

LES SERIFS, C'EST CACA

The chapter contains the main results of simulation experiments at the individual scale. It provides insights on the impact of the 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 responses of individual root strategies to two gradients of water availability: (1) with constant influx but differences in mean influx to simulate spatial heterogeneity, (2) with a shared mean influx, but contrasting rates of reduction of precipitation to simulate the reduction of the available resource during the growing season.

Début rélecture.

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 on 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 determines the relative sensitivity of variables of interest to specific parameters.

je comprends pas trop de la sens de la phrase "bien ut-lisé".

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 requires 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.

→ because of?
→ problème de mise en forme?
(+ espace manquante)

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.

normal?

POT DATA

Simulated plants 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 48 days, followed by the treatment phase when plants are watered (soil saturation) either once a week or once a day. The light level and water influx are simulated following the experimental conditions (Peterson and Billings, 1982) by a lighting of 1850 Watts per square meter, and soil saturation. Plants have default geometry parameters, reproduction is ignored and it is assumed that 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 1.1) defined both thanks to the literature and constraints dictated by desired behaviours from the model. When necessary the sample is log transformed. Because of the 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

Out

As explained in the 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 chapter III, 4.2. Once the parameters are generated, a first filtering is applied to save simulation time and avoid unrealistic trait values. The computed initial trait values considered out of range (see table ?? for ranges extracted from LES data (Wright et al., 2004) in the alpine biome) are excluded, modifying the initial distribution of the parameter values (see figure 1.2). 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, 1982 experiment setup.

The results from the finished simulations (i.e. the plant lives until the end and do not exceed model's internal size limits) are then compared to the experiment data species by species. The parameters of logistic distributions are computed from the species means and standards deviations for RSR and total biomass. The use of this distribution form is justified by the intrinsic form of the RSR variable and the need to reject negative values for total biomass variable. A parameter set is accepted for one species if it lies 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*.

The 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 balanced dataset composed of all selected pa-

SENSITIVITY ANALYSIS

Table 1.1: Global parameters of *MountGrass* with units and extreme values used during the parameter filtering process.

name	min	max	unit	full name
u_max	0.36	10	cm ³ .cm ⁻² .h ⁻¹	Maximum root uptake rate
beta_o	0.002	0.2	AU	Soil absorption limitation strength
P_max	0.00001	0.0001	gCO ₂ .cm ⁻² .s ⁻¹	Maximum photosynthesis
alpha	0.00001	1.0001	AU	Photosynthesis curvature
mob	0.0005	1	fraction total green biomass	Maximum growth rate
m	0.1	0.5	AU	Leaf light transmittance
r_g	0.1	0.5	gC.gMO ⁻¹ .h ⁻¹	Growth respiration rate
r_i	0.003	0.03	gC.gMO ⁻¹ .h ⁻¹	Active tissue respiration rate
ls_so	5.7658	7.9628	day	Log of maximum shoot lifespan
ls_si	-1.2325	0	day	Shoot lifespan slope
ls_ro	4	7	day	Log of maximum root lifespan
ls_r1	-1.5	0	day	Root lifespan slope
sd_s_rate	0.05	1	per year	Seed survival rate
WUE	0.001	0.01	GCO ₂ .gH ₂ O ⁻¹	Water Use efficiency
LCC	0.39	0.5	gC.gOM ⁻¹	Leaf carbon content
alpha_d	10	30	AU	Drought mortality
gamma_d	1	3	AU	Drought mortality
th	0.0124	0.0437	cm	Leaf thickness
s_r	0.0019	0.05	cm ²	Root section (area)
rho_as	0.005	0.1	g.cm ⁻³	Volumic mass of shoot active tissue
rho_ss	0.8	1.5	g.cm ⁻³	Volumic mass of shoot structural tissue
rho_ar	0.005	0.1	g.cm ⁻³	Volumic mass of root active tissue
rho_sr	0.8	1.5	g.cm ⁻³	Volumic mass of root structural tissue
vt_s	0.7	0.75	AU	Volume occupied by the tissue in total leaf volume
k_os	0.001	0.01	cm ³ .cm ⁻³	Shoot volume occupancy
k_or	0.01	0.5	cm ³ .cm ⁻³	Root volume occupancy
k	0.4	0.6	AU	Light extinction parameter

trait	min	max	unit
SLA	20	400	cm ² .g ⁻¹
SRL	1000	15000	cm.g ⁻¹
LLS	10	400	days
RLS	100	1200	days

Table 1.2: Extreme values of traits related to exchange area per biomass and organ longevity for both shoot and root.

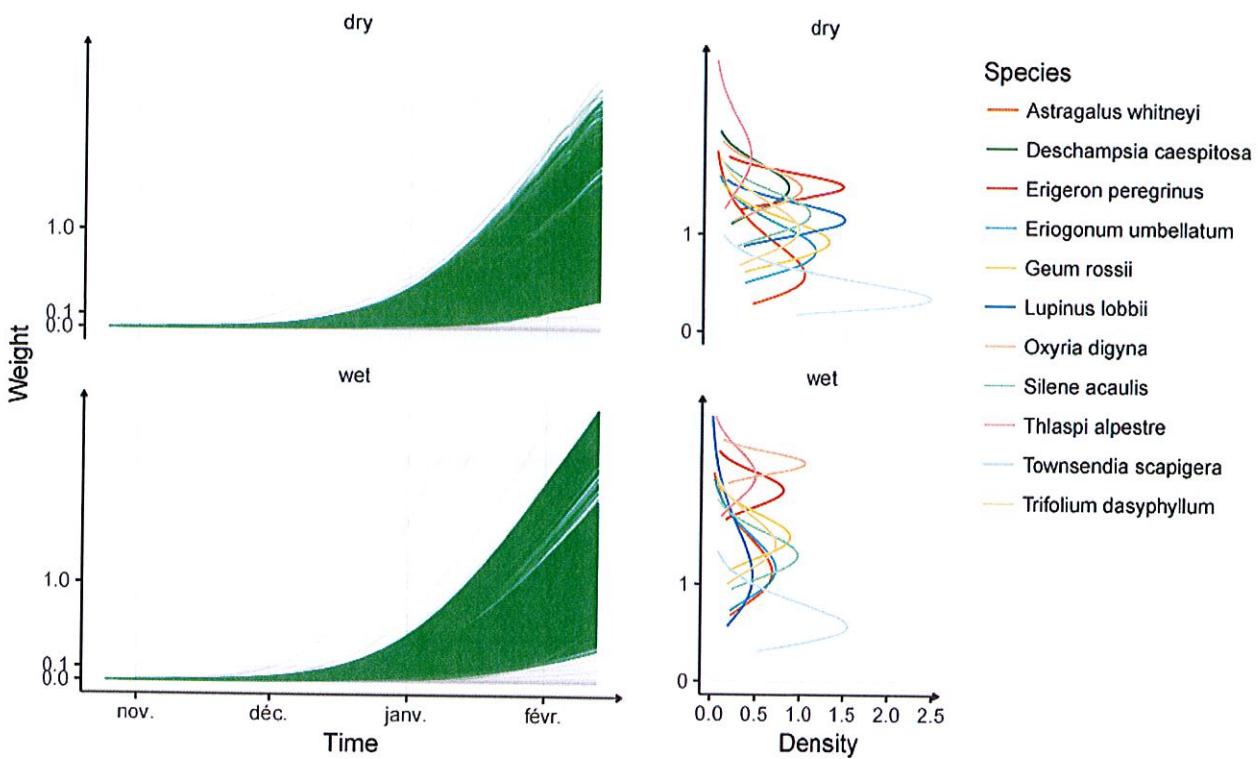


Figure 1.1: Comparison of simulated weights with distribution of weights of real alpine species for contrasting conditions.

parameter sets and a random sample of rejected sets of equal size. Importance is assessed on the results of the random forest.

1.1.2 Results

Parameter filtering process resulted in the selection of a low number of parameter sets (below 0.2%) for each allocation algorithm ~~X~~. 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 extent 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 shows relatively tight distribution with little overlap between the conditions for both variables (see figure 1.1 for comparison between simulations and data for total weight).

Despite the low selection rate, a difference can be noted between the *fixed-equilibrium* algorithm and the two other algorithms with an 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 the 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

SELECTION RATE

an accepted rate

Oups !
peut-être
pas

a

Table 1.3: 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

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 a 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 (βeta_0), organ exchange rates (P_{max} and u_{max}) and soil coverage by roots (ρ_{ar} and k_{or}).

SENSITIVITY ANALYSIS

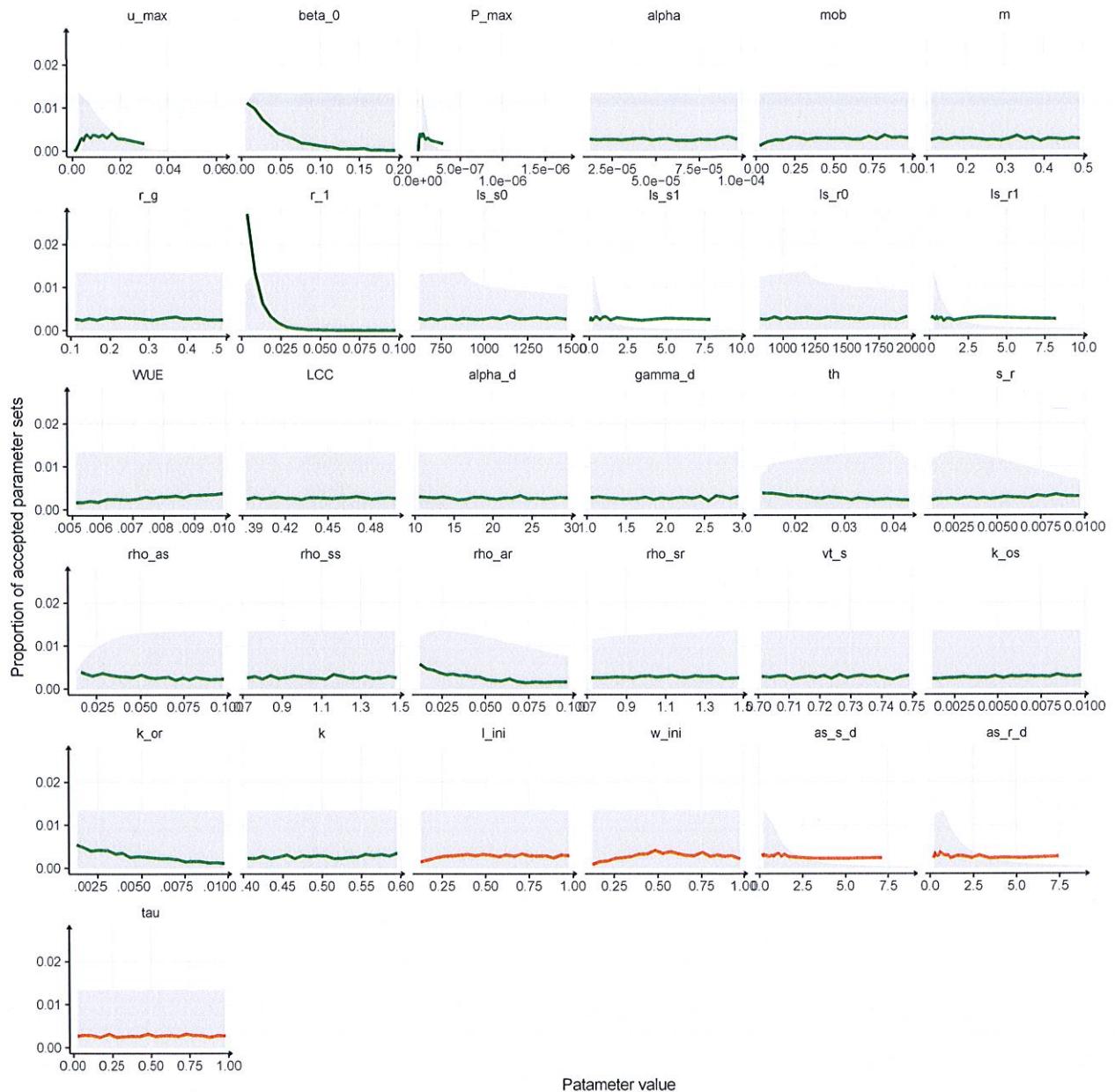


Figure 1.2: Selection rate (coloured lines) per parameter (global and species specific) for the individual growth. The grey area illustrates the prior distribution after the first filtering step (see method form ore details. Non plastic.)

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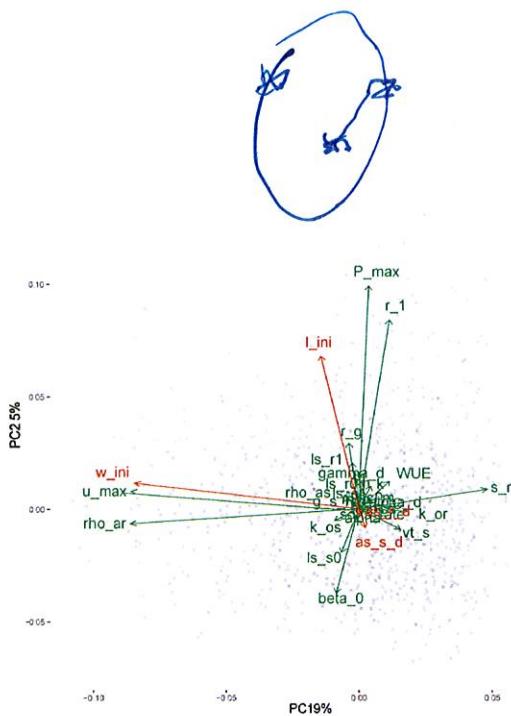


Figure 1.4: Representation of the PCA of parameter sets selected in parameter filtering process on the first principal components. *Non plastic*.

Relative mean decrease accuracy

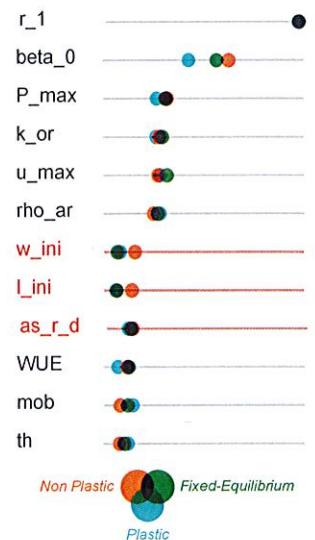


Figure 1.3: Relative importance of main parameters for selection under the three main allocation algorithms: (non plastic, fixed-equilibrium & plastic).

The PCA performed for *non plastic* algorithm only on parameter values reveals that important parameters are also the dominant variables that shape the selected subspace. The two first axis explain only 14% of the 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} , $as_{\text{s_d}}$, $as_{\text{r_d}}$, $as_{\text{r_d}}$ & $as_{\text{s_d}}$) 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) is plotted against the most important variables in figures 1.5 and 1.6.

VARIABLE RESPONSES

The total biomass is particularly sensitive to the tissue respiration cost (r_{-1}), but also to the maximum exchange rate parameters. There is a notable difference in growth maxima between the two conditions in favour of the wet condition, in line with observed data. This difference is observed for the three algorithms 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 parameter tau controlling the balance between genetic and environmental control does not emerge as an 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 a stronger influence on the ratio than the root maximum exchange rate.

spaces?

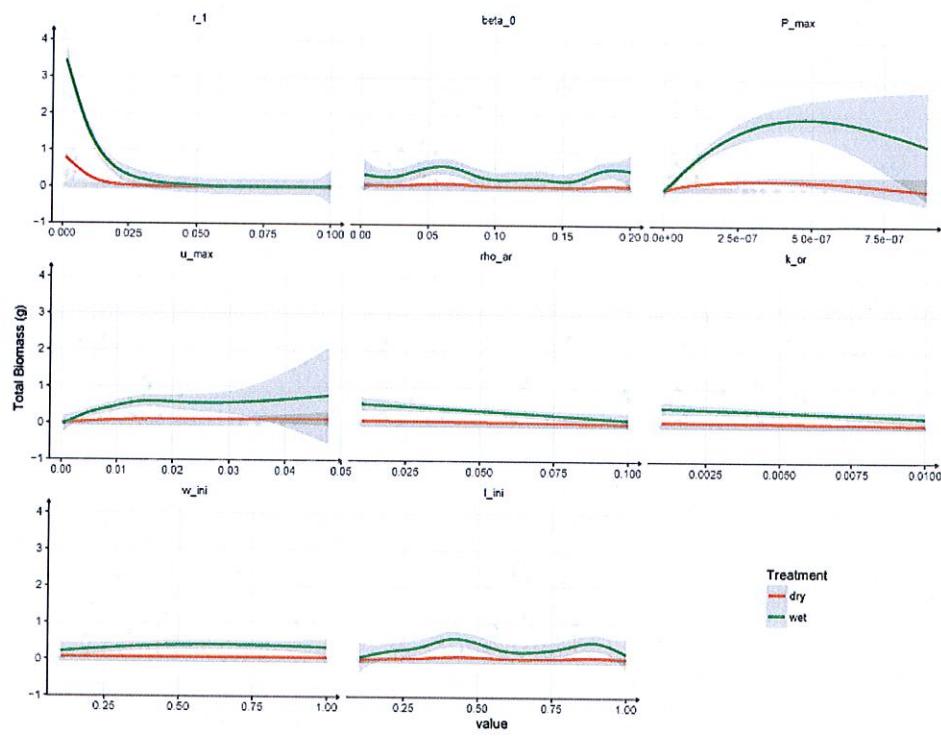


Figure 1.5: Main parameters effect on the total plant biomass. *Non plastic*. One dot represents a parameter set. Not all parameter set are represented as the y axis is limited around the smooth function (loess). Coloured points represent selected parameter sets in the two treatments (dry and wet).

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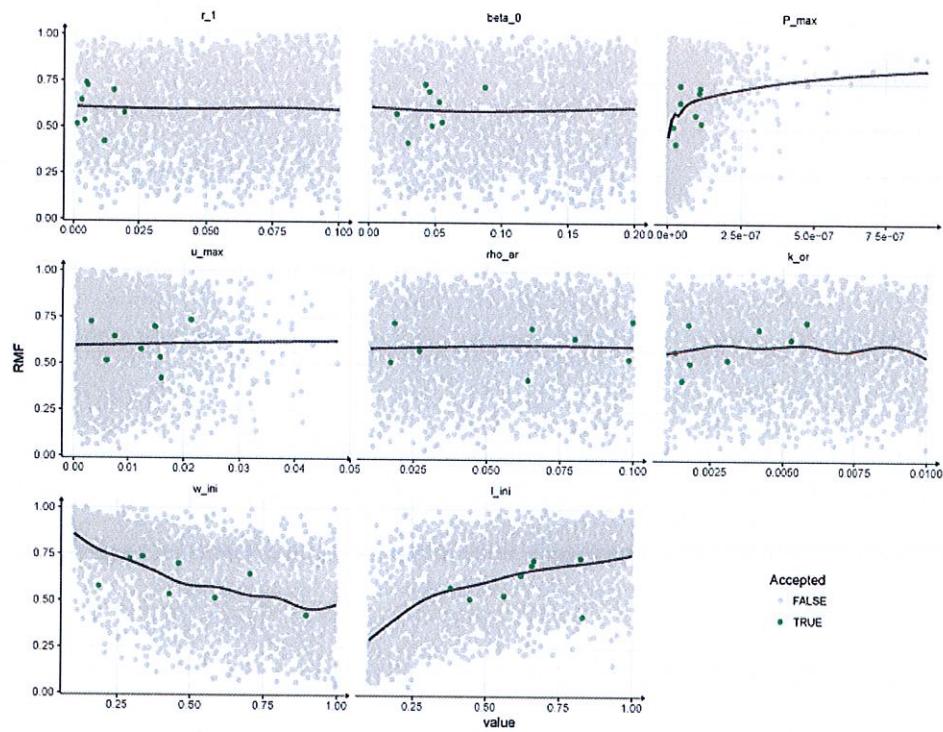


Figure 1.6: Main parameters effect on the total plant Root Mass Fraction (RMF). *Non plastic*.

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

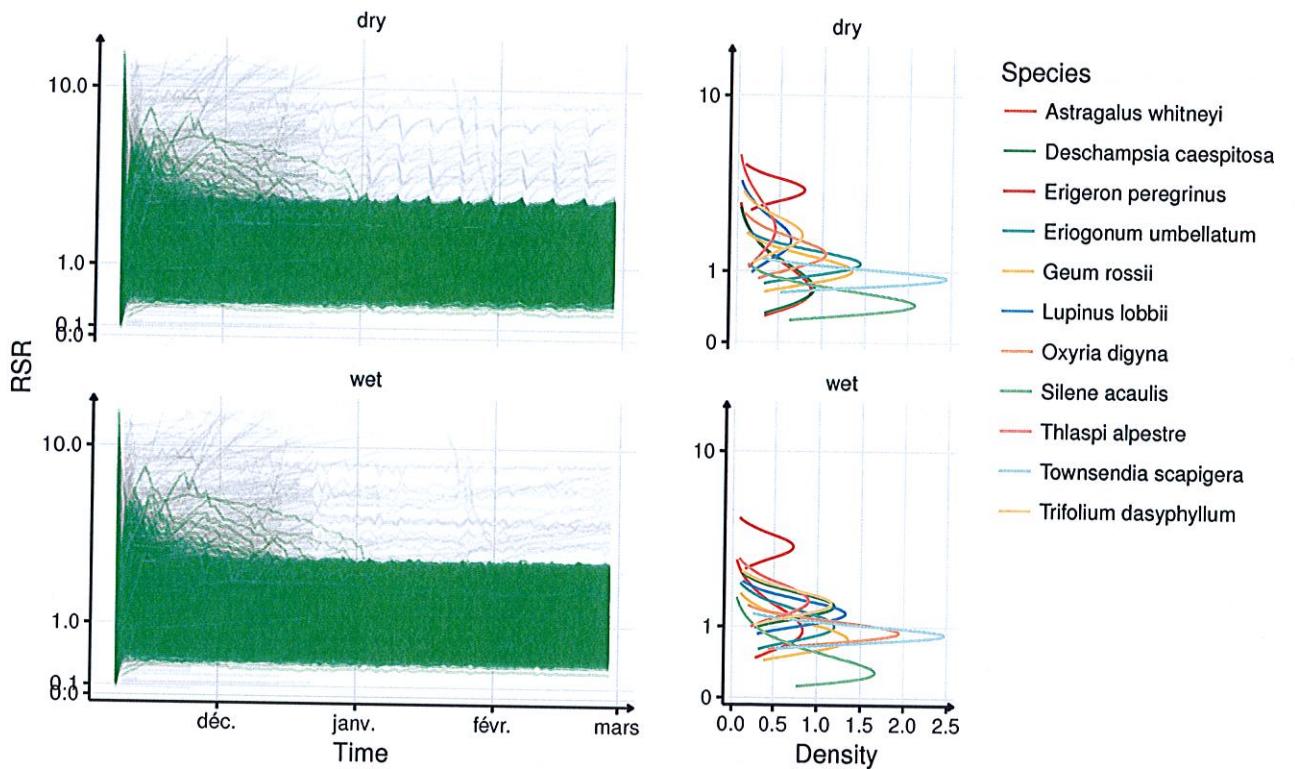


Figure 1.7: Comparison of simulated values of RSR with real species RSR in two contrasting conditions. Because there is no plasticity or ontogeny, the simulated plant do not express any changes in RSR. Fixed-equilibrium.

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

GROWTH AND STRATEGY SPACE

higher

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 of functional potential diversity) and the main trade-off between resource acquisition and efficiency.

Sous le paré,
la page



?? the memory parameter?

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 analysed in further simulations within the same set of model parameters.

Because of the model complexity and the number of species-specific parameters, in addition to long simulation time, Bayesian calibration could not be performed. In the Bayesian paradigm, the information is contained in the data and revealed by the structure of the model. An alternative modelling approach is to use the parametrisation phase to accept certain parameter sets, and learn about the system through simulation experiments. The simulated data is analysed rather than empirical data. The patterns emerging from the simulation experiments inform us of the impact of the modelled mechanisms (even if they do not totally match the data). Therefore the model is still an understanding tool and can inform ~~the~~ ^{on? about?} effect of plasticity on ecological processes.

The growth is reproduced in contrasted conditions, but only partially as one ~~per~~ parameter set is tested. The number of species and dimensions in the strategy space would not allow for a calibration of all species for one parameter set. The plastic response of the root:shoot ratio is not correctly reproduced and would require a different implementation (stress based). However, the plasticity as implemented improved the acceptance rate because of a better growth. Therefore the effects of plasticity can still be investigated with simulation experiments.

If the parameter filtering step does 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 experimental data of drought events, it is no surprise that parameters related to water economy show a strong influence on the selection rate and model behaviour. In the context where the model has been developed, water shortage is expected to be an important factor for the community dynamics. In this perspective, the ability of *MountGrass* to reproduce the differences in productivity between 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 sensitivity of the different variables to the parameters align with the two criterion of selection (that work with the independence of trade-off). In contrast with forest, the light is not the most important factor and water plays a more limiting role. A particular focus on below-ground resources should drive the simulation experiments with this model.

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 the 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 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* fluctuate between two "states", or phenotypes associated with the dry and the wet conditions. The value of the RSR following a 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 rates. While the net growth rate is limited by the comparison during the filtering process of the total weight of plants with the empirical data, the assimilation rate is not and can be compensated with a 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 (but lower turn-over). 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.

This generalised high phenotypic flexibility allowed by high assimilation rates to compensate high turn-over rate highlight a problem within the calibration. The reproduction of growth patterns gives us confidence in the good functioning parameter filtering process, so wrong priors are certainly the cause of this behaviour. The uncertainty around the exchange rates for shoot and roots lead to the definition of relatively wide priors informed by parametrised models (Kleidon and Mooney, 2000; Reineking et al., 2006; Taubert, 2014). In the other hand, the turn-over parameters are relatively well informed by modelling approaches but also empirical studies (Ryser and Urbas, 2000; Wright et al., 2004; Tjoelker et al., 2005; Luke McCormack et al., 2012), leading to more constrained priors. The value of these priors is not discussed, it is rather how they are translated

PHENOTYPE FLEXIBILITY

plutôt guillemets
simples en anglais.

elle fait mal celle-là...
si sujet = flexibility
alors => "highlights"

on Teria
au pluriel
je cours.

idem

within the context of the model leading to an over-estimation of the cost of leaf senescence. Because the lifespan is integrated at the daily time-step as a constant turn-over rate, instead of a late decrease in biomass as in natural systems, the biomass is reduced early in the growth (from day 0). This can be a problem when the growth is non-linear, especially when growth is higher early in the growth period. In this context, fairly narrow priors can lead to an over-estimation of the turn-over cost as the non-linear growth is not properly integrated by the integration of the tissue senescence. This over-estimation is then compensated, during the parameter filtering process by a higher assimilation rate and a higher tissue flexibility.

The particular design of the experiment from Peterson and Billings, 1982 with cycling wet and drought periods can also explain this effect. Other experiment designs with shifts in the mean influx of water would limit the role of the phenotypic flexibility and show more consistent differences in RSR between wet and dry conditions.

Moreover, the fact that plants are more productive during periods where they may not want to invest in roots reduces the possibility for a strong durable shift of RSR. 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 on 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 phytohormones.). 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.

The high flexibility of the plant phenotype given by the high assimilation and turn-over rates reduces the inertia of the model and its capacity for modelling lasting changes in RSR. The modelling of the plastic response also reduces the capacity of the model to well capture changes in RSR.

The parameter filtering process successfully captures the growth pattern, showing convincing patterns of parameter sensitivity and variable response. However, limitations in the plastic response modelling, coupled with high phenotypic flexibility and a particular experiment-design do not allow a solid representation of the RSR differences between the conditions. Neverthe-

less, the *MountGrass* still offers a way to interrogate the effect of plasticity on growth patterns, optimum strategies and potential diversity.

1.2 Individual level behaviour and properties of plastic allocation algorithm driven by the plant memory

Calibration and sensitivity analysis gives information on the main processes of plant growth, but the general effects of the allocation rules on plant growth are not fully identified. Moreover, because the parameter filtering processes were limited to individual plants and the effects of the species-specific parameters are depending on the 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 of the role of the **allocation rules** and species **memory** on plant development as the basis for interpretation of plasticity effects in following chapters.

The challenge of the framework presented in the 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 extent to which different species memory lead to different phenotypes under full genetic control (not influenced by the external conditions) is explored through simulation experiment under *plastic optimisation* allocation algorithm with no effect of conditions on traits ($\tau = 1$), only on growth.

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, 8mm and 16mm per day. To avoid drift in the phenotype due to allocation algorithm (see paragraph 2.2.1 on phenotypic determination), simulations were 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*.

The 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 is visualised by fitting loess curves between memory values and individual trait values.

1.2.2 Results

The allocation algorithm affects the way the organic matter is distributed between the different tissues of the plant. With partitioning coefficient pre-established

ALLOCATION ALGORITHMS

MEMORY & PHENOTYPE

ALLOCATION ALGORITHMS

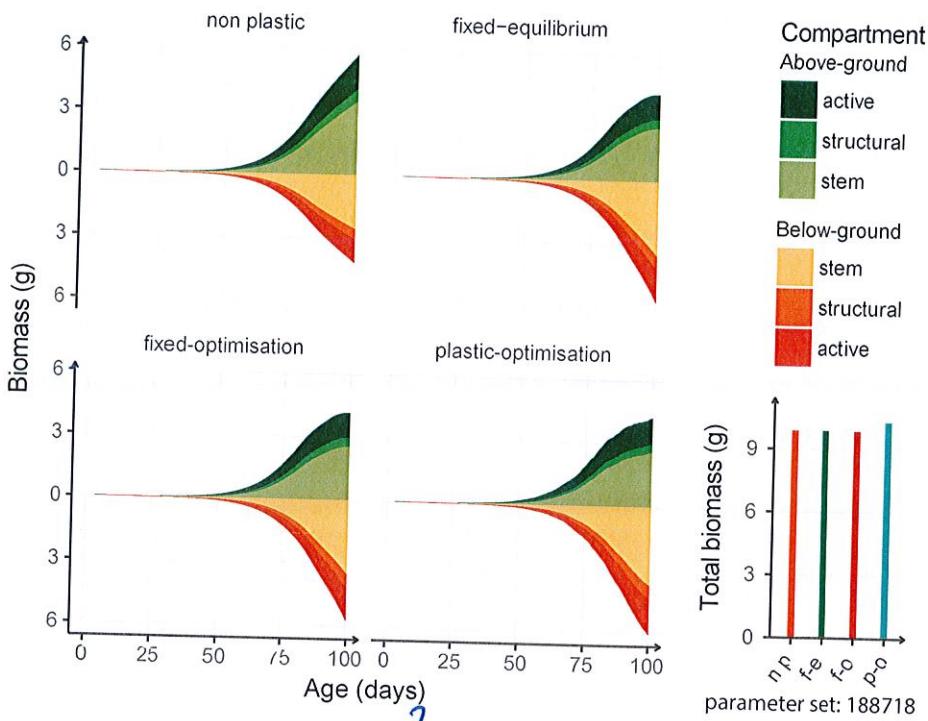


Figure 1.8: Effect of the different allocation algorithms on the different biomass compartments of the plant. The fraction of organic matter allocated to the stem (ensemble of supporting tissues for shoot and roots) are increasing over time for all algorithms. The *non plastic* algorithm show constant allocation coefficients between above-ground and below-ground compartments and between active and structural tissues. All others show different coefficients for the above-ground - below-ground partitioning, and the *plastic-optimisation* algorithm have changing proportion of active and structural tissues. The bottom-right panel shows the total biomass for the four allocation algorithms after 100 days.

for the given conditions, the algorithm shows very similar performances (see figure 1.8). The difference in allocation algorithm is mostly noticeable in figure 1.8 mostly on the shift toward root allocation at the end of the simulation when the water becomes to be limiting. The plant under *plastic-optimisation* allocation benefit from a slight improvement in performance (mean: +10%, median: +3.4% relative to *non plastic*).

The *plastic-optimisation* algorithm allows changes in the proportion of active tissues in organs. This may have repercussions on the allocation between shoot and root but also can lead to non-specific variability within plants with no perception of resource fluctuations ($\tau = 1$). The median variability of the RMF (root mass fraction) along the 100 simulated days is 0.015, that is five times higher than the variability of the other plastic algorithms (*fixed-optimisation* and *fixed-equilibrium*) (see table 1.4). This variability is much higher (around 0.028) for the plastic plants in all three plastic algorithms, while it is null for the *non plastic* allocation rule. The range of the RMF follows a similar trend, with a higher value for the *plastic-optimisation* than the other algorithms when plants do not perceive the resource fluctuations, and wide range for all plastic allocation algorithms when plants take into account the changes in light and water resources.

algorithm	sd		range	
	$\tau = 0$	$\tau = 1$	$\tau = 0$	$\tau = 1$
none	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$	$< 10^{-12}$
fixed-equilibrium	0.0278	0.00212	0.173	0.0155
fixed-optimisation	0.0279	0.00221	0.173	0.0161
plastic-optimisation	0.0283	0.0150	0.174	0.0839

Table 1.4: Median of variability and range of the RMF for simulations of 100 days, for 100 different parameter sets and three different water treatments (2, 4 and 8 mm per day), in the four different allocation algorithms. sd: standard deviation.

The plastic algorithms show similar levels of variation and range, while the *non plastic* one is stable as expected. The *plastic-optimisation* allocation show more

instability for non plastic plants ($\tau = 1$) but that is lower than the variability observed in plastic plants ($\tau = 0$). The allocation (and therefore phenotype) is controlled by the allocation rules (plastic dimensions and objective functions) and the estimation of conditions. Before investigating the effects of varying conditions, it is important to understand the effect of memory on plant strategy and phenotype.

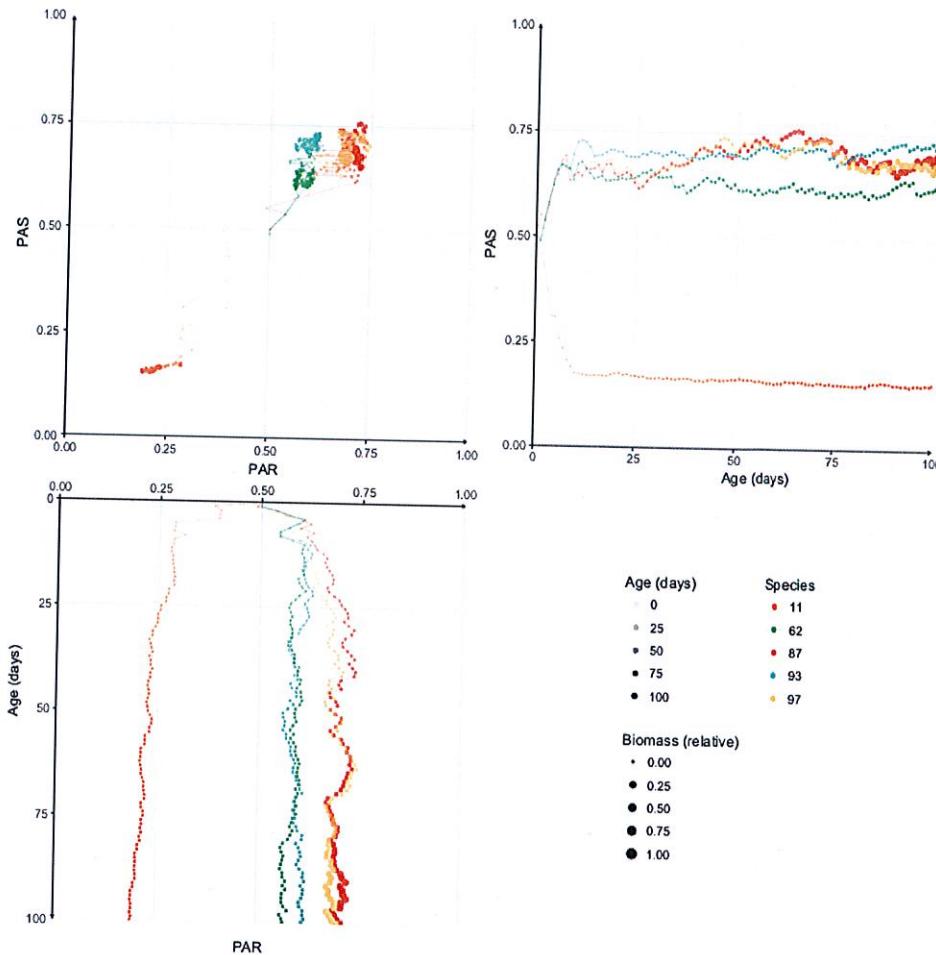


Figure 1.9: Trajectories along time in the strategy space of 5 plants with different memories. After 10 days, all plants have converged toward the estimated optimum.

The kinetics of the phenotypic shift is first visualised for one parameter set on the two main phenotypic axes (proportion of active tissues in roots: PAR and proportion of active tissues in the shoot: PAS). From the same starting point, the five species show a 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.

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 the increase in water availability memory (figure 1.10). This response pattern is consistent between all parameter sets, but

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subspaces?

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 1.11) 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).

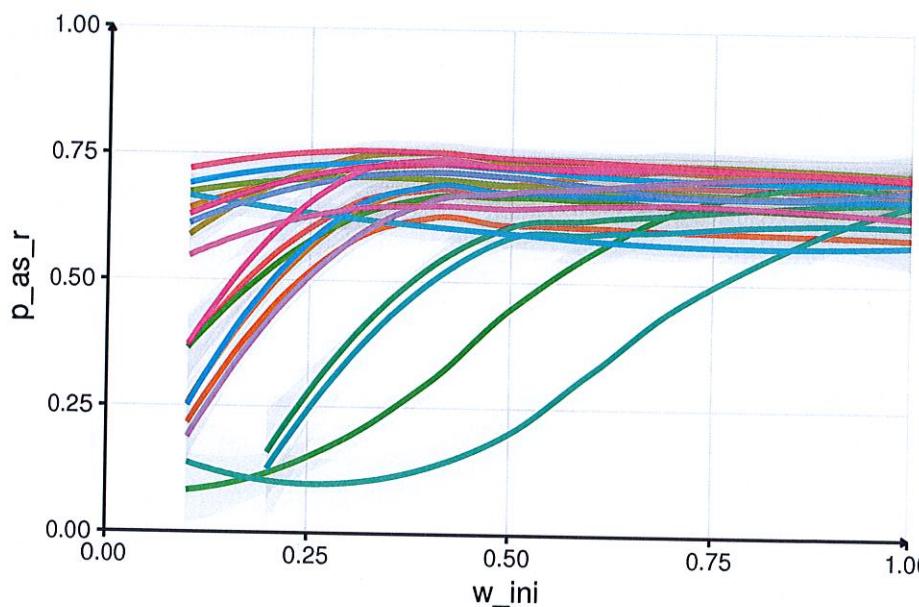


Figure 1.10: Effect of memory of water availability on proportion of active tissues in roots. *Plastic-optimisation*. Each line correspond to a local regression fitted for all memory combinations for a given parameter set. Water availability memory is given in percentage of maximum exchange rate, absolute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

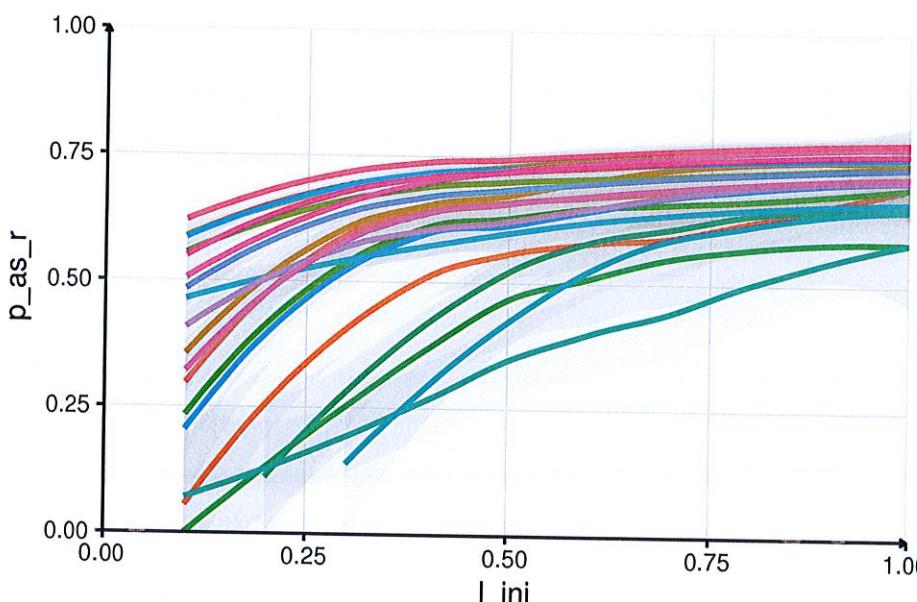


Figure 1.11: Effect of memory of water availability on proportion of active tissues in shoot. *Plastic-optimisation*. Each line correspond to a local regression fitted for all memory combinations for a given parameter set. Light availability memory is given in percentage of maximum exchange rate, absolute values may change between parameter sets.

The combined effect of the two axes of plant resource availability memory is observed by plotting the phenotypes (on the 2D space of active tissue allo-

cation) of four contrasting memories for all parameter sets (figure 1.12). 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". A memory of low availability for both resources drives plant toward very conservative strategies than other strategies. High expected availability of at least one resource increases allocation to active tissues to both organs. This confirms the positive effect of complementary resources (light for roots and water for the shoot) of active tissue allocation in organs (see figure 1.11). 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 (○).

1.2.3 Discussion

The pre-calculation of phenotypes, avoiding any phenotypic drift, allows for all allocation rules to grow plants with close performances. Nevertheless, the plastic algorithms show changes in RMF at the end of the simulation when the light:water balance starts to shift. This consistent shift in RMF for all three plastic allocation rules (with a low variation of the other plastic dimensions) suggests the sensitivity and importance of this phenotypic axis. On the other hand, the other plastic dimensions benefit the plant growth suggesting that they also play a role in the tissue efficiency. While both the RMF and the proportion of active tissues can change the exchange area, only the proportion of active tissues can change the tissue efficiencies. Because the RMF shows similar levels of variation and range in both *fixed* algorithms (RMF is the only plastic dimension) and *plastic-optimisation* algorithm (see table 1.4) the allocation of active tissue in the latter algorithm does not compensate for change in root:shoot allocation and is not used to increase the area of the limiting organ. This is confirmed by the fact that memory of low-light conditions (● in figure 1.12) lead to lower allocation to active tissues than high light conditions (○). In the case of fully plastic plants trying to optimise their growth, the vegetative phenotypic dimensions do not fulfil the same functions: the RMF is used to adjust the balance between the resource exchanges while the changes in active tissue proportions are related to the tissue and whole plant efficiency. This contrast in functions looks opposed to what is often observed in empirical studies where shoot:root ratio and SLA (here controlled by the proportion of active tissues) respond in the same direction to increase the leaf area and compensate low incident light (Ryser and Eek, 2000; Poorter, Niinemets, et al., 2009; Poorter, Niklas, et al., 2012). This discrepancy reveals a limitation within the plastic-allocation algorithm: the balance function is mostly supported by changes in root:shoot ratio while the proportion of active tissues (controlling SLA and SRL) controls the tissues efficiency. The low proportion of active tissues in low resource (● in figure 1.12) indicates a selection of

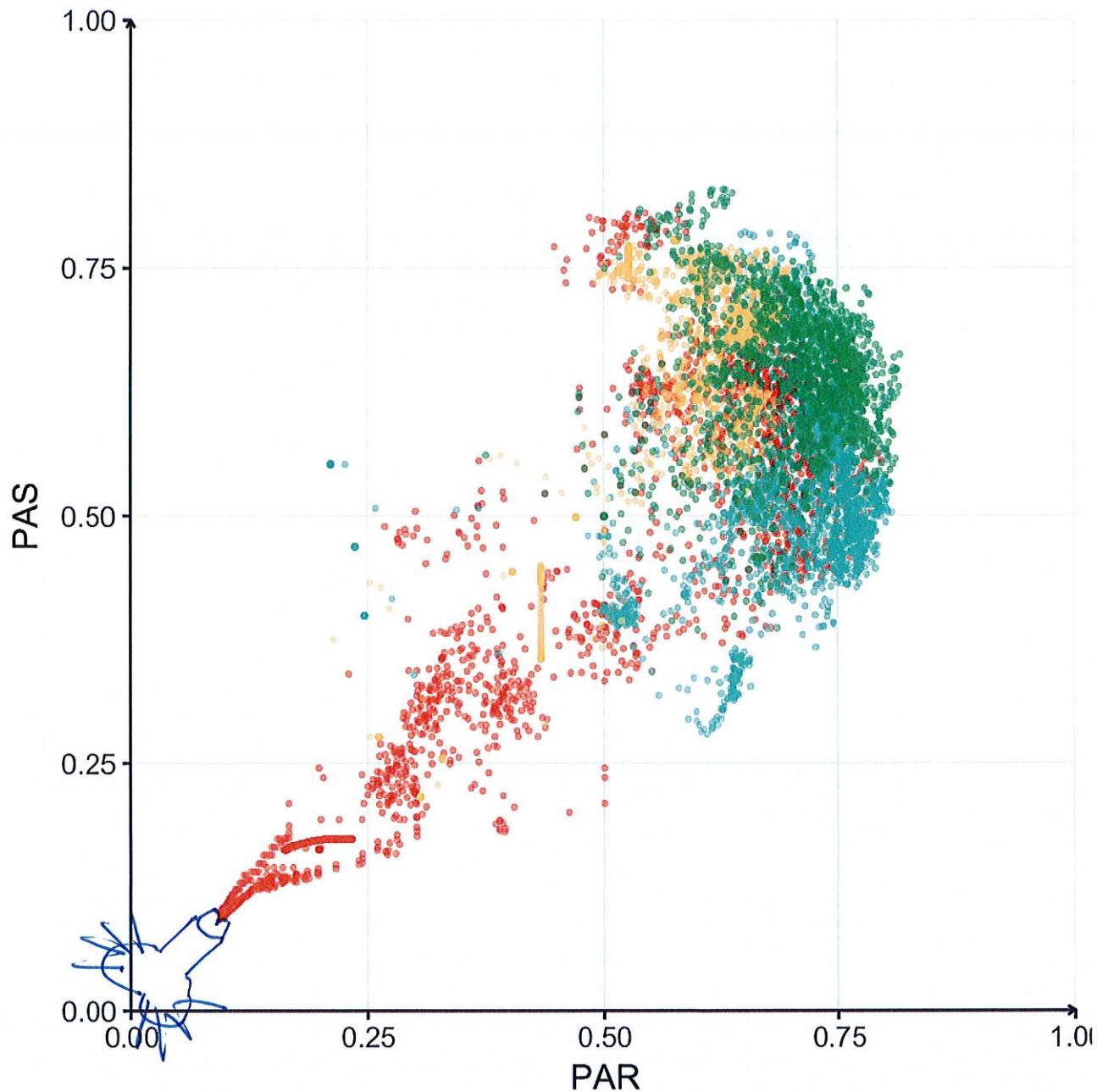


Figure 1.12: Impact of species memory on final phenotype in case of fully plastic allocation. *Plastic optimisation.* Each point corresponds to a plant phenotype for a memory syndrome for a given parameter set. Colours denote the memory syndromes.

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

more conservative phenotypes when the resource is scarcer. This is in agreement with the Grime's triangle (Grime, 1977) and large-scale empirical studies (Wright et al., 2004). In contrast with the conclusions of Ryser and Eek, 2000, here the full phenotypic plasticity of the *plastic-optimisation* algorithm is driven by similar constraints than the long-term selection processes. This can be explained by the design of the trade-offs that drive the gain function (see chapter III). Therefore there are strong constraints on the tissue allocation, but low constraints on the root-shoot allocation. An additional constraint of this dimension can be added by considering other functions of each organ (such as nitrogen absorption by roots), or more artificially by increasing the cost of the displacement along the RMF axis. The fact that traits and allocation may be constrained in different ways has been observed by Freschet, Swart, and Cornelissen, 2015, highlighting contrasted types of response between shoot and roots (Poorter and Ryser, 2015). Also, it appears here that studying the long-term effect of a fixed estimation of conditions is probably not the best way to understand how the plastic responses of plants to an abrupt change in conditions. However, in *MountGrass*, the plasticity is driven by the same mechanism, so such interpretations can be made. But, this discrepancy suggests that mean phenotype and plastic responses should probably not be driven by exactly the same mechanisms.

In addition to this imbalance in constraints, the mean organ approach can also explain this behaviour. Approximating the properties of the canopy by considering one mean organ leads to a low impact of the plastic allocation on the SLA and SRL if the already existing compartments are large relative to the growth, a high importance of old tissues, while most of the exchange activity is generally produced by freshly grown tissues. Also, the rapid growth and turn-over in numerous parameter sets also authorise rapid plastic response on the RMF dimension (see also the rapid oscillations in the figure 1.7 top left panel), diminishing the need for tissue-specific adjustments. A stronger calibration of gross production and turn-over rates, as mentioned in the previous section, should reduce this effect. Finally, the optimisation function may be too strong and plants may not always go for the optimum allocation but for the fastest and most competitive choice (see Farrior, 2011; Dybzinski et al., 2011; Farrior, 2014). If this is not a problem in the context of this simulation where the memory is used to drive the default phenotype of the plant, it would be problematic in the context of plastic responses.

The different allocation algorithms impact the vegetative phenotype in different ways, but with a similar performance when any phenotypic drift is avoided. But, the plasticity along the three main dimensions of the plant vegetative phenotype (PAR, PAS & RMF) seems to have different objectives. While the RMF is the main adjustment variable to respond to changes in equilibrium, the proportion of active tissues is more closely related to the amount of resources and tissue efficiency. However, it does not reproduce increases in organ area by changes in traits when the related resource is limiting. Multiple factors can explain this partial discrepancy with empirical results. The model still can be used to better understand the role of the memory as a driver for the phenotypic development, and the effects of the plasticity (particularly the RMF dimension) on plant performances.

The *plastic-optimisation* allocation algorithm allows for interesting insights into how the different resources affect the theoretical optimum phenotype. The in-

crease in resource levels leads to an increase in the allocation of organic matter to the active tissues. While this is commonly demonstrated, the indirect effect of one resource on an organ that is not limiting for this resource is less often studied. A higher perceived resource availability drives plants to have a higher proportion of active tissues in both gathering (*i.e.* leaves for an increase in light availability) and other organs (*i.e.* roots for an increase in light availability). The direct effect on the related organ shows a rapid shift from low to a maximum value. This rapid shift can be explained by the fact that the increased resource availability both increases the slope of the exchange rate per biomass (gain function) and reduce the importance of the maintenance costs relative to the productivity, favouring the exploitative strategies.

In the other hand, the indirect effect of an increased resource level on the non-gathering organ can be explained by two mechanisms: a shift in the limiting organ requiring an increase in the exchange area of the newly limiting organ or an increasing gross productivity reducing the need for efficient organs. The former mechanism is related to the equilibrium maintenance. The balance between the two organs can be maintained by increasing the exchange area of the newly limiting organ (or reducing the exchange area of the non limiting organ, see Liu and Stützel, 2004 for an example, or Grassein, Till-Bottraud, and Lavorel, 2010). However this type of response is unlikely considering this implementation of phenotypic plasticity. The changes in exchange area are mostly driven by the organ biomass rather than its proportion of active tissues (see previous paragraph). The latter mechanism is more in line with the observations of the behaviour of *MountGrass* (figures 1.12 & 1.11). It explains the increase in active tissues in both organs by an increase in the exchange rate of the gathering organ and in the productivity at the plant scale, decreasing the relative importance of maintenance costs and allowing for a more exploitative strategy of the organs.

Such allocation pattern could explain coordination between organs, as the cost of the respiration and turn-over are compensated globally by the gross productivity, and allows divergence from the optimum of the isolated organ functioning (see chapter III for details on the trade-offs at the organ's scale). However, this coordination along a fast-slow axis asks the question of the stability of this strategy. Indeed, the high investment in active tissues observed suggests that the turn-over and respiration costs are high, and a loss in efficiency based on an incorrect estimation of condition could have strong negative effects.

The allocation trade-off allows for strategies from the fast-slow spectrum to arise for the shoot and roots based on the perceived condition availabilities with some degrees of coordination, in a coherent framework. Such allocation mechanism can explain coordination thanks to shared cost and increase efficiency when the resource is available. The potential instability of the phenotypes may lead to discrepancies between the optimum defined by the *plastic-optimisation* algorithm and the realised performance landscape.

The model *MountGrass* brings a new approach to agent-based models and plasticity by integrating the resource availability estimation directly as a parameter for the plant development strategy. Despite requiring certain adjustment for an integration with full plasticity (in RMF and organ-specific traits), it reproduces a certain pattern of coordination and overall resource use strategy along resource gradients. It also makes a bridge between the mechanistic approaches, that use species-specific parameters measure on individual plants and species

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distribution models (SDMs) that focus on abiotic conditions¹ and how species distribution match climatic variables. This new framework can allow more exploration at bigger scales with numerous species, that is often the limitations of such agent-based models. However, to make this step, further work is needed on the general assumption that the estimation of conditions coupled with the gain function gives a good proxy to the plant development. There must be a strong positive correlation between the memory, the developed phenotype and the plant performance.

While this verification seems obvious, difficulties can arise if you consider plant with different levels of plasticity. A non plastic plant will certainly require the same memory as a plastic plant that will be able to adjust this memory. The former should conciliate the memory (and therefore the phenotype) matching the conditions of it growing period with values that limit risks of negative growth outside this favourable period. A mean value of the experienced condition during the growing period is certainly a good value for the memory. This also raises the question of the ontogeny in these models that often consider fixed allocation parameters. In *MountGrass*², ontogenetic shifts can be mimic under *plastic-optimisation* by having default allocation parameters different from the ones computed by the optimisation algorithm². On the other hand, plastic plants should better have a memory that matches the conditions at the early stages of growth, and let the plasticity drive the allocation for the continuation of the development. Also, while the structure of the model lets a door open for the integration of heritability mechanisms (through epigenetic modifications) that are expected to play an important role in the adaptation to the global change, those differences between plastic and non plastic plants may impact the integration of plasticity. This argument also encourages to find alternative solution to model plastic traits. Based on the review by Crisp et al., 2016, the concept of memory can be conserved but adapted to be more driven by stress levels and stress response/recovery than actual resource availability values. The knowledge of molecular mechanisms of the plant functioning must better inform the modelling routine that is too focused on mathematical and theoretical approaches. The advantage of such specific memory mechanism is that it can be stress specific³ and allows the integration of heritability.

The concept of memory, even if it allows the contrasting phenotype in a continuous space, should take a different form to suit multiple plasticity strategies and integrate a form of heritability. The molecular mechanisms of plastic responses are better understood and provide solid foundations for new organ-specific plasticity.

The model *MountGrass* integrates trade-offs in resource use driven by the memory in resource availability. The investigation of the allocation patterns driven by the *plastic-optimisation* algorithm under the assumption of maximisation of the daily growth demonstrates different roles of the phenotypic axes: the RMF largely controls the equilibrium between shoot and root total activities, while the proportion of active tissues are related to the tissue efficiency as well as the overall plant efficiency and resource use strategy. While the fast-slow gradient along resource gradients is reproduced, and organ partial coordination explained, plastic responses to answer quick changes in resources are likely to not be reproduced due to a lack of constraints on the RMF dimension. The effect of the different algorithm, plasticity strategy and

¹ new SDMs now integrate biotic interactions as well as other ecological processes, as suggested by Guisan and Thuiller, 2005.

² limited here by a first simulation cycle, see methods for details.

³ as suggested in the chapter III.