Adaptation of the GreenLab growth model to plants with complex architectures and multi-scale analysis of source-sink relationships for parameter identification.

Adaptation du modèle de croissance GreenLab aux plantes à architecture complexe et analyse multi-échelle des relations source-puits pour l'identification paramétrique.

Véronique Letort

Laboratoire MAS - Ecole Centrale de Paris

28 May 2008

Collaborations

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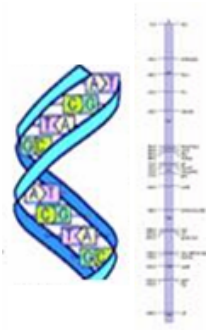
- DigiPlante project, INRIA
- AMAP, CIRAD
- LerFob, INRA Champenoux
- MAPI team, INRA-Supagro Montpellier
- LIAMA
- China Agriculture University (CAU)
- Chinese Academy of Forestry (CAF)
- Wageningen University

Global flowchart

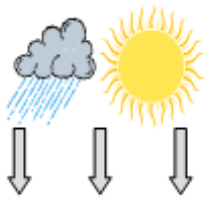
Plant genome



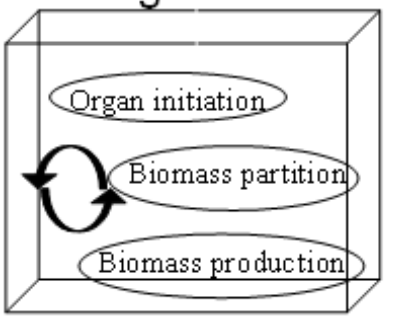
Genetic model

Input parameters
architecture, sources, sinks

Control variables
(environment)



Plant growth model

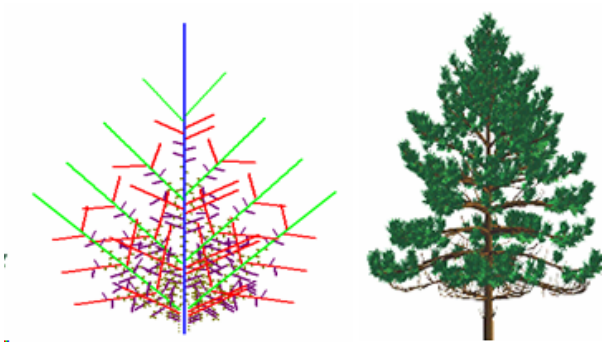


GreenLab

Outputs
3D growth, organ weights, plant height, yield...

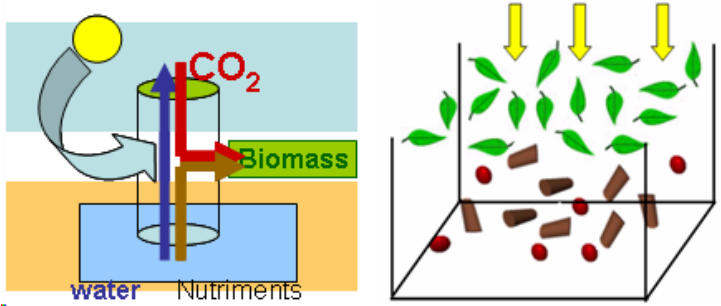
Functional-structural models

Geometrical models:
Simulation of 3D architectural development



Organogenesis + empirical geometry rules
Applications: video games, landscape/urbanism, design

Process-based models
Yield prediction as a function of environmental conditions



Biomass acquisition (Photosynthesis, root nutriment uptake) and allocation,. . . Compartment level

$\Longrightarrow$ functional-structural model

Assets of functional-structural models

- Interactions architecture $\Longrightarrow$ functioning:
  - e.g. assimilate production depends on light interception (related to crown structure or leaf orientations)
- Interactions functioning $\Longrightarrow$ architecture:
  - organ (e.g. fruit) abortion
  - tillers or branches appearance

Importance for applications

Yield prediction under environmental stresses in agronomy, simulation of forest management practices, prediction of wood quality and biomechanical stresses,...

But: Until now, most FSMs used for teaching and research only.

Partly because of problems for parameter identification.

Parameter identification for FSMs

How to handle plants with complex architectures for growth modelling, parameter identification and experimental protocol ?

- How to model topology-physiology interactions ?
- How to analyze the model behaviour ?
- Which levels of topological description are relevant :
  - in terms of data ?
  - in terms of modelling ?

Outline

1. Modelling
   - Plant development
   - Interactions topology-physiology
2. Model behaviour and limit analysis
   - Limit production of the model
   - Conditions for invariances of biomass production with different topologies
3. Model identification for plants with complex architecture
   - Procedure
   - Multi-scale data aggregation
   - Multi-scale model aggregation
4. Discussion and perspectives

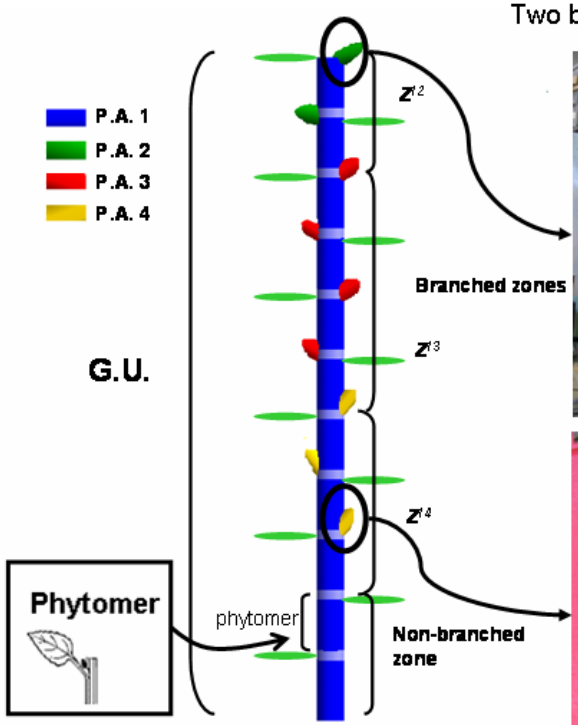
Outline

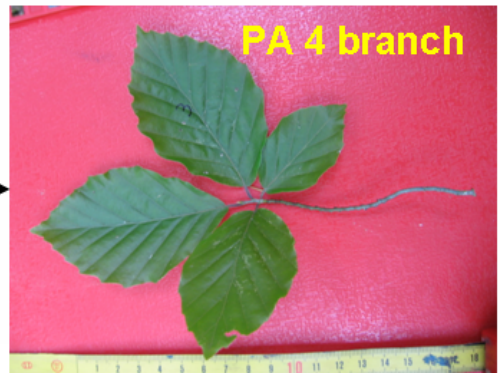
A discrete dynamic model

- Spatial unit = phytomer (meso-scale)
- Time step = growth cycle (rhythmic or continuous growth)
- Physiological age = characterization of the meristem differentiation state.

e.g.: Beech tree (LERFoB)

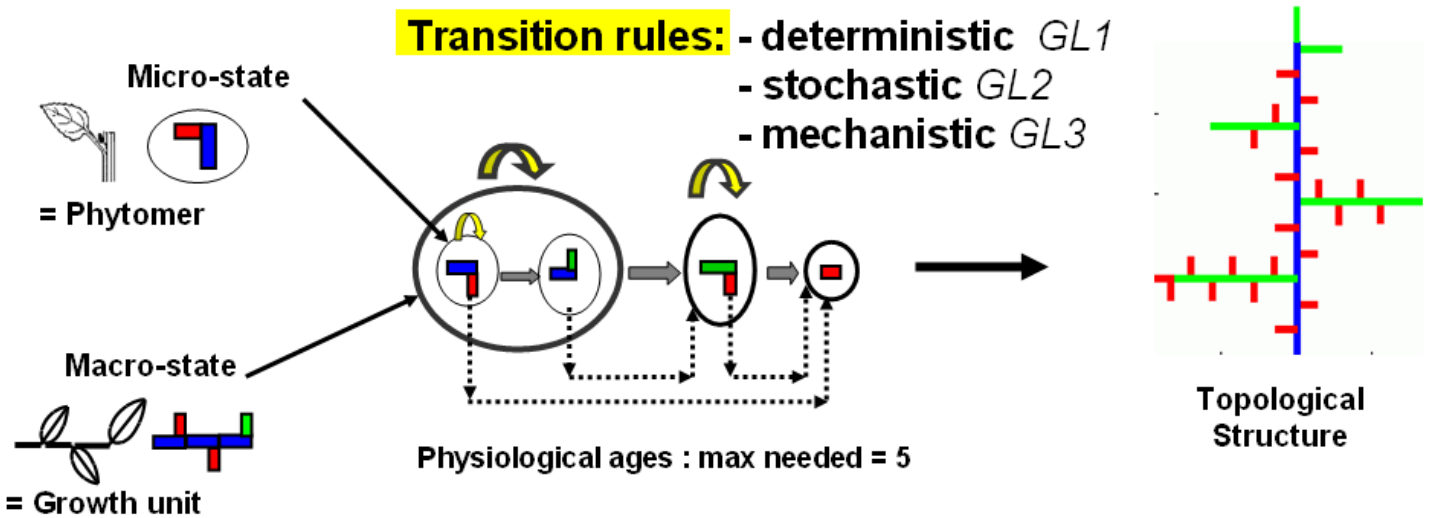
Two branches with same CA but different PA:





Development rules

- Dual-scale automaton



- Structure factorization
  - Simulation time proportional to maximal PAs and CAs
  - Structure formalism :

$$S_p(n,t) = \left[\prod_{p \le q \le P_m} (m_{pq}(n,t))^{u_{pq}(t+1-n)} \, (S_q(n-1,t))^{b_{pq}(t+1-n)}\right] S_p(n-1,t)$$

u_{pq}: number of metamers; b_{pq}: number of lateral branches

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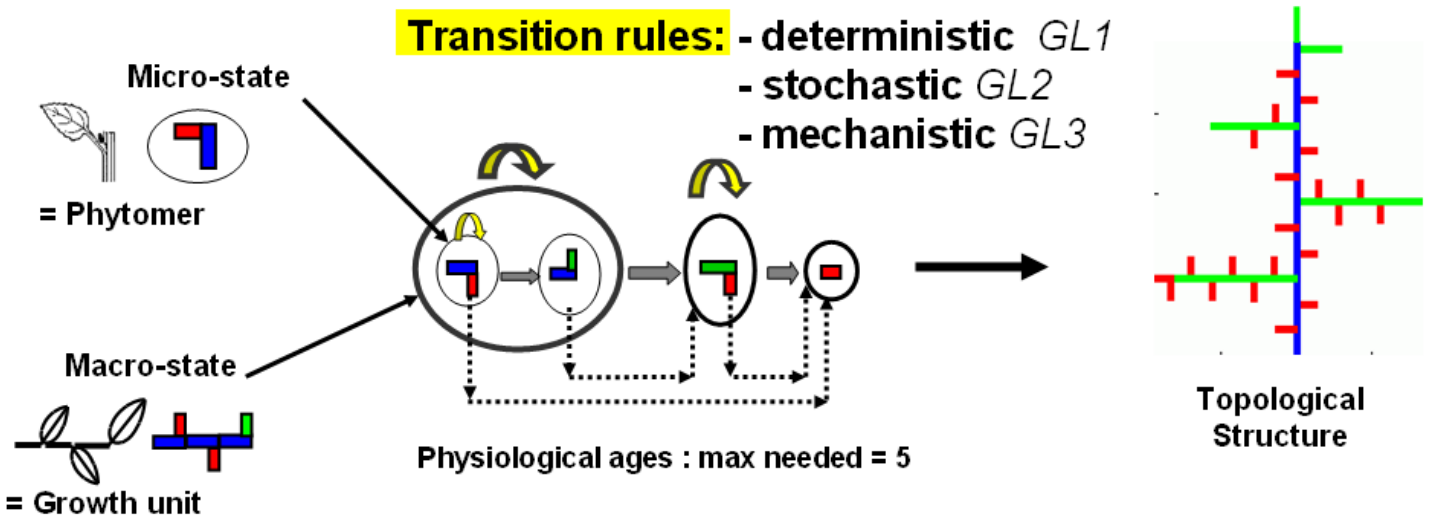

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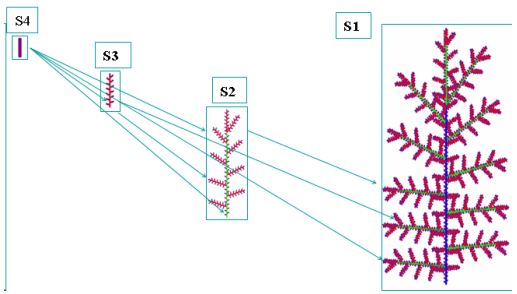

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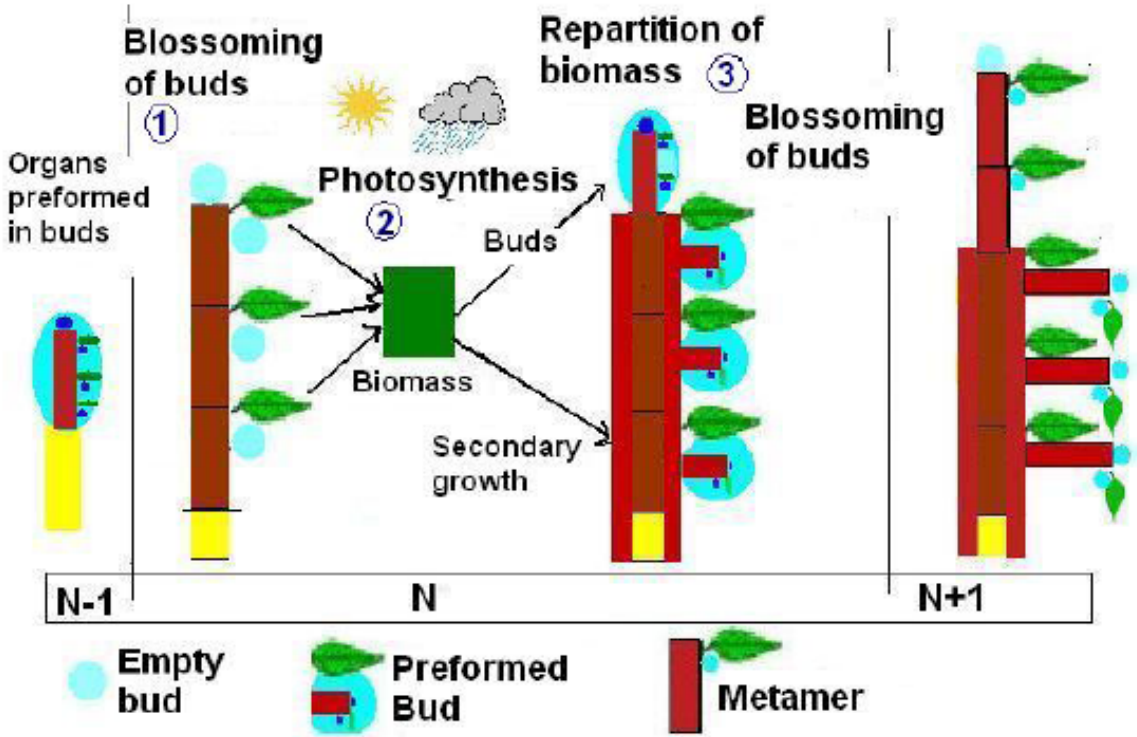
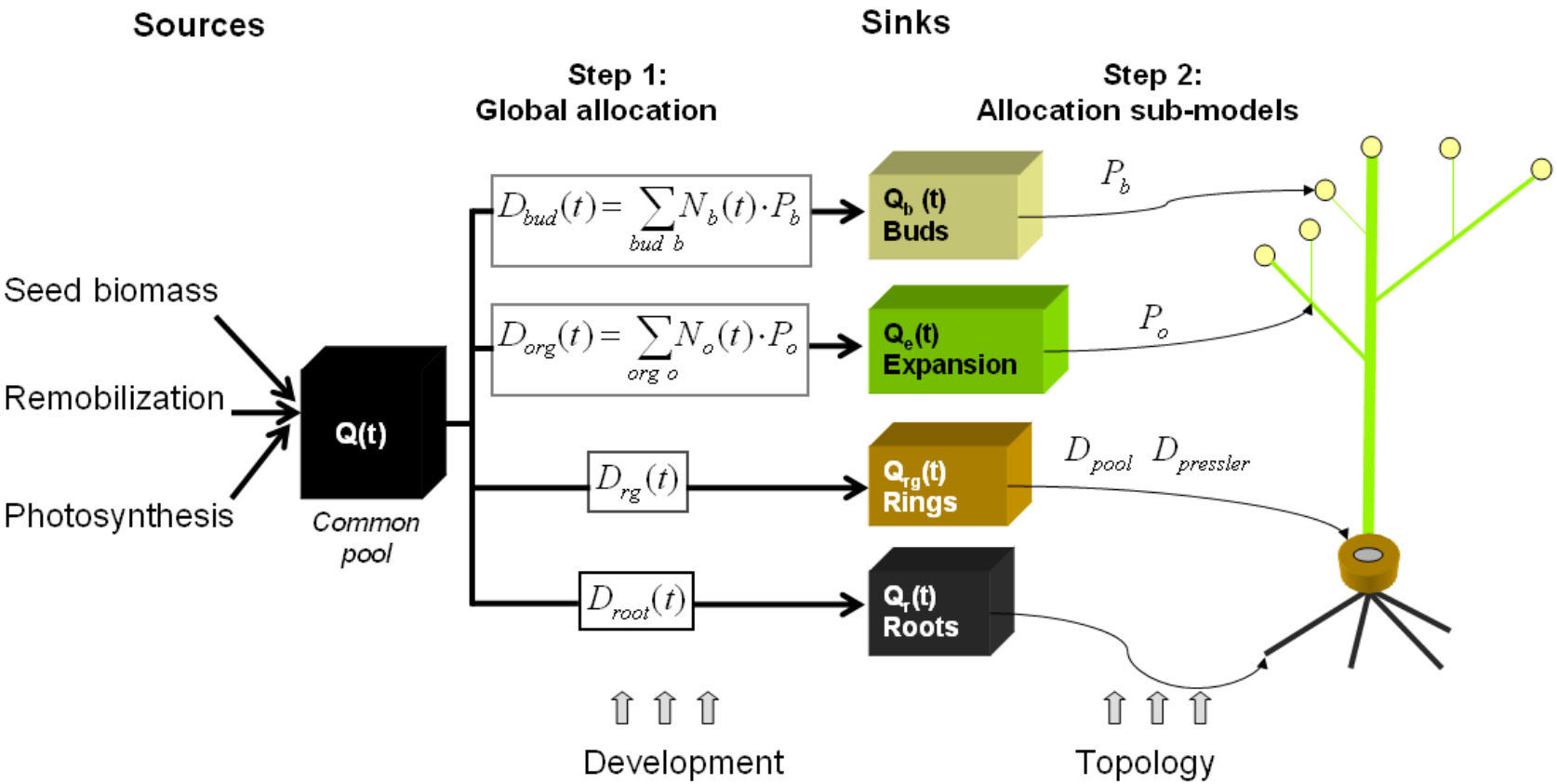
Flowchart of growth cycle



[A. Mathieu]

Source-sink model



- $Q(t)$: Biomass production at cycle t
- $D(t) = D_{bud}(t) + D_{exp}(t) + D_{ring}(t) + D_{root}(t)$: Plant demand at cycle t
- P^o: sink strength of organ o
  $(D_k^o(n) = P_k^o \phi^o(n),\ k \in \{1 \dots P_m\},\ n \in \{0 \dots t\})$
- N^o: number of organs

Biomass production

Plant production at growth cycle t (with negligible axis resistances):

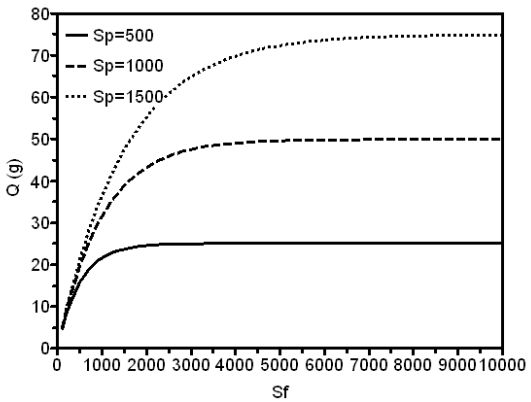
Parametric equation of the variable $S(t)$ = blade area at cycle t, with the environment $E(t)$ as control variable.

$$Q(t) = E(t)\gamma\left(1 - e^{-\nu \cdot S(t)}\right)$$

Analogy with Beer law and LUE models:

$$Q(t) = E(t) \cdot \mu \cdot Sp \cdot \left(1 - e^{-k \cdot \frac{S(t)}{Sp}}\right)$$

$Sp/k, \mu Sp$: parameters of the parametric equation;

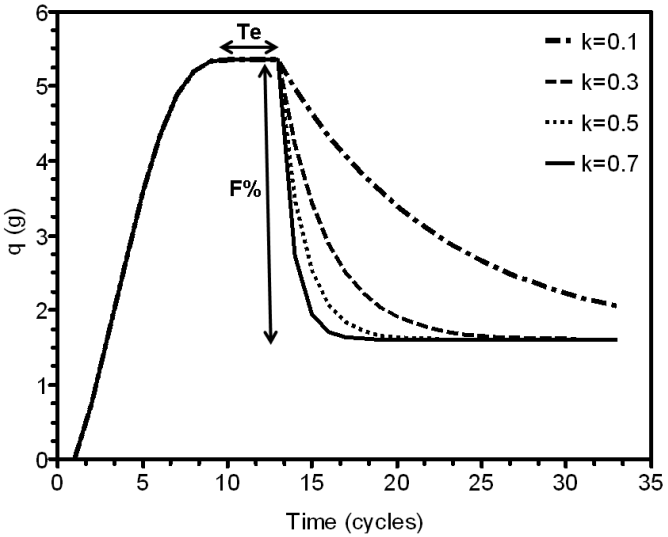


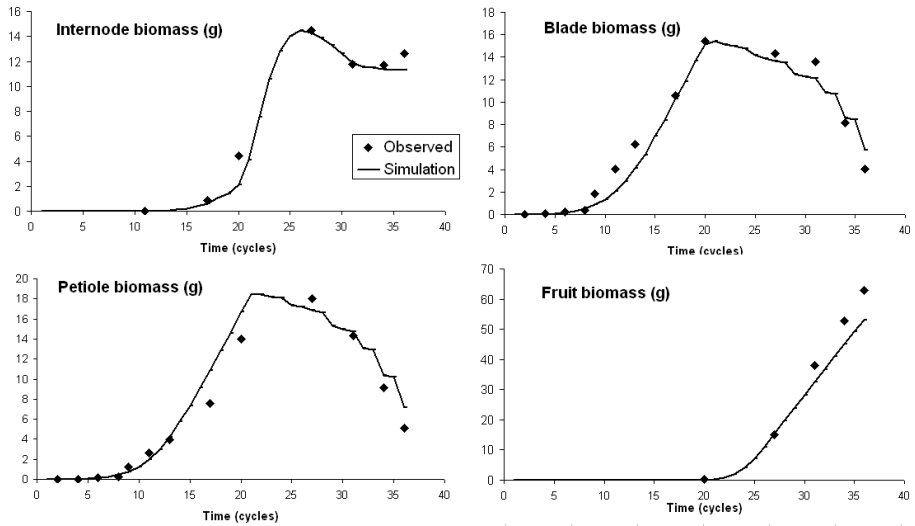
Production independent of the plant topology.

Biomass remobilization at organ senescence

Mass of organ of CA n after the end of its expansion ($n \geq T_{exp}$) :

$$\forall n \geq T_{exp} + Te,\ q(n) = q_{max}\left(1 - F \cdot \left(1 - (1-k)^{n - Te - T_{exp}}\right)\right)$$





[Data Rice Zheng BangYou, CAU]

Te: beginning of emptying after end of expansion

F: proportion of emptying

k: speed of emptying

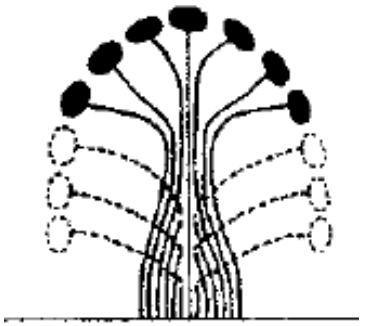
Allocation to secondary growth: global demand

3 modes to compute the global demand for ring growth:

1. **Pipes**.

Ring demand proportional to numbers of leaves $N^a(t)$.

$$D_{ring}(t) = \left(P_0^{rg} + P_1^{rg} \cdot \frac{Q(t)}{D(t)}\right) \cdot N^a(t)$$



[Shinozaki et al., 1964]

2. **Mode Q/D**. Ring demand determined by the plant trophic state Q/D: $D_{ring}(t) = P_0^{rg} + P_1^{rg} \cdot \left(\frac{Q(t)}{D(t)}\right)^{\gamma}$
   - If $\gamma \neq 1$, the plant demand is solution of : $D = D_0 + D_1 \cdot \left(\frac{Q}{D}\right) + D_2 \cdot \left(\frac{Q}{D}\right)^{\gamma}$
3. **Mode Q**. Ring demand determined by the plant production Q: $D_{ring}(t) = P_0^{rg} + P_1^{rg} \cdot Q(t)$

P_0^{rg} and P_1^{rg} are parameters to identify.

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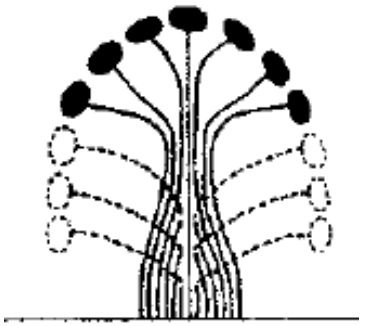

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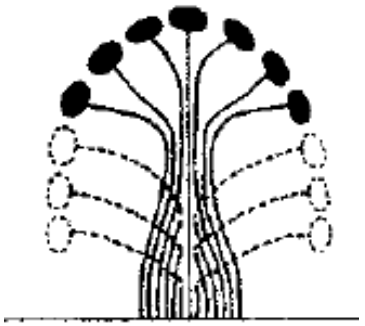

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P_0^{rg} and P_1^{rg} are parameters to identify.

Secondary growth: allocation sub-model

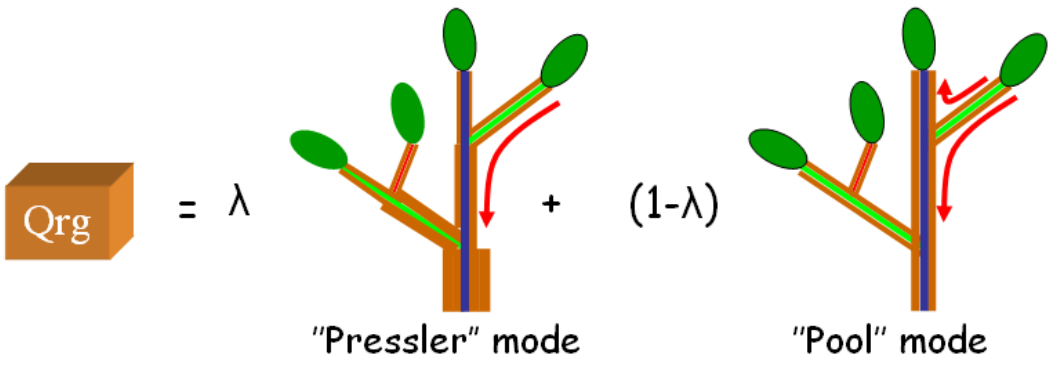
Pressler law and limitations

$\Longrightarrow$ Ring biomass increment of phytomer of physiological age p, chronological age n, at growth cycle t:

$$q_p^{rg}(n,t) = \left(\frac{1-\lambda}{D_{Pool}(t)} + \frac{\lambda \cdot N_p^{a,a}(n,t)}{D_{Pressler}(t)}\right) \cdot p_p^{rg} \cdot l_p(n,t) \cdot Q_{ring}(t)$$

with: $D_{Pool}(t) = \sum_{p=1}^{P_m} \sum_{n=1}^{t} N_p^m(n,t) \cdot p_p^{rg} \cdot l_p(n,t)$,

$D_{Pressler}(t) = \sum_{p=1}^{P_m} \sum_{n=1}^{t} N_p^m(n,t) \cdot N_p^{a,a}(n,t) \cdot p_p^{rg} \cdot l_p(n,t)$

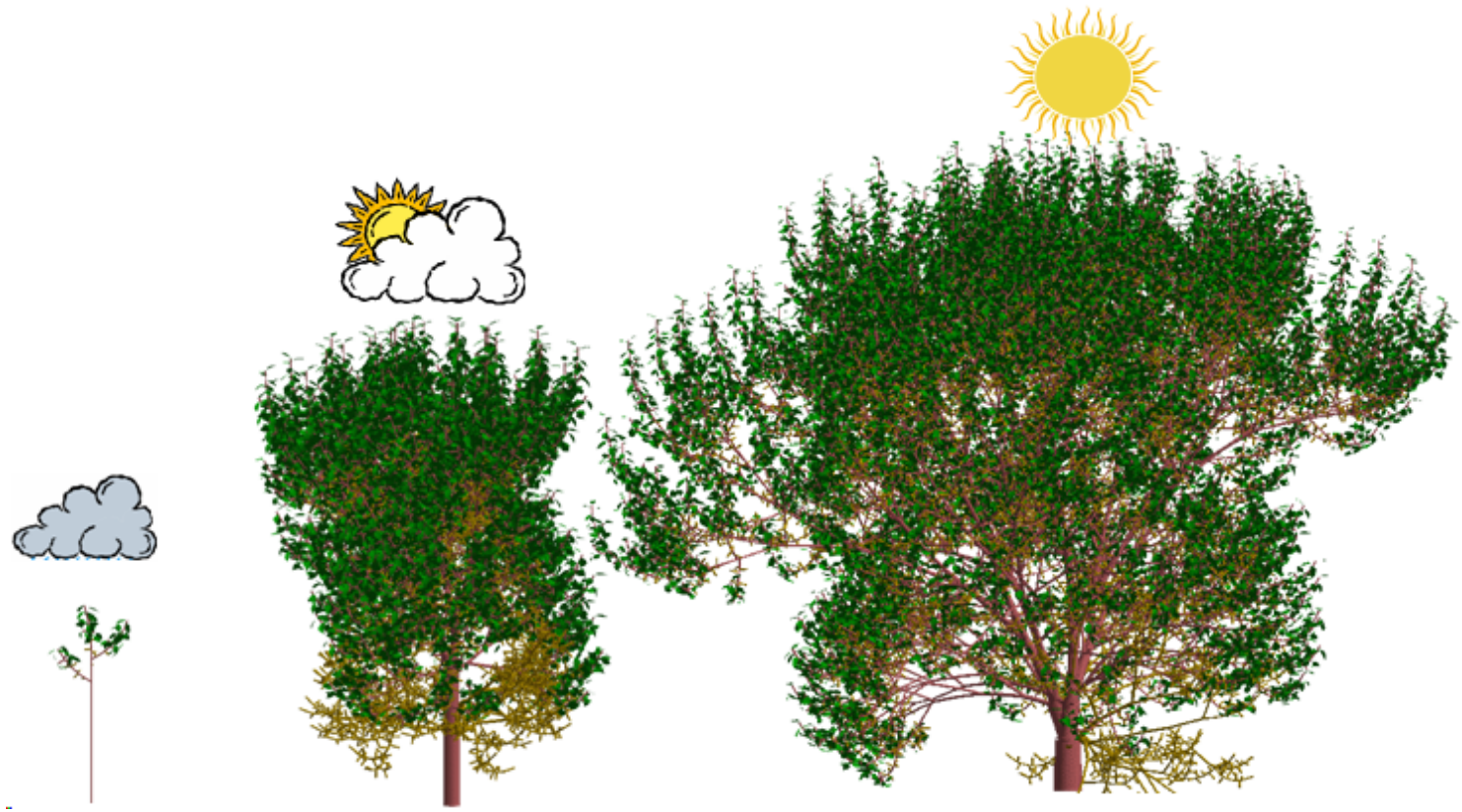


$\lambda \in [0;1]$.

- $N_p^{a,a}(n,t)$: Number of active leaves located above the phytomer of PA p and CA n at GC n.
- p_p^{rg}: linear sink strength of ring growth for phytomers of PA p.
- $N_p^m(n,t)$: number of phytomers of PA p and CA n at GC n.
- $l_p(n,t)$: length of phytomers of PA p and CA n at GC n.

Feedback interaction of physiology on topology

Simulation of plant architectural plasticity in response to environmental or ontogenic changes (GL3) :
$u_{pq} = f_1(\frac{Q}{D})$, $b_{pq} = f_2(\frac{Q}{D})$



[Mathieu, 2006]

Outline

Analytical studies

Dynamic system for biomass production: $Q_t = f(Q_{t-1}, \dots Q_{t-t_a})$
with t_a: functioning duration of leaves.

$$Q(t) = E(t)\mu Sp \left[1 - \exp\left(\frac{-k}{eSp} \cdot \sum_{i=1}^{t_a} \sum_{k=1}^{P_m} N_k^a(t-i+1) P_k^a \cdot \sum_{j=1}^{i} \frac{\phi^a(j) \cdot Q_{t-(i-j)-1}}{D_{t-(i-j)-1}}\right)\right]$$

$N_k^a(t)$: number of PA k leaves appeared at GC t; $P_k^a \cdot \phi^a(j)$: sink strength variation of PA k leaves at CA j; e: SLW

(Case of negligible resistances of internodes)

$\Longrightarrow$ analysis of limit behaviour.

Limit production and architectural models

- Limit production with D independent of Q
- Limit production with D function of Q
  $\Longrightarrow$ Influence of global demand mode for ring growth
- Influence of the value of leaf functioning duration

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Limit production

The production is bounded:$\forall t,\ Q(t) \leq E(t)\mu Sp$

Case D independent of Q

The limit production is solution of : $Q_\infty = A(1 - e^{-B \cdot Q_\infty})$ where $A = E_\infty \cdot \mu \cdot Sp$ depends on the environmental conditions and $B = \frac{k}{eSp} \sum_{i=1}^{t_a} \sum_{j=1}^{i} \phi^a(j) \cdot \sum_{k=1}^{P_m} P_k^a \cdot \left(\frac{N_k^a}{D}\right)_\infty$ depends on the plant topology.

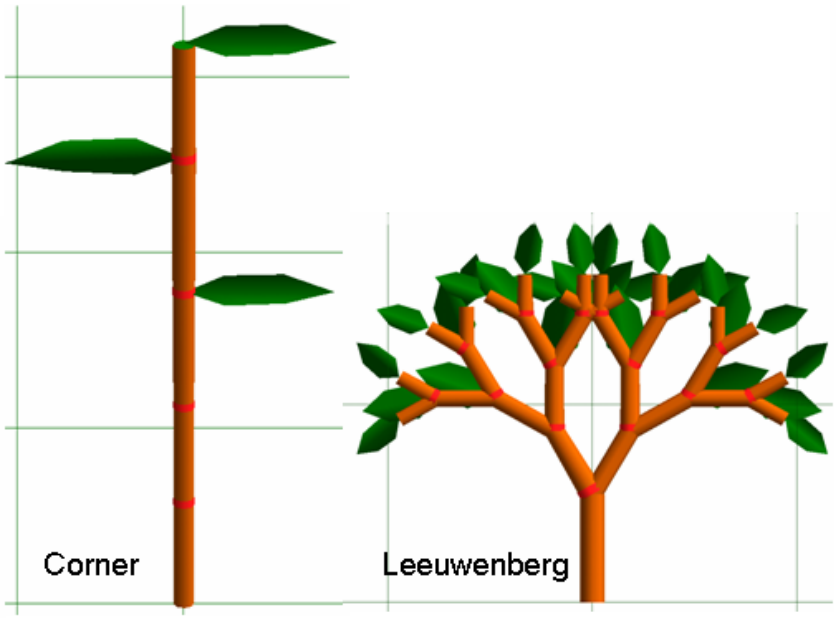
Solution if $AB > 1$: $Q_\infty = A + \frac{1}{B} \cdot W_0\left(-AB \cdot e^{-AB}\right)$ where W_0 is the principal branch of the *Lambert function*

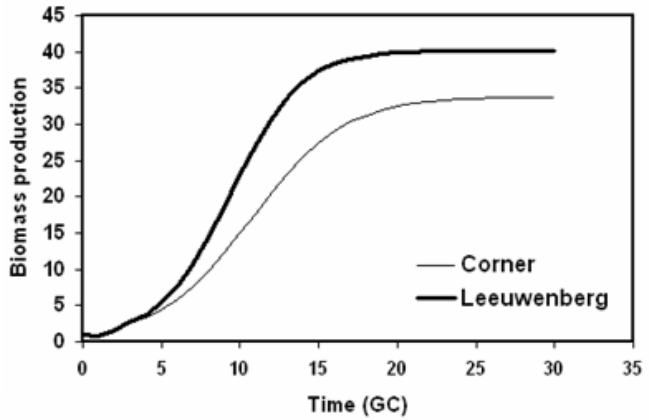
Lambert function = multivalued inverse function of $h(x) = xe^x$.
Approximations of W_0 given by truncations of its Taylor serie:
$\forall |x| < \frac{1}{e},\ W_0(x) = \sum_{n=1}^{\infty} \frac{(-n)^{n-1}}{n!} x^n$.

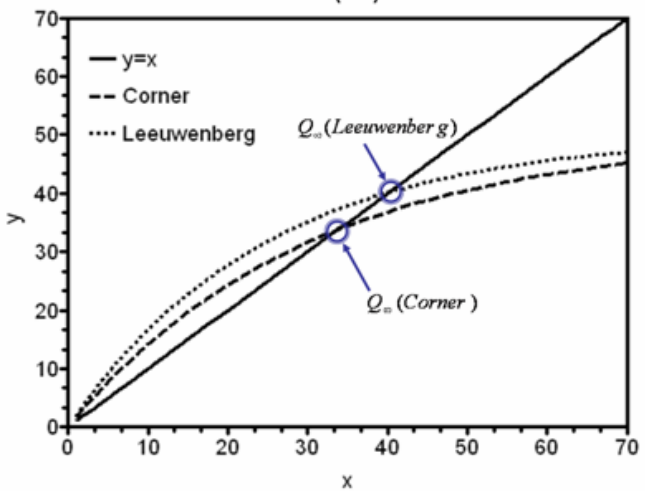
Limit production for Corner and Leeuwenberg models

Values of B indicate the performance of architectural models:

$$B_{Corner} = \frac{k \cdot P^a}{e \cdot Sp} \frac{2}{P^a + P^i} = 0.033,\ B_{Lee} = \frac{kP^a}{e \cdot Sp(P^a + P^i)} \left(\frac{3M^2 + 2M + 1}{M^2 + M + 1} \right) = 0.04$$







Invariances of biomass production

Invariances with topological changes

Is it possible to identify topological parameters from data on biomass ?

Conditions for similar production sequences for plants with different topologies:

- Immediate expansion ($t_{exp} = 1$), $P_m = 1$, no rings (or ring demand proportional to the number of leaves and a constant number of leaves)
- Expansion duration for several cycles ($t_{exp} \geq 1$), $P_m = 1$ and same sink variation shape for all organs, if:
  - Leaf functioning is infinite
  - or Leaf senescence is proportive every branch remains active during exactly t_{exp} growth cycles

$\Longrightarrow$ Possible difficulties to identify.

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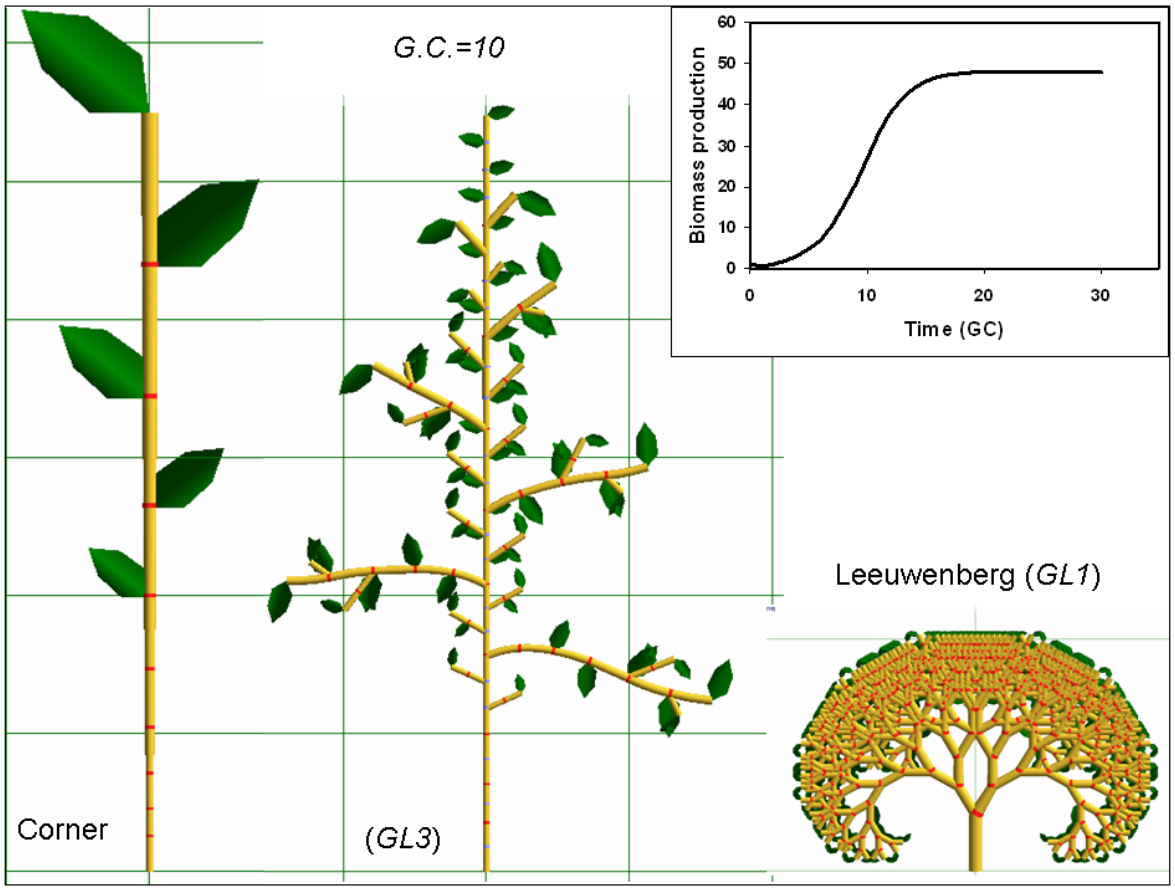

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Invariances with topological changes

Is it possible to identify topological parameters from data on biomass ?

Conditions for similar production sequences for plants with different topologies:

- Immediate expansion ($t_{exp} = 1$), $P_m = 1$, no rings (or ring demand proportional to the number of leaves and a constant number of leaves)
- Expansion duration for several cycles ($t_{exp} \geq 1$), $P_m = 1$ and same sink variation shape for all organs, if:
  - Leaf functioning is infinite
  - or: Leaf senescence is progressive: every unit of leaf biomass remains active during exactly t_a growth cycles.

$\Longrightarrow$ Possible difficulties to identify.

Outline

Procedure

- Objective criteria $Y \in \mathbb{R}^n$ = observed data ; F = model. Estimator $\widehat{U}$ minimizing $J = {}^t(Y - F(U))\Omega(Y - F(U))$ with $\Omega_i = \frac{\sum_{j=1}^{n_i} y_{i,j} - \widehat{y_{i,j}}}{n_i} \cdot \frac{n}{n-p}$
- Generalized Least Squares Algorithm + Heuristic algorithms for discrete optimization: simulated annealing, particle swarm optimization.
- Parameters: $\tilde{Y} = F(P_t, P'_t, P_f, P'_f)$
  - P_t: topological parameters to fit (e.g. GL2 probabilities, GL3 coefficients)
  - P'_t: observed topological parameters (e.g. GL1 number of phytomers per growth units)
  - P_f: functional parameters to fit (e.g. source parameters, sink strengths)
  - P'_f: observed functional parameters (e.g. expansion durations, SLW)

Vector of observation data

Y consists of two kinds of data :

- *Biomass data* = measurements of organ (or compartment) weights and sizes.

- *Topology data* = information on numbers of organs and their hierarchical organization.

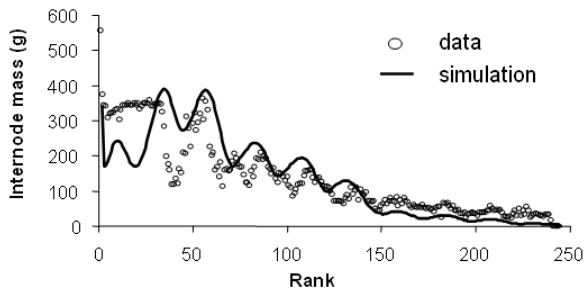
Multi-date fitting (several growth stages for the same individual)
Multi-plant fitting (different individuals sharing the same parameter values).

Applications and experimental protocol

Plants analyzed with **complete** set of data:

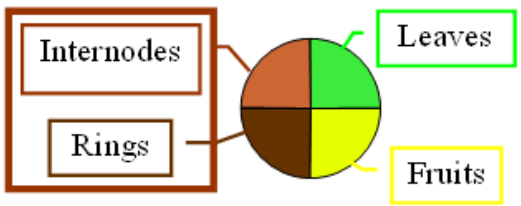
- Young chinese pines [Guo Hong, Hong LingXia, CAF]
- Rice [Zheng BangYou, CAU]
- Cotton trees [Li Dong, CAU]
- Tomato [Zhang BaoGui, CAU]
- *Cecropia sciadophylla* [Patrick Heuret, Camilo Zalamea, AMAP]
  - 6 persons
  - one week
    $\Longrightarrow$ 1050 metamers measured

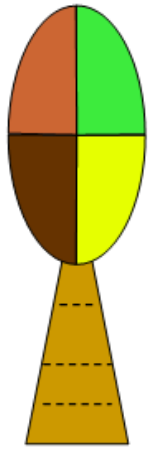
Heavy protocol.

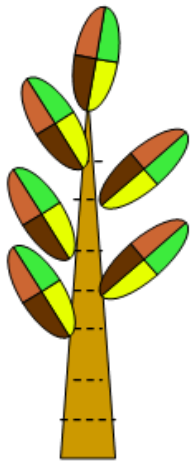


Different levels of data aggregation

Regarding biomass data, 3 levels of data aggregation were considered:







Cumulated Target (B0)

Only compartment weights

'Lollipop' Target (B1)

Trunk at G.U. level

Compartment weights for crown

'Rattle' Target (B2)

Trunk at G.U. level

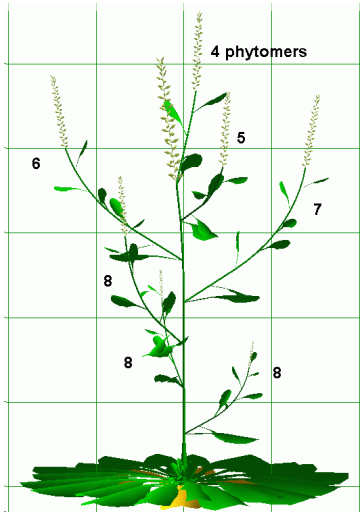
Compartment weights for branches separately

Complete Target (B3)

Metamer level

Different levels of topological description

T2 Topology fully observed: no topological parameters to fit ($dim\ P_t = 0$), GL1: e.g. *Arabidopsis thaliana* [A. Christophe, LEPSE], *pinus tabulaeformis*



Axis	Numbers of phytomers		
	av. observed nb	std dev	simulated nb
Axis 1 (top)	4.1	0.3	4
Axis 2	4.8	1.0	5
Axis 3	6.2	0.4	6
Axis 4	6.5	1.0	7
Axis 5	6.4	1.0	8

T1 Topological data = mean and variance of numbers of organs, topological parameters to fit P_t = GL2 probabilities: Wheat with tillers, Cotton tree [Li Dong, CAU]

T0 No topological data: default botanical rules (P'_t), topological parameters to fit P_t = GL3 coefficients (using biomass data only): Beech tree

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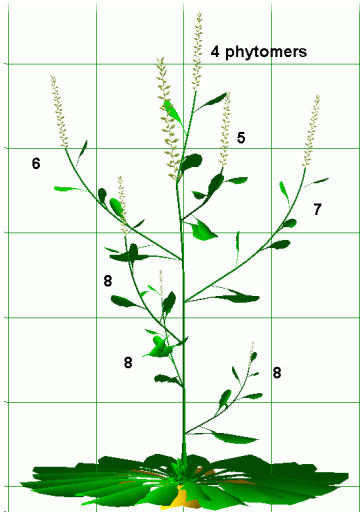

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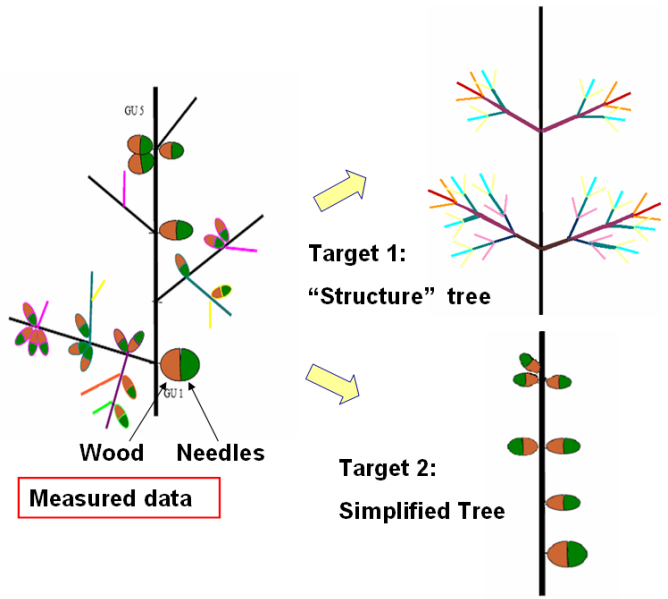
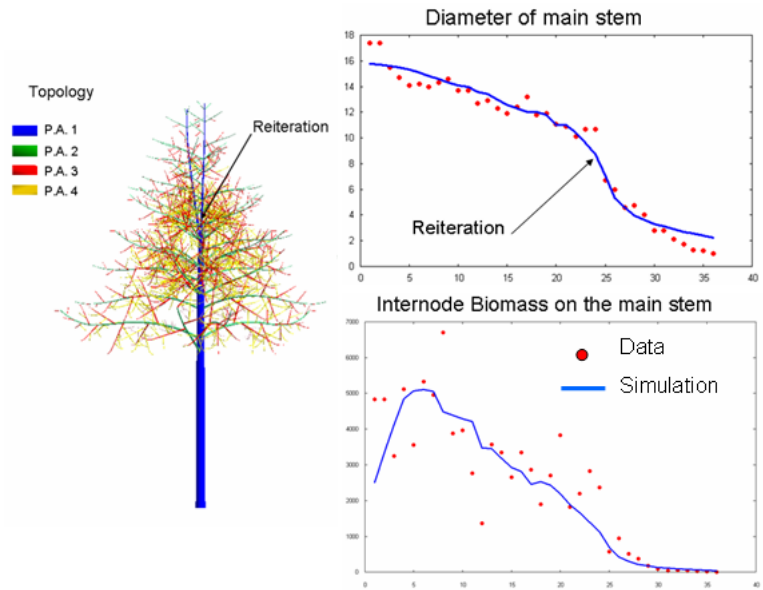
GL1. Targets for adult Chinese pine [Guo Hong, CAF].

Two kinds of target formats:



Fitting results:



Param.	Meaning	Values	
		Complete target	Rattle target
$R_1 = 1/\mu$	Needle resistance	7.4	7.6
P_1^{rg}	Cambial sink (mode Q)	0.037	0.038
λ	Leaf influence	0.57	0.59
	on ring biomass partitioning	young pines: 0.14	

GL2. Parameter identification of stochastic development

Application to wheat with tillers [Data from Wageningen University, Kang MengZhen]

Procedure:

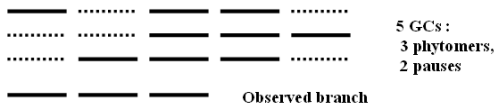
- Topological data: means and variances of numbers of organs $\Longrightarrow$ topological parameters (probabilities of apical growth, branching, apical death, fruit abortion)
  using the expression of theoretical demand expectation:
  $D_{th}(t) = \sum_{o\ organ} \sum_{p=1}^{P_m} \sum_{n=1}^{t} \underbrace{\left(M_{S_1^p(n,n)} - M_{S_1^p(n-1,n-1)}\right)} \cdot P_p^o(t-n+1)$

  $M_{S_n^{1,1}} = \dfrac{p_C\left(1-p_C^n\right)}{1-P_C} \cdot p_A \cdot \mu \cdot p_I$: Expectation of numbers of organs
- Computing the plant production from the theoretical demand expectation.
- Compartment mass at different growth cycles $\Longrightarrow$ parameters of theoretical mean biomass production.

GL2. Parameter identification of stochastic development

- Organ weights for branch tips only (sorted according to their rank) $\Longrightarrow$ parameters of sink variation functions

E.g.: probability of apical growth. Problem = how to relate phytomer ranks to their chronological ages ?
Y_i = stochastic variable of weight of rank i organ,



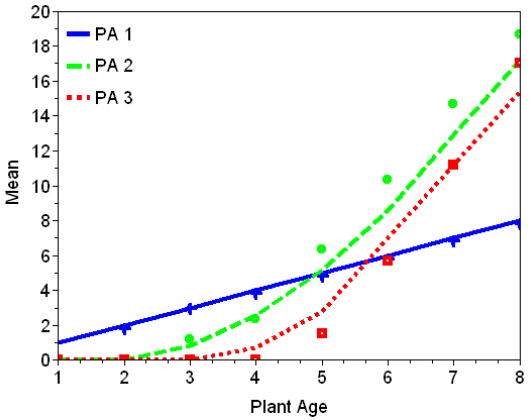
W_k = weights of organs appeared at GC k ($i \leq k \leq t$):

$$E(Y_i) = \sum_{k=i}^{t} C_{k-1}^{i-1} a^i (1-a)^{k-i} \cdot W_k(t)$$

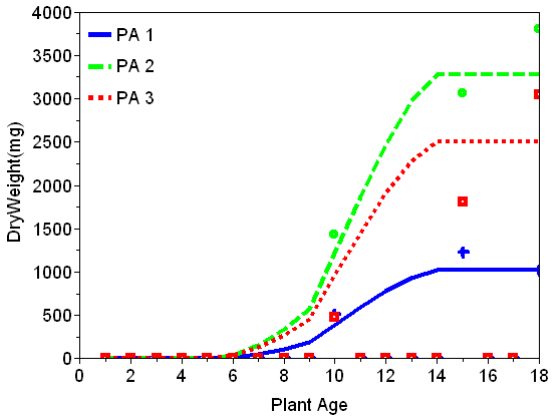
Results :

Parameter	PA 1	PA 2	PA 3
Apical growth proba	1	0.86	0.80
Fruit proba	1	0.81	0.50

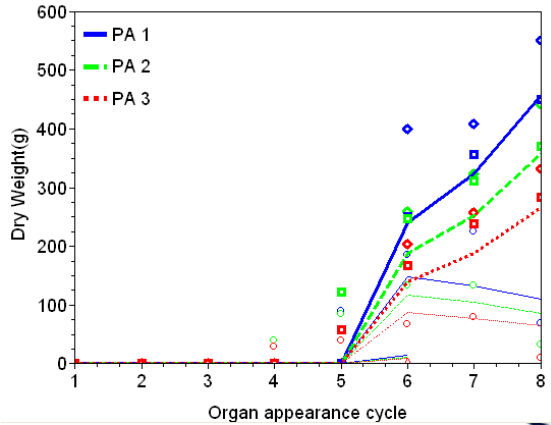
Mean Numbers



Internode compartment



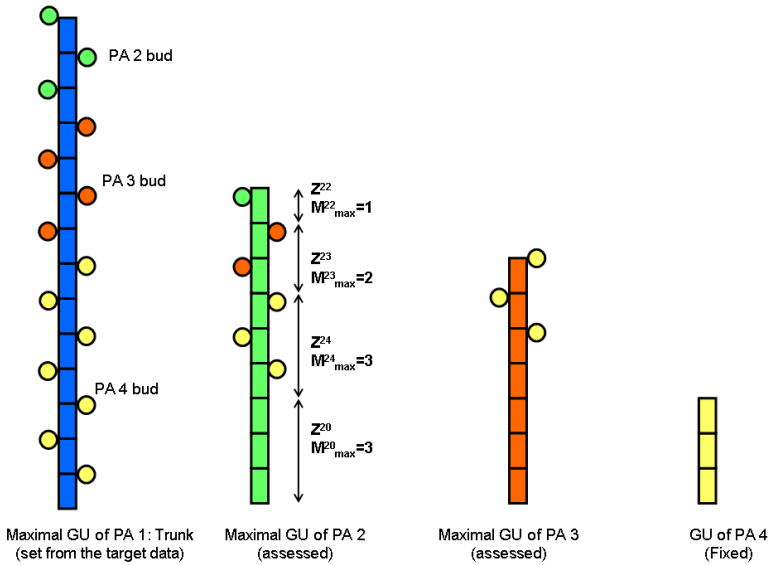
Internodes at branch tips



GL3 topology

Two beech trees (21 and 46 GC) [data from LERFoB, Thiéry Constant]

- Default topology from botanical analysis :



- Fitting of GL3 development parameters:
  Total number of new axes $a_{pq}(t)$ appearing on zones Z_{pq} instead of numbers of axes per growth unit:
  $a_{pq}(t) = \left[N_{pq}(t) \cdot \left(A^1_{pq} + A^2_{pq} \cdot \frac{Q}{D}(t)\right)\right]$

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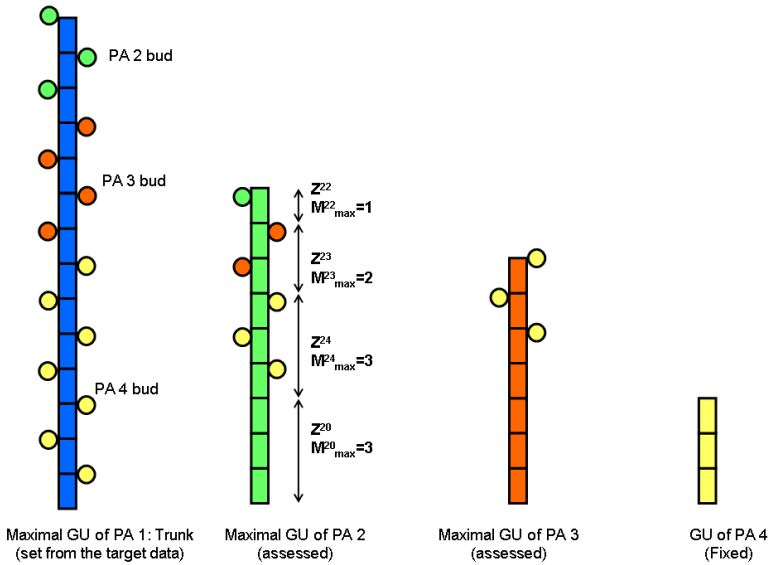

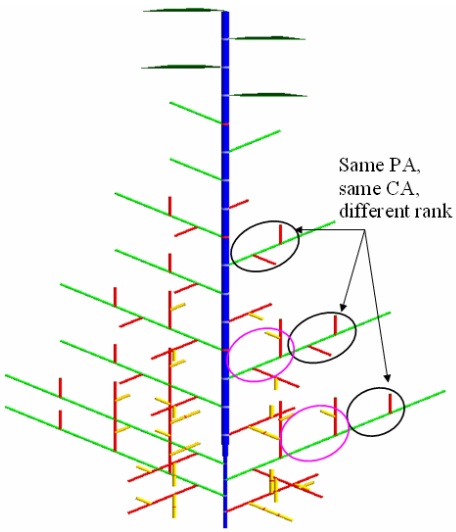

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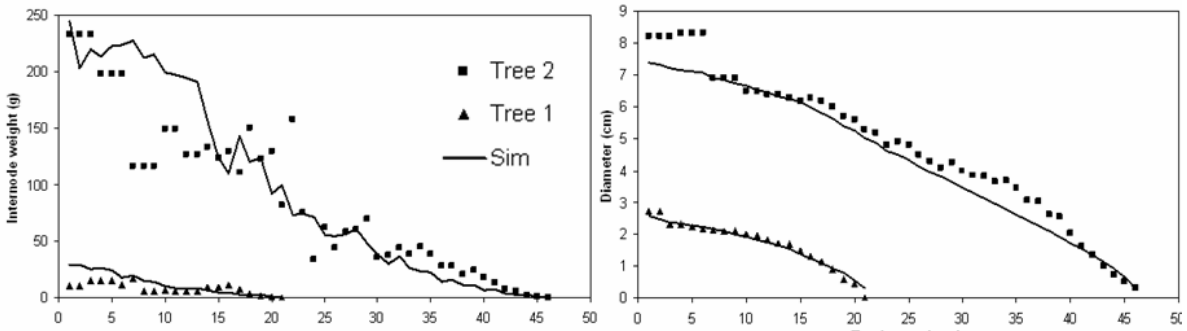
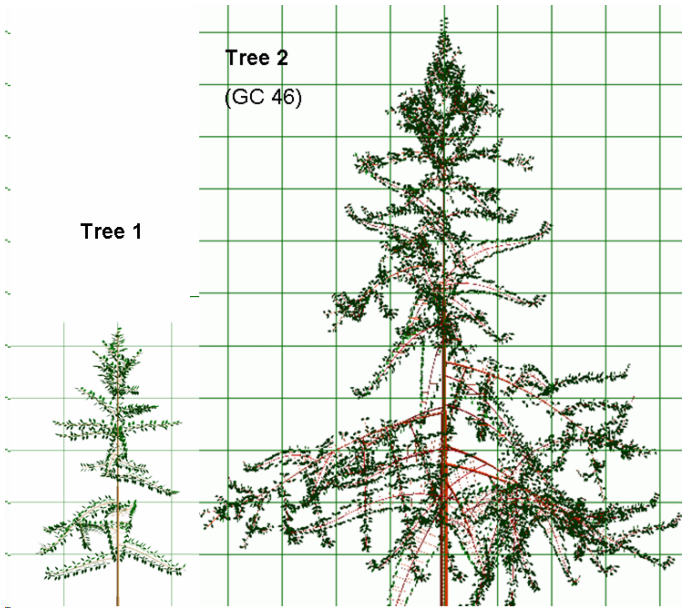
GL3 topology

Fitting results: trunk

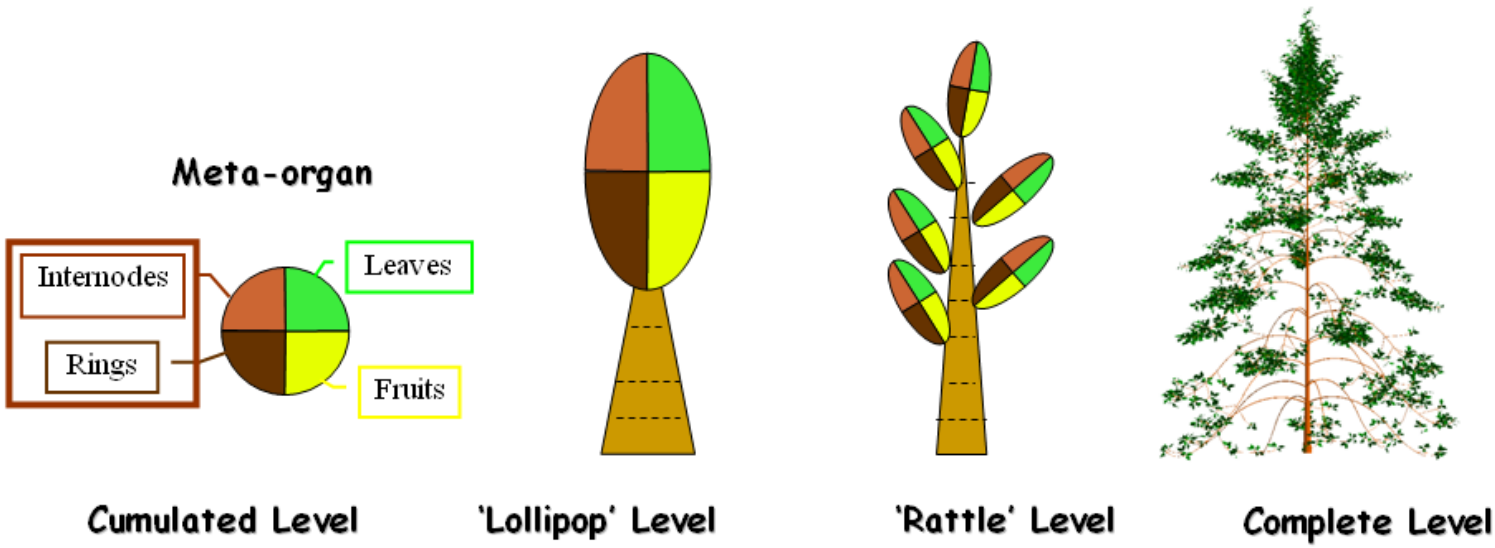




Problem: several solutions, parameter significance.

Model aggregation

Meta-organ : $\omega : \widetilde{S}_t \longrightarrow \Omega_t$



Conservation of key-variables

- Total biomass production of the plant at every growth cycle
- Allocation to biomass compartments
- Trunk description

Conservation of key-variables

- Expansion is immediate for all organs ($t_{exp} = 1$)
- Leaf functioning time is one growth cycle ($t_a = 1$)
- SBM (specific blade mass) does not depend on leaf position in trees

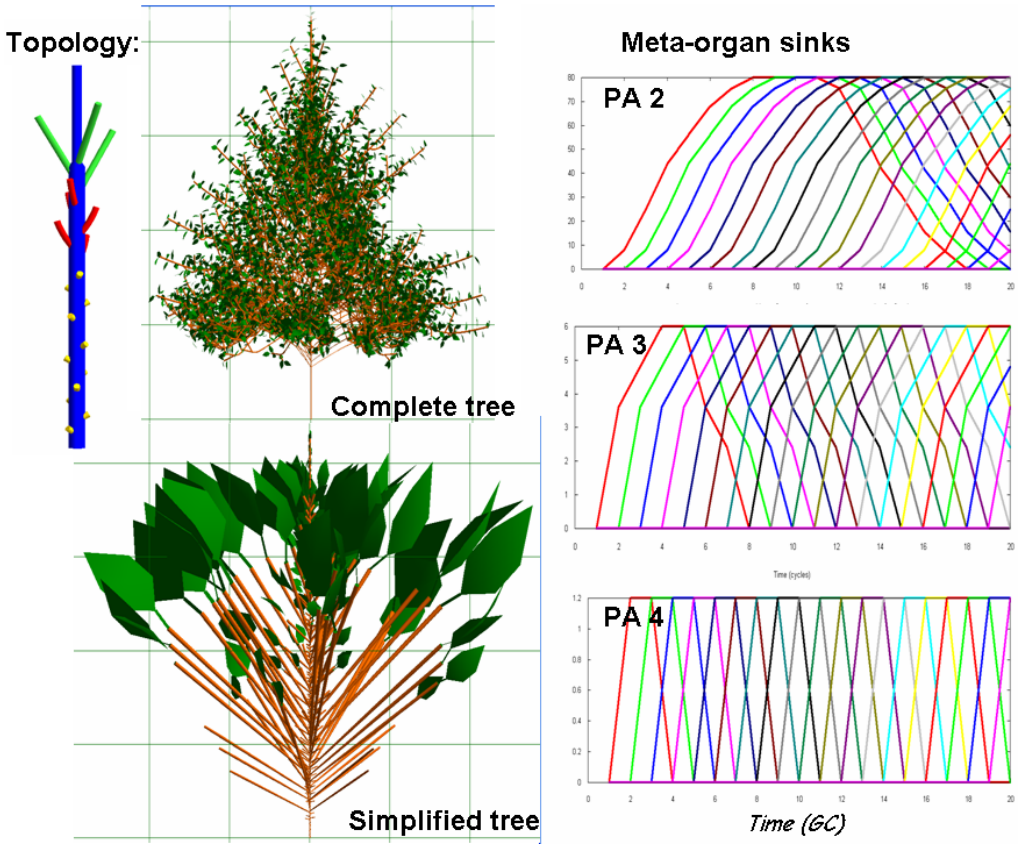
$\omega = \omega(S_p(n,t))$:
Conservation of biomass production:

S_ω = meta-organ blade surface ($= \sum_{i \in S_p(n,t)} S_i(t)$).

$$Q(t) = E(t) \cdot \mu \cdot Sp \cdot \left(1 - e^{-k \cdot \frac{S_\omega(t)}{Sp}} \right) \Longrightarrow \text{same equation.}$$

Biomass allocation

Rattle level:



Meta-organ sinks for primary growth:

$$\begin{cases} P^i_\omega = \sum_{k=p}^{P_m} [\psi'^i(S_p(n,t))][k] \cdot P^i_k \\ P^a_\omega = \sum_{k=p}^{P_m} [\psi'^a(S_p(n,t))][k] \cdot P^a_k \end{cases}$$

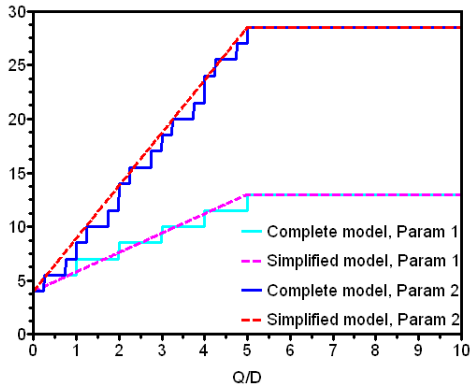
From compartment data:
$\forall n \in \{1..d\},\ \forall k \in \{1..P_m\},$

$$\begin{cases} P^i_\omega(S_k(n,d)) = \dfrac{W^i_k(n,d)}{W^a_k(0,d)} \\ P^a_\omega(S_k(n,d)) = \dfrac{W^a_k(n,d)}{W^a_k(0,d)} \end{cases}$$

Biomass allocation

- Same method for allocation to ring compartment but more complex expressions.
- GL3 buds:

$$\begin{cases} B^1_{p,\omega} & = \sum_{k=p}^{P_m} \sum_{q=k}^{P_m} \psi_\omega[p][q] \cdot P^{pb}_q \cdot \min\{b^{pb}_{pq}(t),\ \lfloor B^1_{pq} \rfloor\} \\ B^2_{p,\omega} & = \dfrac{\sum_{k=p}^{P_m} \sum_{q=k}^{P_m} \psi_\omega[p][q] \cdot P^{pb}_q \cdot \left(b^{pb}_{pq}(t) - \lfloor B^1_{pq} \rfloor\right)^+}{\max_{p,\ q} \left\{ \dfrac{b^{pb}_{pq}(t) - B^1_{pq}}{B^2_{pq}} \right\}} \end{cases}$$



$\Longrightarrow$ perspectives for simplified models:

- GL1 potential topology and meta-organ default primary sinks
- active meta-organ sink: $P_\omega = P_{\omega,GL1} \cdot (B^1_p \cdot q^b_\omega(t-1) + B^2_p \cdot \frac{Q}{D}(t))$
- allocation to meta-organ ring compartment: similar equation.

$\Longrightarrow$ No equivalences but consistent with the GreenLab approach.

Outline

Discussion

- Influence of topology in the model: preliminary analysis. *Further work= a more systematic study, effect of hydraulic resistances to consider for old trees.*
- Different levels of data aggregation for biomass and for topology $\Longrightarrow$ start of plant typology.
- Different approaches have been defined to handle plant topology: choice of default rules, fitting the GL2 or GL3 parameters. *Further work = detailed statistical analysis on the consequences of data aggregation, in particular significance of parameters.*
- Introduction of variable aggregation and proposals for simplified models. *Further work = to test these approaches on simulated and real data.*

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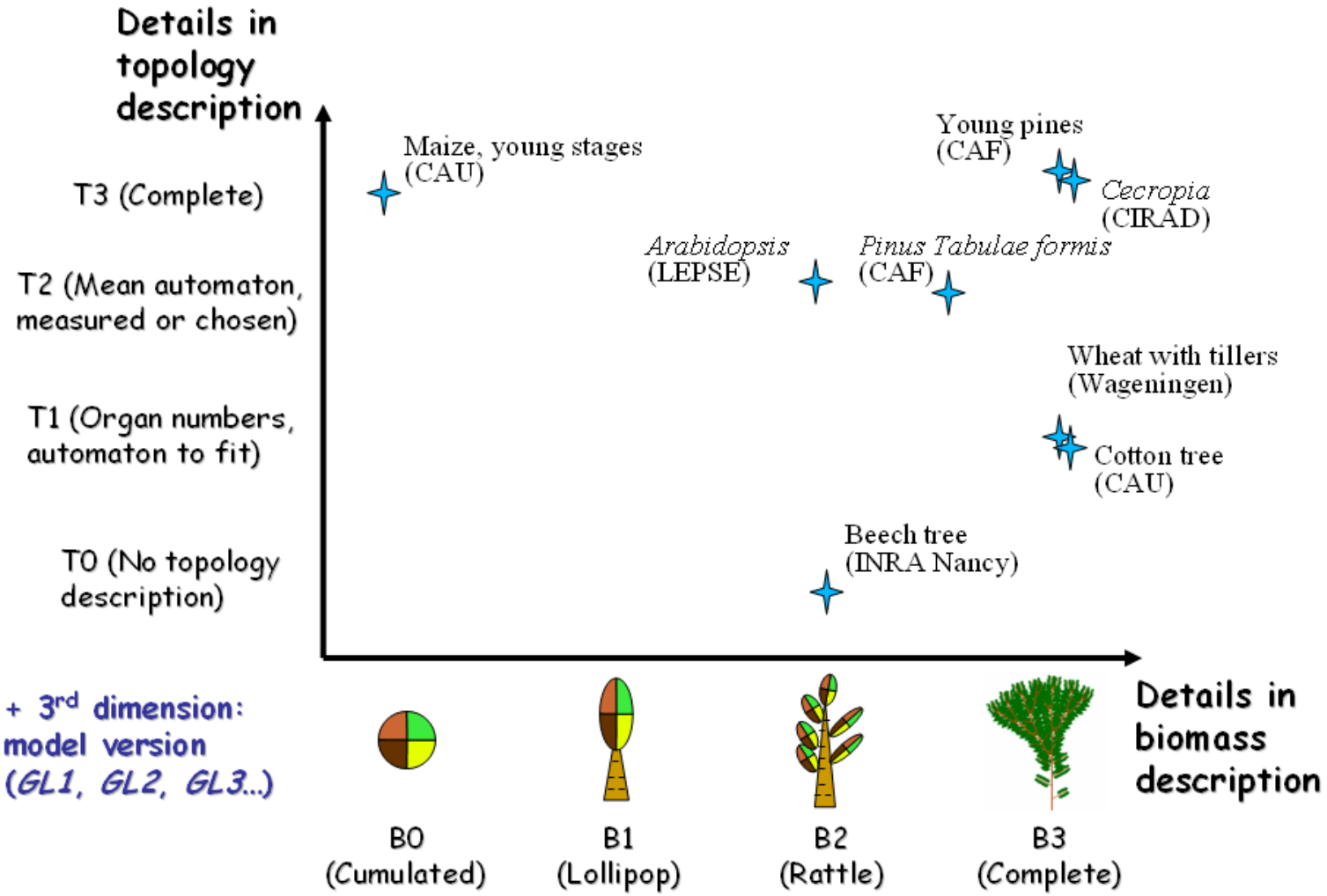

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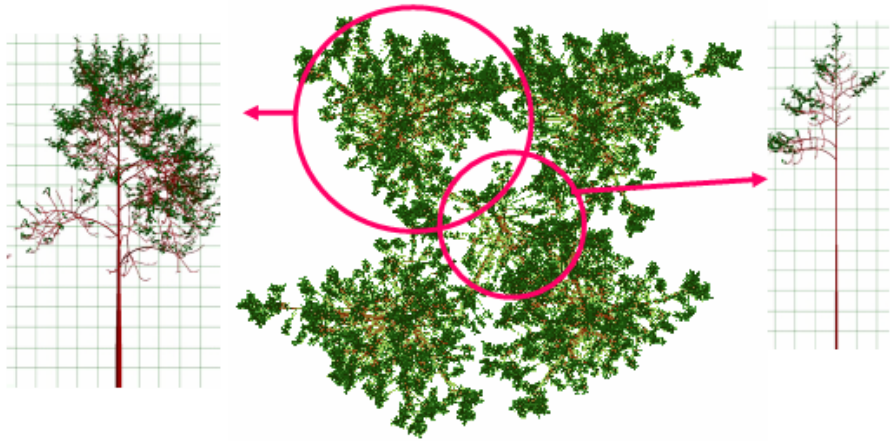
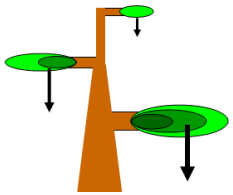
Perspectives: fields of applications

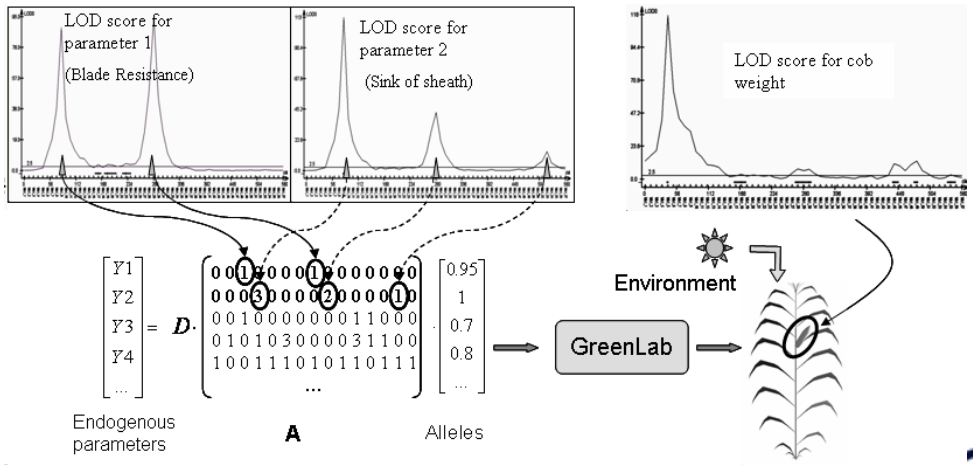
- Stand simulation, functional lanscape



- Biomechanics



- QTL detection



Merci de votre attention !

Thanks for your attention !

谢谢！