth in early stages of development for *fixed* plasticities (when *plastic-optimisation* is more efficient than *fixed* plasticities) that delay the time when the total volume is reached (time t in figure 2.11), and in average lower active tissue allocation in roots that leads to lower loss due to non-equilibrium.

Plastic exhaustion is a specific limit of phenotypic plasticity as implemented in *MountGrass* that relies on the assumption of constant exchange rate per exchange area. It has a large effect in the specific case of pot simulations. However, this phenomenon can be mitigated by plasticity cost linked to changes in traits, and can have adaptive value in a context of competition. Therefore, I argue that *plastic-optimisation* algorithm has low information value in the context of pot simulations with constant resource influx, but should still be studied in the context of community dynamics.

results from this part

As expected the resource availability and the resource balance are key components of the plant growth, to which the plant phenotype needs to match. Aside from the increase in biomass, an increase in "speed" of optimum phenotypes can result from higher resource availability. This observation is in agreement with

¹ this is different from a lag because it is not the result of slow changes in phenotype but comes from a default in the estimation of optimum phenotype.

RESOURCE AVAILABILITY

empirical data that demonstrate higher SLA and faster physiology in favourable conditions. This aspect was less obvious in the response of species under *plastic-optimisation* allocation that shifted more in term of balance and RMF. This may be due to a change in the relative balance between both resources as their availability (from the plant perspective) are linked to the global resource levels by non linear relationships.

The fact that plastic plants (for *fixed* allocation algorithms) show shifts of optimum strategies toward more exploitative phenotypes, in addition to the *non plastic* optimum shifts, in conditions of higher productivity demonstrate the importance of these strategies for plant growth. However, the extend of this effect of conditions on optimum phenotype is susceptible to vary along a gradient. Indeed, because of the non linearity of relationships between resource levels and exchanges rates, and between exchange rates and growth rates, the link between the optimum phenotype and a resource gradient is likely to be non linear itself. In addition, phenotypic plasticity might also change the sensitivity of the phenotype to the resource level.

2.1.4 Extended discussion

Limits exposed in this section and the previous can be explained by default of phenotypic plasticity mechanisms. Relies on assumptions that link partial information and strategy. There is no perfect informaiton (that would not even guarantee best strategy).

Can functional diversity be measured for plastic traits: different effects on plastic and non plastic traits.

This analysis was conduced with drastic parameters of plasticity with plastic plants relying only on their perception of external conditions to develop their phenotype. The different results ... different directions and impact on potential diversity.

Also, some species may not benefit from plasticity, especially if it has a cost, while others can benefit a lot from plasticity.

The contrasting responses of the different algorithms highlight the importance of the allocation mechanism. However, the unique framework implemented in *MountGrass* creates a variety of nuanced responses that are not all explored here. But, the continuous gradient of strategy between species relying on species memory only and species following their perception of external condition should be kept in mind during the interpretation of these results and following.

Subsection conclusion: bla bla bla

PLASTICITY AND INFORMATION

ON FUNCTIONAL DIVERSITY

NUANCES AROUND PLASTICITY

2.2 Plasticity and variability of conditions

The heterogeneity of conditions is an essential mechanism for plant coexistence. Plasticity is likely to alter the effect of this heterogeneity on plant coexistence and relative performance. The impact of plasticity on this relationship between spatial and temporal **heterogeneity** of resources (here limited to water) and strategy dominance is explored with the model *MountGrass*.

The phenotypic plasticity can impact the optimum strategy, but how does this effect impact the optimum phenotype along a resource availability gradient?

Is the contraction effect on species richness, functional diversity and productivity changing along such gradient?

2.2.1 Method

Because the coordination is shown to be less important than the equilibrium, the below-ground resource acquisition is expected to be important in mountain grassland under climate change scenarios, and extensive simulation plan come with high computational cost, only root strategies sampled in this part.

For each of the 20 selected parameter sets, growth of 400 plants (20 PAR values between 0.25 and 0.95, and 20 memory values between 0.1 and 1) is simulated for 100 days in square pots of 12 centimetres deep and 90 centimetres wide (to avoid quick self-competition) in a temperature of 20 degrees celsius during the day of 15 hours, and 10 degrees during the night. The radiance is set to the high values of 122 Watt per hour and per square metre. Because *fixed* algorithms showed similar results, and the *plastic-optimisation* algorithm show strange results, only two allocation algorithms are simulated: *non plastic* and *fixed-equilibrium*.

SIMULATION SET-UP

Spatial heterogeneity of water level is mimicked by a gradient of water influx. The growth of all 400 species described above are simulated for *non plastic* and *fixed-equilibrium* algorithm independently in separated simulations where the water influx is regularly sampled between 0.05 and 7 mm per day (20 values).

SPATIAL HETEROGENEITY

Similar set-up is used for temporal heterogeneity simulations. Because the range of water influx used in the previous simulation is too wide, a lower value is chosen as the mean water influx. This value of 1.3mm per day corresponds to a point around which there is variations in the optimum strategies for most parameter sets. It is also relatively close to average rainfalls in the Alps during summer.

TEMPORAL HETEROGENEITY

2.2.2 Results: gradient of homogeneous precipitation conditions

To study the effect of plasticity on community identity along a precipitation gradient, we can look at the position of the optimum strategy (PAR) along such gradient with different allocation algorithms.

OPTIMUM STRATEGY

The effect of allocation algorithm is observed on all species by plotting the position of the median *optimum* along the watering gradient that translates what part of the strategy spectrum (from conservative to exploitative) benefit from the simulation conditions. At the low end of the gradient, conservative species exhibit higher growth than exploitative species with a median optimum around 25% of active tissues in roots for both the *non plastic* and the *fixed-equilibrium* plastic allocation. In the other end of the spectrum, for watering values above 1 mm per day, the *optimum* reaches a high point (median around 90% of active tissues for both algorithms) demonstrating better performance of the exploitative species in high resource availability conditions. There is not apparent differences between algorithms and the optimum is conserved along the gradient. There is a similar shift with an increase of optimum water availability memory for *non plastic* algorithm.

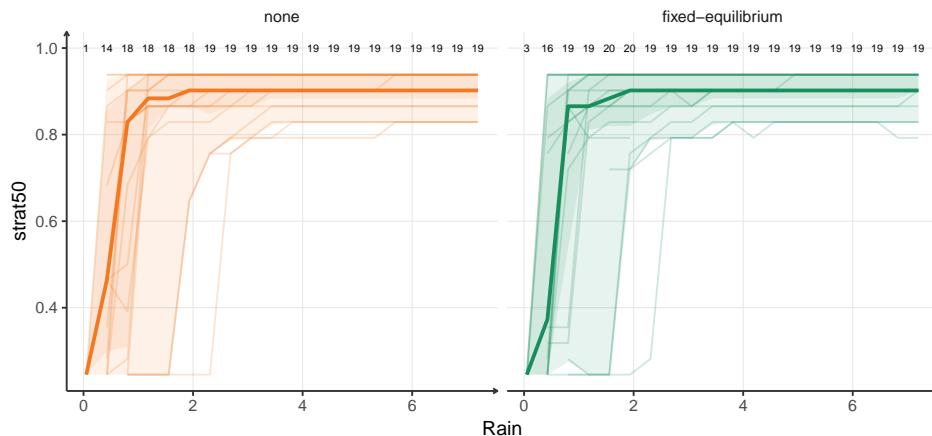
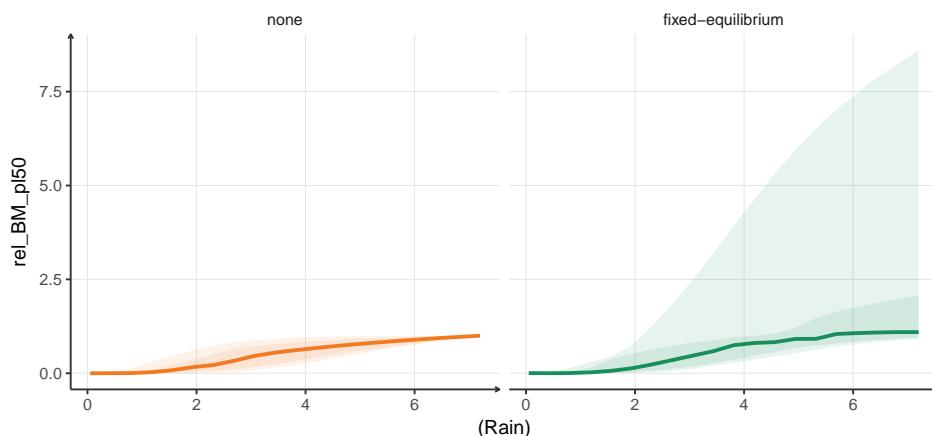


Figure 2.12: Median (dark line -) optimum root strategy along the water treatment gradient for *non plastic* and *fixed-equilibrium* allocation algorithms. The light lines (-) correspond to the 20 independent parameter sets. The color ribbon marks the band between the 5th and 95th percentiles.

The total cumulative biomass of all plants increases along the precipitation gradients. The plastic simulations have a cumulative biomass that is twice the biomass of *non plastic* simulations.

The effect on the maximum biomass is also investigated. For most simulation the maximum biomass is unchanged, and the median of the maximum biomass follow the same path for both conditions. However, the 75th and the 95th percentiles of plastic simulations shows a high increase in maximum biomass.



BIGGER PRODUCTIVITY?

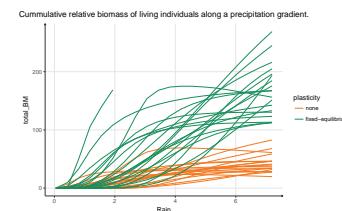


Figure 2.14: Total biomass of all individuals along a precipitation gradient for all tested parameter sets for each condition, showing plasticity treatments: *non plastic* & *fixed-equilibrium*. Color distinguishes plasticity treatments: - *non plastic* & - *fixed-equilibrium*.

Similarly to the previous results, the potential diversity is estimated with the number of species, or the functional volume, of the species within the 90%-100% range of the maximum biomass for the given conditions.

The species richness decreases along the gradient for the two plasticity treatments. The medians of species richness reach the low point for the same precipitation values than the medians of the optimum reach the highest values. The *fixed-equilibrium* simulations show highest species richness along the whole gradient (except for one parameter set).

The functional volume occupied by the top species, also decreases for both plasticity when the precipitations increase. For low watering values, the functional volume of *non plastic* simulation is higher, however this difference disappear when both group of simulations reach low functional diversity.

WHAT ABOUT DIVERSITY?

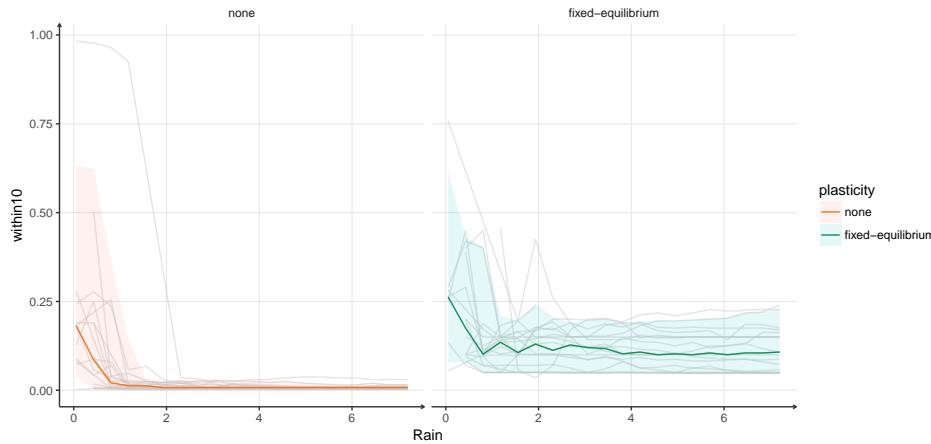


Figure 2.15: Species richness of the species within the range 90%-100% of highest biomass for any given condition (parameter and precipitation) along a precipitation gradient. Colour distinguishes plasticity treatments: - *non plastic* & - *fixed-equilibrium*.

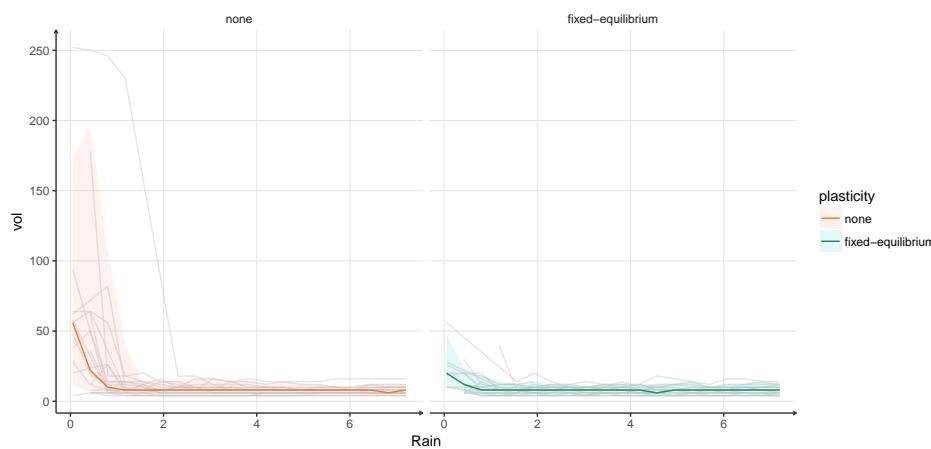


Figure 2.16: Estimation of the functional volume occupied by the species within the range 90%-100% of highest biomass for any given condition (parameter and precipitation) along a precipitation gradient. Colour distinguishes plasticity treatments: - *non plastic* & - *fixed-equilibrium*.

The potential effect of plasticity on niche breadth is visualised here for one representative parameter set. The best performing phenotypes

WIDER POTENTIAL NICHES

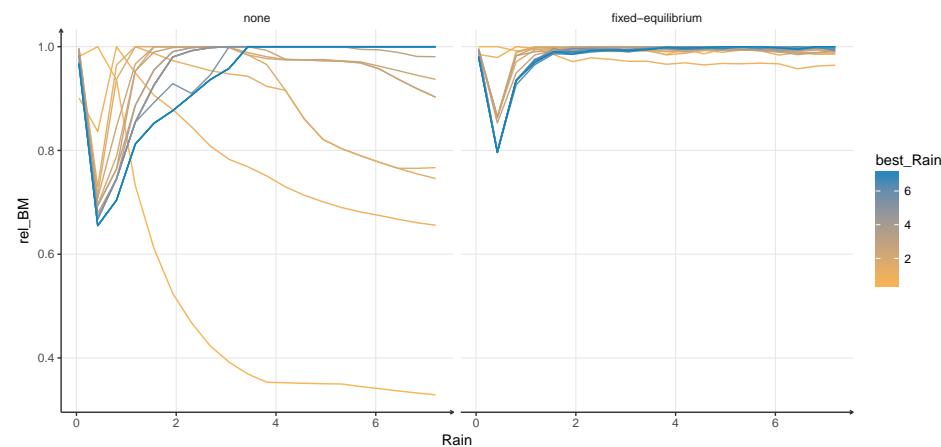


Figure 2.17: Median relative performance of best phenotypes along a precipitation gradient for 20 parameter sets.

Changes in the niche ... but see:

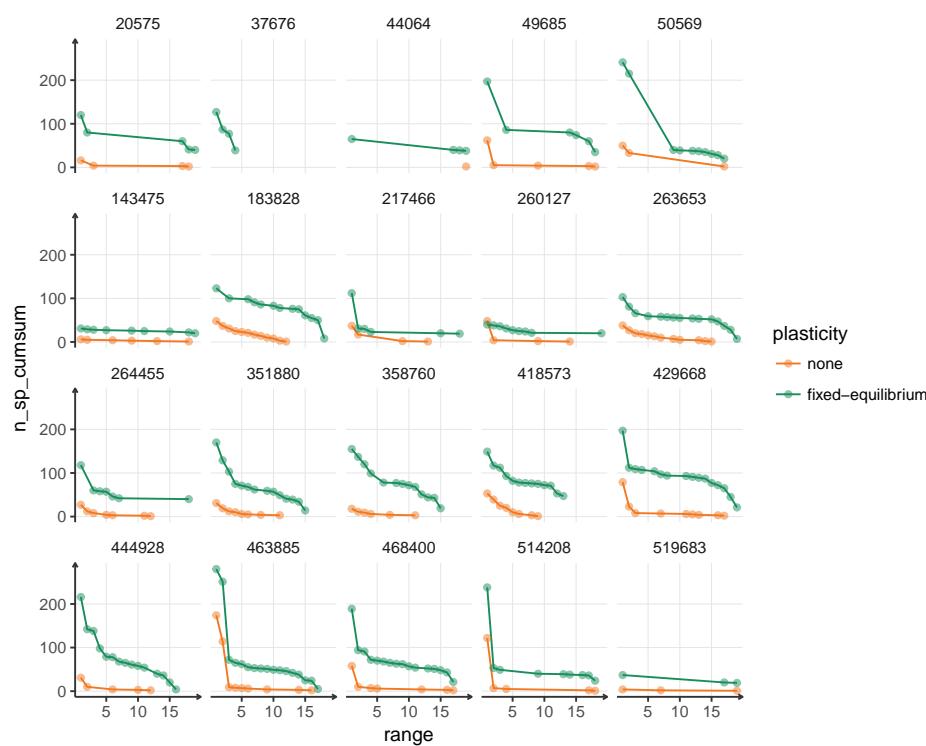


Figure 2.18: Changes in the dominance structure for the evaluated parameter sets. The dominance structure is illustrated by the cumulative number of species along diminishing number of conditions where they are within the top 90%-100% range of highest biomass for any given condition.

2.2.3 Discussion: gradient of homogeneous conditions

Along the watering gradient, the optimum strategy (active tissue allocation in roots) changes from conservative toward exploitative. This shift demonstrates that the trade-off between active and structural tissues allocation allows different strategy to dominate in contrasting conditions (). This shift occurs for low values of the gradient and exploitative strategies are dominant over a large part

STRATEGY SHIFT

of this gradient. This can be explained by high precipitation values disconnected from the precipitation values observed in nature. Also, the low resolution of the strategies (15 values for the proportion of active tissues in roots) limits the possible number of different dominant strategies along such gradient.

Gains from the plasticity can be distinguished between static and dynamic gains. The lower value of the *center of gravity* in conditions of low water availability under *fixed-e*"quilibrium algorithm seems to indicate that conservative strategies benefit from plastic allocation more than exploitative species. However, this effect is mostly due to static gain as the optimum strategy does not change. This effect is due to a growth landscape flatter than in better conditions (more species within the 90-100 % of maximum growth, lower growth difference with best strategy) and asymmetric, that has two effects:

- it reduces the growth gain for species with strategy close to the optimum, but not at the equilibrium (figure ?? panel A);
- increases the potential gain (relative to less flat growth landscape) for species with strategies more conservative than the optimum (figure ?? panel A).

The phenotypic plasticity of the RMF leads to an important widening of the potential niche. This widening is, however, asymmetric because there is a transition of the limitations that define a species niche. Without plasticity, in a given homogeneous environment, the optimum phenotype is defined by both the adequate resource use and its balance. With costless plasticity in RMF, the balance is almost guaranteed and the resource use becomes the main limitation of a species niche. Conservative species are less efficient in high resource availability conditions, while exploitative species are more efficient, but this efficiency decreases quickly as the resource availability does not meet the levels required for these species to maintain high productivity. ... try to expand discussion on this idea.

If costs are low, the effect is likely to reduce potential species diversity. An established species can, thanks to static gain, maintain relatively high growth rate in a habitat where the balance is different but the optimum strategies closed. This is particularly true for rich environments where the optimum strategy for roots is quite stable. The effect on coexistence is better illustrated with an example. Given two species, *species a* and *species b*, with optimum strategy (PAR) and RMF for two distinct conditions, respectively *A* and *B*, in a heterogeneous environment composed of majoritarily condition *A* and minorly condition *B*, ... where do I go with that ? ...

Fitness evenness leads probably to greater competition if there is great overlap of potential niches. However, hard to tell what is the impact on competition and stabilizing effects. Probably negative: so hard to tell effect on coexistence.

Who cares. The ones that are close to the optimum, unless there

Mostly static gain, but even if there is gain, increases the potential niche of species that are settled. Bigger niche: favourable for conservative species of rare habitats.

Hard to tell anything on coexistence, except wider niches

**STATIC AND DYNAMIC GAIN
WHO BENEFIT FROM PLASTICITY**

NICHE WIDENING

FITNESS EVENNESS

WHAT STRATEGIES BENEFIT FROM PLASTICITY?

2.2.4 Results: gradient of heterogeneous precipitation conditions

Along the temporal heterogeneity (increasing negative slope of water influx) gradient the median biomass of the optimum phenotypes decreases under all allo-

cation algorithms when the variability increases despite the same mean water influx. The amplitude of reduction varies with the allocation mechanism: *non plastic* algorithm shows the largest decrease while *fixed traits* algorithms show slower decrease. *Plastic-optimisation* simulations have more constant performances with low initial performances in constant condition (between 5% and 55% on the *non plastic* simulation), but they end with slightly better performances than *non plastic* simulation for the extreme case of variation (two extreme regimes).

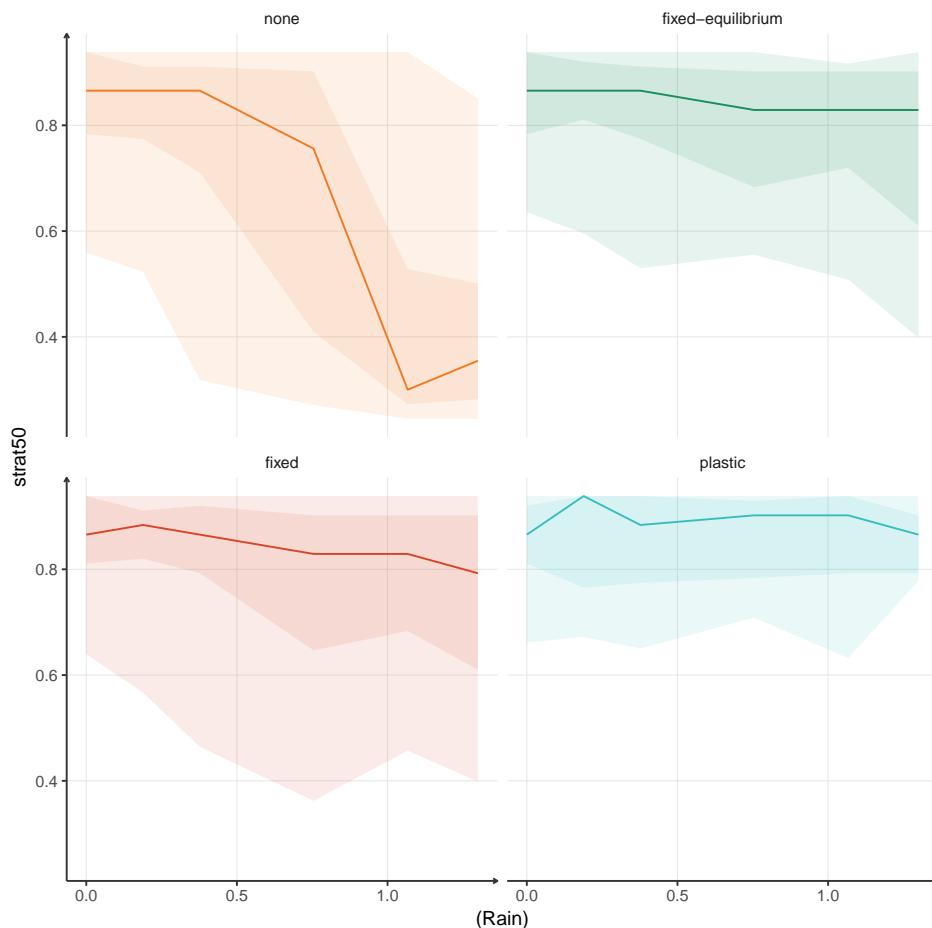


Figure 2.19: Strategy shift of the best performing species along a gradient of resource variability for four plasticity treatment.

In addition to a reduction of biomass, the increasing slope of the water influx reduction lead to a shift of the optimum strategy in *non plastic* simulations. This reduction of optimum toward more conservative strategies is offset in most of *fixed-equilibrium* and *fixed-optimisation* simulations. A reduction (around 25%) of the 5th and 25th percentiles of the optimum root strategy can be observed between the extreme conditions (constant flux and two distinct regimes) for these two algorithm. This shift in optimum strategy can better be observed on the plan of the proportion of active tissues in root (PAR) and root mass fraction (RMF) in figure 2.20 where all trajectories¹ along the variability gradient are plotted. *Non plastic* allocation trajectories by a linear shift toward more conservative strategies with higher allocation to roots, while *fixed-equilibrium* and *fixed-optimisation* trajectories are non linear and can be divided into two phases: (1) increase in RMF, (2) reduction of PAR. *Plastic-optimisation* algorithm shows no consistent pattern in trajectories.

¹ trajectory of the optimum, not of the species.

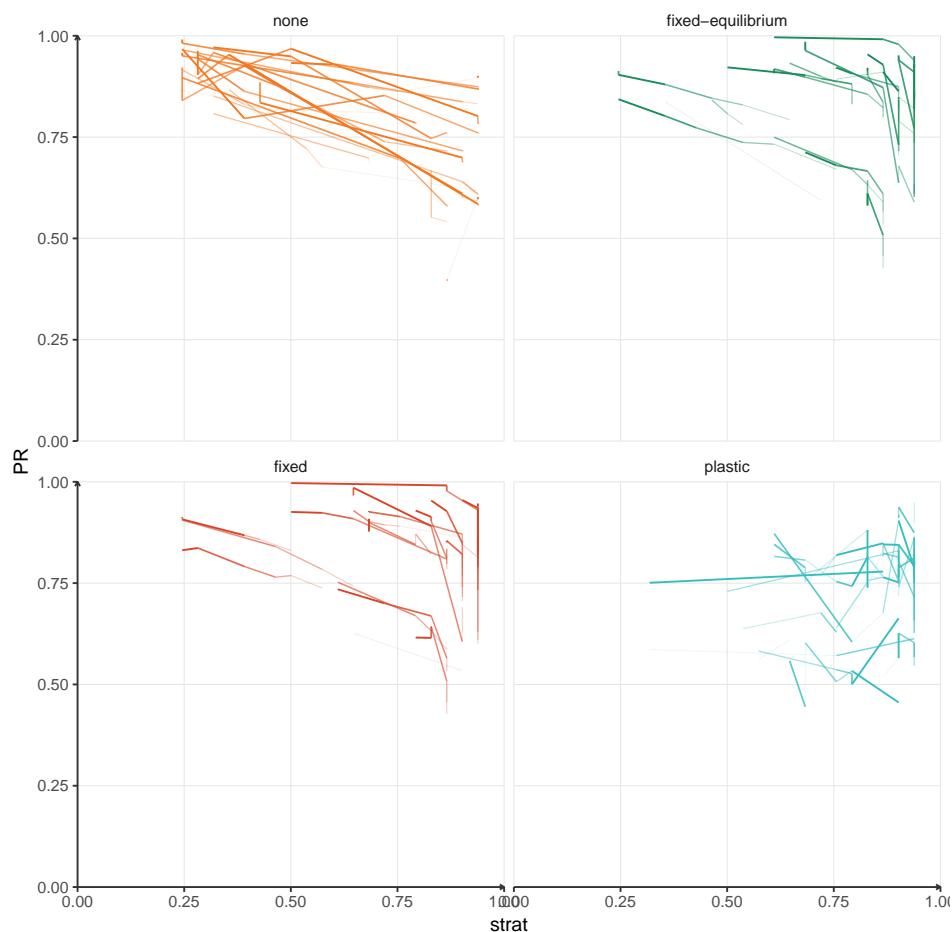


Figure 2.20: Best phenotypes along water resource variability gradient. Thinner lighter lines indicate low water variability, while the thicker lines indicate strong temporal heterogeneity.

As previously seen, plasticity can affect diversity in a drastic way, reducing the functional diversity by contracting the phenotypic space, but also increasing the potential species diversity by the same mechanism. The effect of static gain¹ and dynamic gain must be disentangle. The

DIVERSITY

¹ refers to the gain due to convergence toward a good static phenotype and no temporal changes.

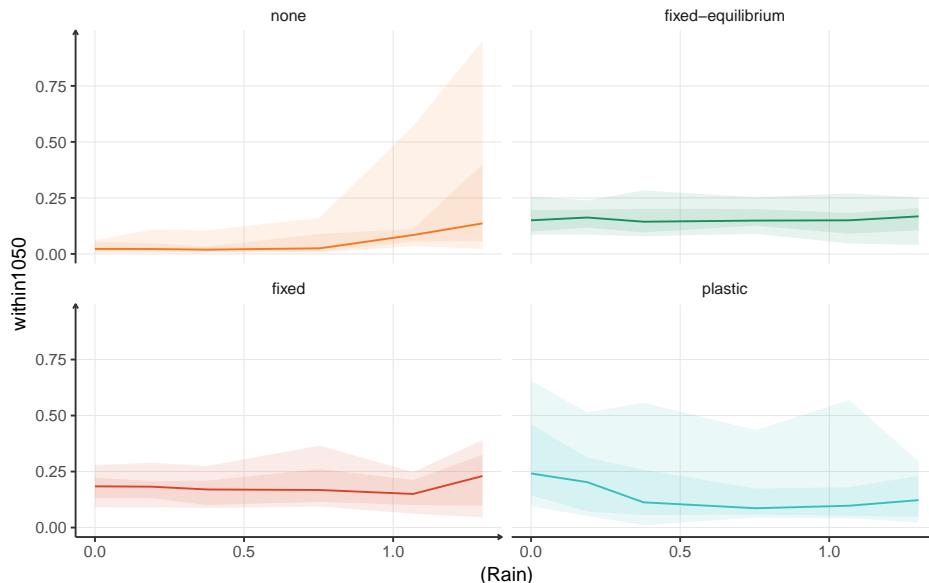


Figure 2.21: Species richness of the species within the range 90%-100% of highest biomass for any given condition (parameter and precipitation) along a water resource variability gradient. Colour distinguishes plasticity treatments: - non plastic & - fixed-equilibrium.

Changes in optimum, but does it affect evenness ? Same pattern as before with the trade-off between species and functional diversity. What happen if you filter down stuff ?

2.2.5 Discussion: gradient of temporal variations

Plasticity has a positive effect on exploitative strategies in low resource availability conditions. As said earlier in the document, plant performance depends on multiple things: effectiveness of organs, global resource usage and equilibrium. If plasticity improve the performance of the exploitative species, it is unlikely to be because of the contraction of the space since it is the optimum only that is looked at. Also means it is probably dynamic gain, if the filter was static, plasticity shouldn't have change much. And there is gain, even in the high end of the gradient where the optimum does not move, saying that the optimum is fairly conserved despite increase in resource (but low resolution of the strategy space, and match the function).

IMPROVEMENT IN VARIABLE CONDITIONS

Change in optimum strategy can be explained by: an assymmetry in efficiency (better a but more conservative in exploitative favourable conditions than exploitative in conservative favourable conditions) or an assymmetry in imbalance cost (better be imbalanced when conservative than when exploitative). The first option is not consistent with previous results (see subsection 2.1, figures ...) that show higher fitness for species more exploitative than the optimum, compared to species more conservative. In the other hand, following results show positive effect of functional equilibrium over conservative strategies. Nevertheless, this effect certainly results from an artefact and the contraction of the phenotypic space not in favour of exploitative strategies. The sensitivity of exploitative

strategies to low conditions is visible in figure ??

Shift of RMF then strategy explain quite well that the equilibrium is more important than the resource usage and the organ efficiency. How does that inform us on the real world ?

- potentially reduces the meta community diversity if spatial heterogeneity has a less drastic effect on strategic dominance. - talk about that in diversity part /!

may come from a lack of coordination with shoot. Since shoot activity is suppose to be relatively high. == might not have been a good choice to look only at root strategy. But, since there is adjustment of RMF that allow to maintain equilibrium and resource usage, it should be fine to interpret these results.

Phenotypic plasticity give exploitative species an advantage in variable conditions because their growth rate rely more on productivity and therefore equilibrium than conservative species.

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. However, this effect should be limited by plasticity cost. Indeed, if the growth gain due to plasticity is only static, any species with a fixed phenotype closer to the optimum than the focus species has a better growth rate and exclude the focus species. . a few words on dynamics... 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.

2.3 From model behaviour to competition and coexistence in the real world

2.3.1 Plasticity: new functional diversity

functional diversity of plastic traits? Should them be excluded?

Impact of traits, and abundances: the need to account for it!

May still be useful especially for invasion, and works well despite low flexibility (see (Forsman 2014)). May allow more diversity if some correlations with other non plastic traits.

2.3.2 Plasticity as a strategy: cost and correlations

and limits ? what about exhaustion

One of the argument to say this is new, however not really explored, neither with plasticity cost perspectives (a bit with plasticity limits) or with tau. However, used extreme cases: give better understanding and necessary before finer analysis. Still, there are hypothesis on the effect on diversity and the role in phenotypic stability (attention: isn't it just because the formulation of projection is wrong that we can make these conclusions ?).

WHO BENEFIT FROM PLASTICITY?
COST OF PLASTICITY
PLASTICITY AS A STRATEGY

2.3.3 Plasticity and competition: changes in interactions

What about the continuous τ gradient ?

EXTENDED INTERPRETATIONS

What about interactions and cycles ? Little has been discussed on the dynamic of the resource and how it could affect coexistence. Imagine that with cycle, reproduction timing has an importance here...
plasticity will change: performance, sensitivity and impact of the resource.

BIBLIOGRAPHY

- DeWitt, Thomas J., Andrew Sih, and David Sloan Wilson (1998). "Costs and limits of phenotypic plasticity". *Trends in Ecology & Evolution* 13.2, pp. 77–81.
- Forsman, A. (2014). "Rethinking phenotypic plasticity and its consequences for individuals, populations and species". en. *Heredity*.
- Freschet, Grégoire T., Elferra M. Swart, and Johannes H. C. Cornelissen (2015). "Integrated plant phenotypic responses to contrasting above- and below-ground resources: key roles of specific leaf area and root mass fraction". en. *New Phytol* 206.4, pp. 1247–1260.
- Grimm, Volker et al. (2005). "Pattern-Oriented Modeling of Agent-Based Complex Systems: Lessons from Ecology". *Science*. New Series 310.5750, pp. 987–991.
- Peterson, K. M. and W. D. Billings (1982). "Growth of Alpine Plants under Controlled Drought". *Arctic and Alpine Research* 14.3, pp. 189–194.
- Reich, Peter B. (2014). "The world-wide 'fast–slow' plant economics spectrum: a traits manifesto". en. *J Ecol* 102.2, pp. 275–301.
- Van Kleunen, Mark and Markus Fischer (2005). "Constraints on the evolution of adaptive phenotypic plasticity in plants". en. *New Phytologist* 166.1, pp. 49–60.
- Wright, Ian J. et al. (2004). "The worldwide leaf economics spectrum". en. *Nature* 428.6985, pp. 821–827.

V

COMMUNITY DYNAMICS

This second result chapter examines the effects of phenotypic plasticity at the scale of the community. Another parameter filtering processes is performed and described in the first section of this chapter. The second part focuses of the effects of plasticity of the main properties of the community. The impact of plasticity on species diversity is particularly investigated. This chapter gives a glimpse of the potential of the model to answer various questions around the role of intraspecific variations on diverse community properties.

1 COMMUNITY LEVEL SIMULATIONS: NON PLASTIC COMMUNITY

1.1 Parameter filtering

1.1.1 Method

Weather data for the time period between 1959 and 2014 has been computed by the MeteoFrance model SAFRAN by ... using GPS coordinates, slope, azimuth and horizon computed from a digital elevation model. These parameters were also used by the model CROCUS to compute snow accumulation and snow melting. These high frequency data (resolution under 1h) have been averaged on a daily time-step and used to compute input variables for *MountGrass*. The snow in particular defines the length of the growing season starting with the first snow melt of the year and finishing the day of the first snow fall of autumn or winter.

WEATHER DATA

The simulated years above 2014 are randomly sampled from the existing dataset between 1995 and 2014.

Community level parameter filtering is conducted for a new table of parameter sets. These parameter sets are ... from accepted parameters and joined with LHS random sampling for five community level parameters: seed germination density, drought mortality, ageing mortality, plasticity cost for environmental sensing and plasticity cost for trait changes (see chapter 4 for details).

PARAMETER FILTERING

Few words on why plasticity cost parameters: time limits, distinguish the benefit of plasticity itself, not combined effect. Should have done simulations with no cost to have an idea of plasticity cost effect.

The simulations run over 300 hundreds years for 6 sites described in table ?? on squares of ... square centimetres. The simulation is stopped and the parameter set rejected if no individual persist and the seedbank is empty. The seedbank is composed of seeds contained in the seedbank and seeds from the metacommunity. The total of seeds is defined by the seed germination density and the area simulated. The seeds from the simulated community represent up to 80 % of the seedbank, less if the seed production is limiting. The first ... years are not taken into account in the filtering process to let the community settle.

1.1.2 Results

SIMULATIONS

Simulations done. Need to illustrate the results.

On stability and on diversity (functional and species)

EFFECT OF PARAMETERS

Random forest approaches like sensitivity analysis at individual scale.

1.2 Non plastic communities

Trade-off, diversity, stability ...

Is there a selection of some parameters ? Are there ecological trade-off (resource use strategy and reproduction) emerging from the model ?

ECOLOGICAL TRADE-OFF ?

2 PLASTICITY: IMPACT ON SPECIES FITNESS AND DIVERSITY

Plasticity in integrated framework and full community simulations. Plasticity mechanisms, but also plasticity as a strategy (look at the cost and tau).

Effects on productivity and coexistence. Difference in the correlation ?

Effect of tau on persistence.

2.1 Plasticity and diversity

Now

2.1.1 Method

To test the effect of plasticity on coexistence and community dynamics, runs from the parameter filtering are used as starting points to limit the simulation time of the stabilisation phase. For each parameter set tested, 6 different sites were tested during the calibration phases, 77 parameter sets were accepted and a sample of ... were tested, resulting in ... communities. Each of those is the starting point of three parallel runs that differ only by the allocation algorithm used: *non plastic*, *fixed-equilibrium* and *plastic-optimisation*. The *fixed-equilibrium* is favoured to *fixed-optimisation* algorithm because previous part of the document focused on this algorithm and because it is simpler to analyse. The *plastic-optimisation* algorithm is still simulated, despite the relatively poor performance results observed in constant conditions and the high convergence, because the introduction of plasticity cost, continuous species specific plasticity ($0 < \tau < 1$), and temporal and spatial heterogeneity should mitigate the negative sides of this allocation mechanism and give information of processes at stake.

SIMULATIONS

The plasticity costs (maintenance: related to the value of τ , and displacement: relative to changes in phenotypes) defined in the parameter sets are applied to all algorithms. In *non plastic* simulations, this results in artificial additional costs to species with low values of τ but with no potential gain from plasticity as the allocation is non plastic.

The differences of effects between the different types of plasticity on the variables of interest are computed unpaired Wilcoxon tests assuming an independence of the the different data points. This assumption of statistical independence is justified by the normalisation for each parameter set of the variables relative to the mean of the *non plastic* group. This normalisation allows to compare the simulations between the parameters sets. The interactions and other level (site, and autocorrelations) are discussed later in this section.

The normalisation $Vn_{a,p,t,s}$ of the variable V for the allocation algorithm a , the parameter set p , the time t and the site s is given by the following formula:

$$Vn_{a,p,t,s} = \frac{V_{a,p,t,s}}{\bar{V}} \quad (2.1)$$

$$\bar{V} = \frac{\sum_{a=\text{non plastic}} Vn_{p,t,s}}{n} \quad (2.2)$$

where n is the number of observations for the *non plastic* algorithm.

2.1.2 Results

The level of coexistence is evaluated by the number of distinct species that manage to maintain at least one individual or produce at least one seed at the end of the season. This criterion allow to ignore the potential non stable diversity introduced by the "meta-community invasion" (sampling of species in the meta-community pool) and to consider species that can be filtered out sue to seed mortality. The number of species increases in almost all simulated years and sites for both plastic allocation algorithms, with a median of 1.5 times the number of species in *non plastic* simulations (see figure 2.1.2). This factor can go up to 6 for *fixed-equilibrium* and 9 for *plastic optimisation*.

The effect of plasticity on coexistence is driven by the benefits of plasticity at the individual scale. These benefits are mitigated by the cost of plasticity, particularly the maintenance cost that affect all species relatively to their potential plasticity.

Low values of plasticity maintenance cost (see figure ??) show higher diversity for both plastic allocation algorithms. This trend is consistent across sites despitess some inter-annual variability in the diversity. The effect is a bit less stronger for *fixed-equilibrium* than for *plastic-optimisation* (as already observed in figure 2.1.2).

The mechanisms through which the phenotypic plasticity impacts species richness are multiple (refer to the figure 3.7 in chapter II). However it is hard to disentangle them all.

The density can be affected by the phenotypic plasticity leading to higher species diversityLepik, Liira, and Zobel 2005, higher density leading to the sampling of more species. The density, estimated by the number of individual after the reproduction phase (persisting individuals and produced seeds), is consistently higher in *plastic* simulations, but the difference is relatively low (around

STATISTICAL TESTS

EFFECT ON COEXISTENCE

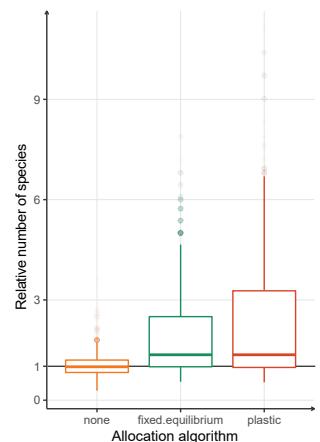


Figure 2.1: Relative species richness in the three plasticity treatment. To negate the variability due to the parameter sets, the realised number of species is divided by the median number of species in *non plastic* treatment for each parameter set. The variability is due to random invasion and climatic variability (inter-sites and inter-seasons).

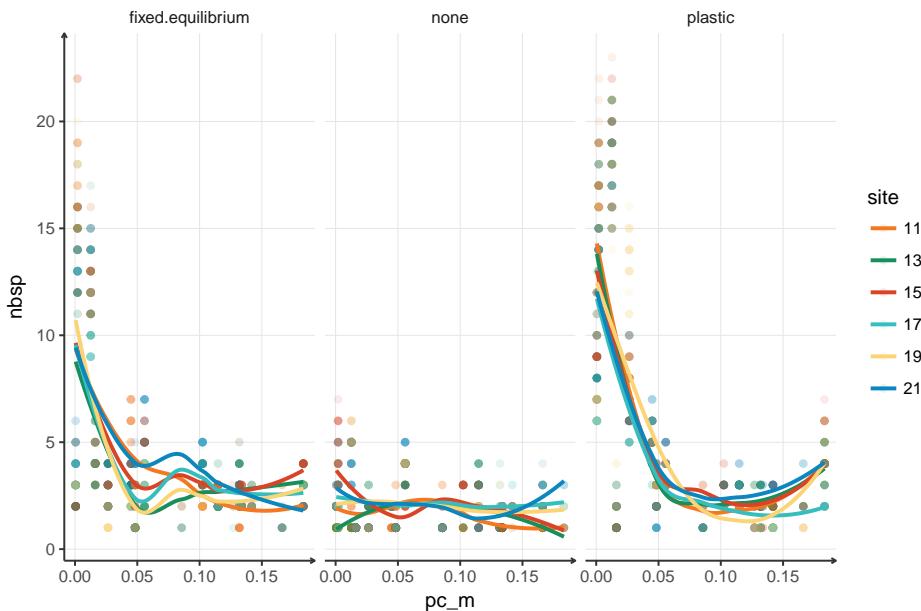


Figure 2.2: Effect of the cost of plasticity-maintenance on the absolute number of species in the three plasticity treatments. Individual season values (points) and site-specific trends (gam smoothing line) are represented.

3% higher than the *non plastic* median density) and an order of magnitude lower than inter-annual and inter-site variations that can go up to 40% difference relative to the median density (for any given parameter set).

If the plant estimated density increases, the number of species relative to the plant density ... with plasticity.

Figure 2.4: Species richness relative to plant density for the three plasticity treatments.

Productivity is also susceptible to be impacted by the phenotypic plasticity at the community level. Multiple mechanisms can be involved, but in any case higher productivity is achieved by high efficiency in the resources given, and plasticity can affect this efficiency at individual level (with positive effects as observed in section 2) or at the community scale with changes in the dominant species and competition intensity.

The productivity of the *non plastic*, *fixed-equilibrium* and *plastic-optimisation* allocation algorithm show little differences. The *non plastic* simulations average biomass tend to be a bit higher in certain cases. Like the diversity and density, the normalised yearly average biomass does not show great variations between plasticity, but higher variability between sites and seasons. *Non plastic* and *fixed-equilibrium* median are quite similar, and the *plastic-optimisation* show lower productivity than the other two algorithms.

The allocation algorithm is expected to alter the fitness of potentially plastic plants. The selective effect of the allocation algorithms is investigated by plotting the τ value of species that are maintained in only one of the algorithms. Because of the plasticity cost, the selection of species with low values of τ signifies an improvement of the fitness due to plasticity. The distribution of τ is fairly high for *non plastic* species and almost 75% of the species have a value above 0.8, whereas *fixed-equilibrium* specific species have lower values ranging from 0.2 to

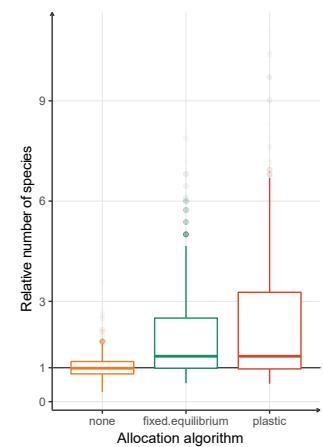


Figure 2.3: Relative plant density in the three plasticity treatment. To negate the variability due to the parameter sets, the realised number of plant is divided by the mean number of plant in *non plastic* treatment for each parameter set. The plant density is estimated with the output of the reproduction process.

PRODUCTIVITY

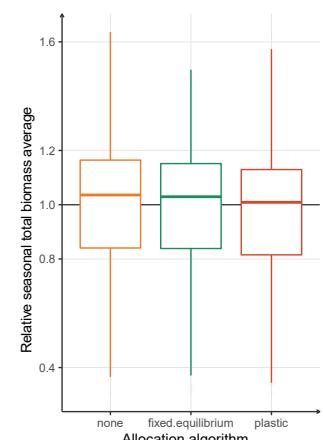


Figure 2.5: Average total biomass relative to *non plastic* simulations, in

1 with the median around 0.7 and the *plastic-optimisation* species have even lower values with a median around 0.55.

Select different strat? meh, from very site specific strats (one dominant species), to more variable within the site, but less differences between the strats. Shift from beta diversity to alpha diversity.

2.1.3 Discussion

Plasticity allows the emergence of new phenotypes that are plastic. Leading to higher density in competitors, and greater evenness. Hard to detect because not the same number of species, or require other experiments.

also, Jung et al. 2014 show contrasting response between species and within species - might not be the best

Plasticity allows for bigger niche (variability dimension), more chance to build enough "growth potential" to persist. Otherwise, other species that are dominant, because other species can settle, take advantage of it. Should look at the growth rates hierarchy for a couple of simulations.

Interaction between plasticity effects and parameter sets, but the interest here, even if it is interesting. Higher variance due to site and weather. The almost perfect knowledge of models allows an extremely precise decomposition of the effects, but at the risks of losing broad effects. The difficulty is to measure the relative strength of these effects, and generalise. But, by essence, the parameters are suspected to have a significant effect that can be identified, otherwise it would not have been included in the model.

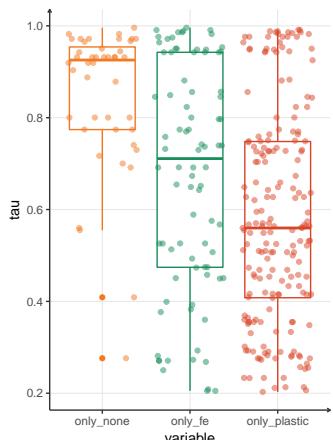


Figure 2.6: Plasticity levels of species that are present in only one type of plastic treatment.

VARIABLE STRATS

COMPETITION EVENNESS

SHIFT IN STRATEGY

WHY HIGHER DIVERSITY

INDEPENDENCE OF POINTS

BIBLIOGRAPHY

- Jung, Vincent et al. (2014). "Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events". en. *J Ecol* 102.1, pp. 45–53.
- Lepik, Mari, Jaan Liira, and Kristjan Zobel (2005). "High shoot plasticity favours plant coexistence in herbaceous vegetation". en. *Oecologia* 145.3, pp. 465–474.

VI

SYNTHESIS & OUTLOOK

GLOSSARY

active plasticity Change in phenotype controlled by internal regulation processes. Opposed to passive response. *i.e.* change in SLA when light is limiting is an active plastic response.

allocation rule The allocation rule is the set of rules that determine the target phenotype of a plant considering its actual phenotype, the biomass available and the projection of external conditions. It can be decomposed in two main parts: the plastic dimensions, and the fitness proxy function (or gain function). Allocation rule is also designated as allocation algorithm, plasticity rule or plasticity algorithm.

Plasticity

4 INDEX

allocation rules, 97
dynamic gain, 110
equilibrium, 108
functional diversity, 110
gravity center, 103
heterogeneity, 113

memory, 97
optimum tissue efficiency, 108
organ tissue efficiency, 109
parameter filtering, 87
parametrisation, 87
performance landscape, 109

plant performance, 107
plastic exhaustion, 112
sensitivity analysis, 87
species diversity, 110
speed, 109
static gain, 110