Simulation of ecophysiological processes using crop and FSP models

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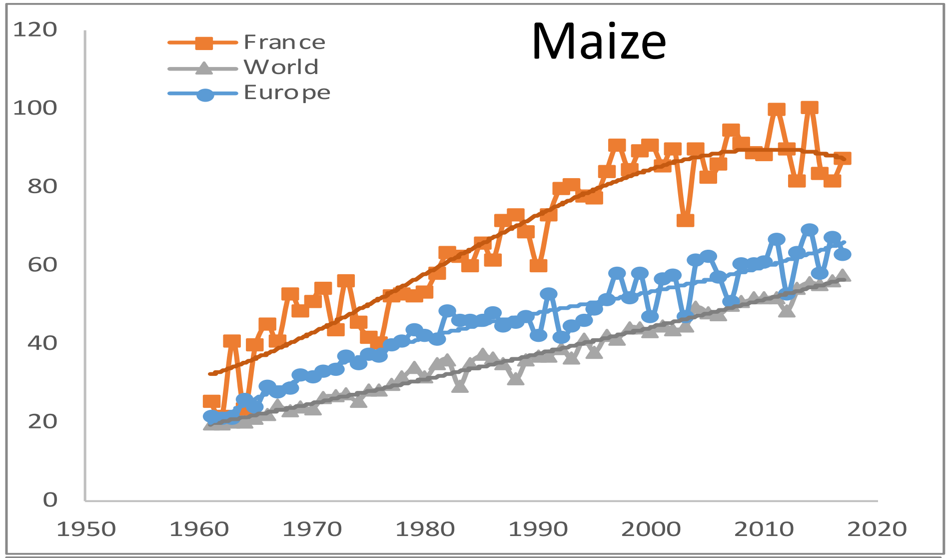
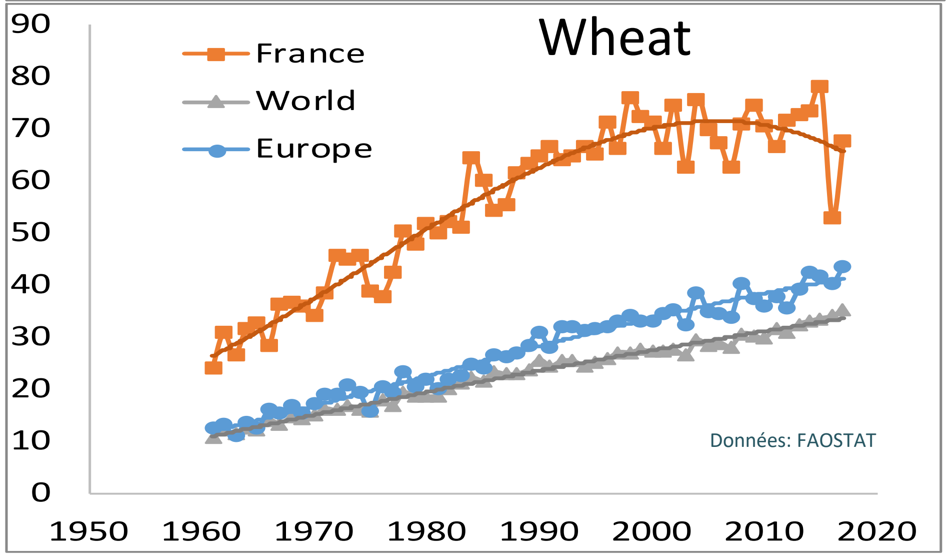
Variation in yield over years

Yield stagnancy but …

Are we far away for the potential yields?

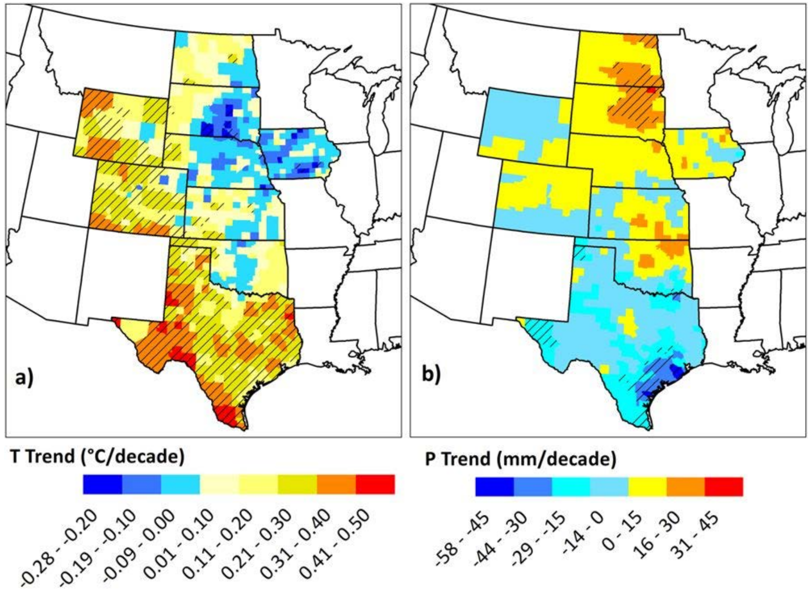


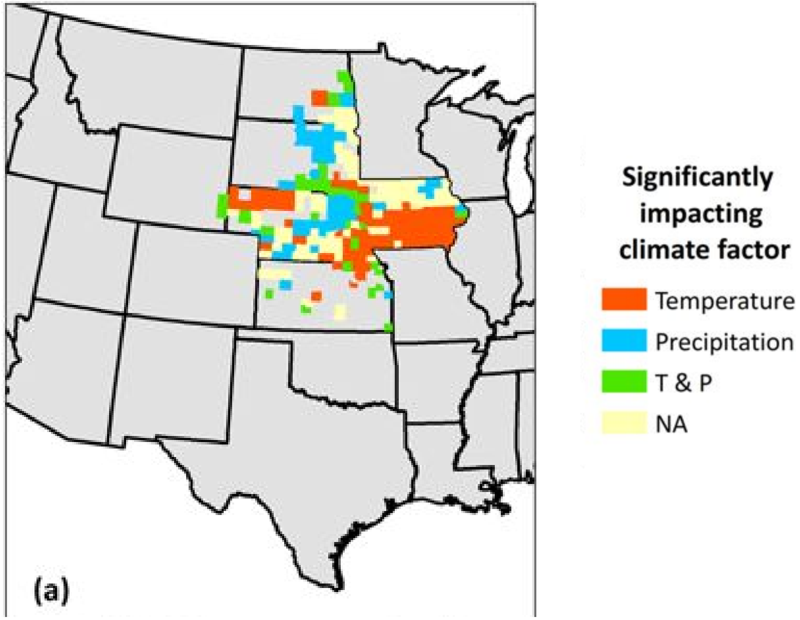


Impacts of climate change on crop productivity

Large spatial variability in climate change characteristics

… with polymorphic effets





From Kukal and Imark, 2018

Impacts of climate change on crop productivity

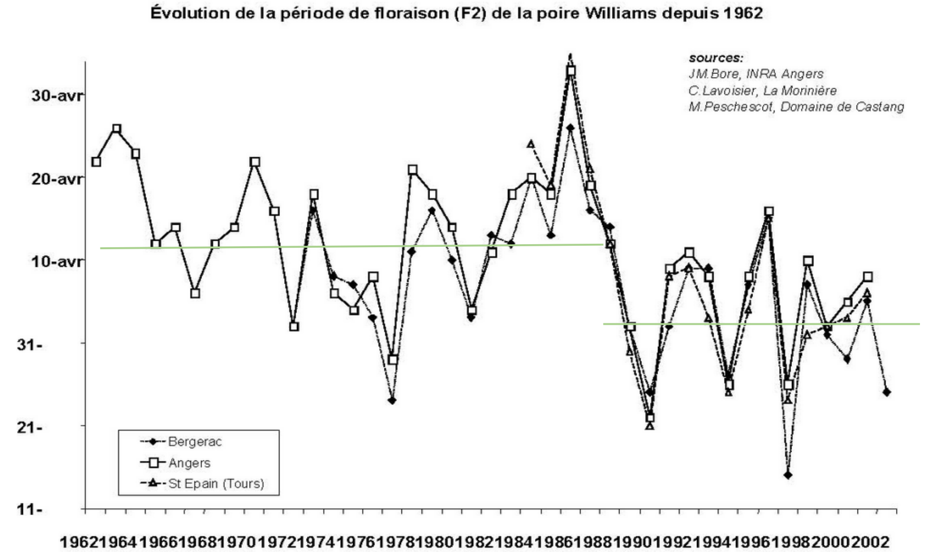
A wide range of negative effects

Decrease in net carbon assimilation

Effect on plant development

Modification of organoleptic properties of harvested organs

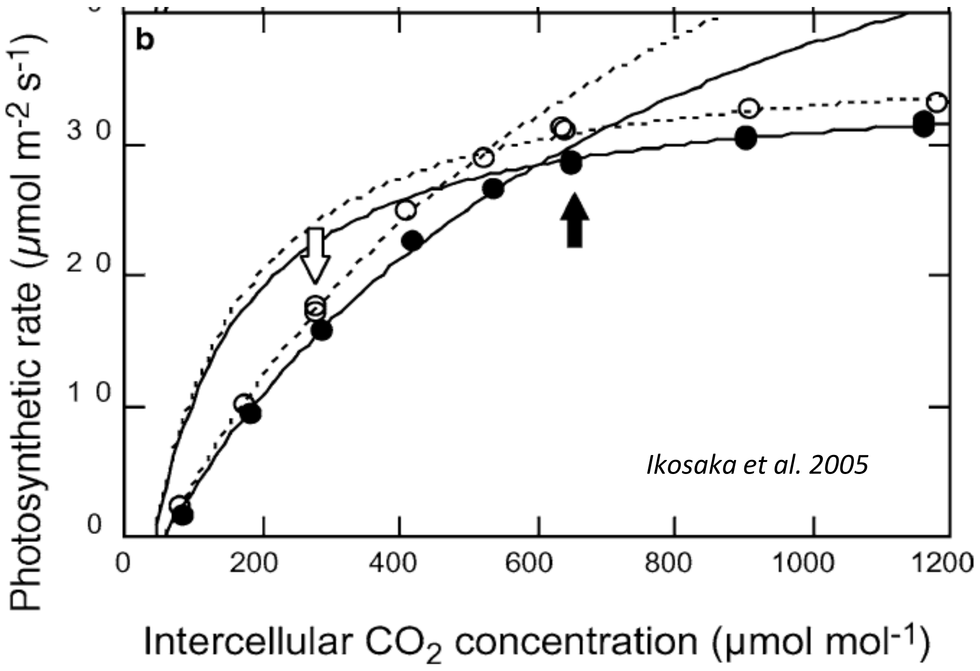
Risk fro the system perenity



Impacts of climate change on crop productivity

A wide range of negative effects

… but with some possible positive effects



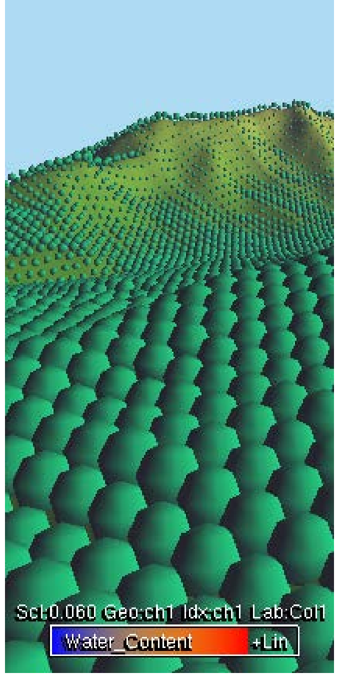
How models can help analyzing the complexity of this system?

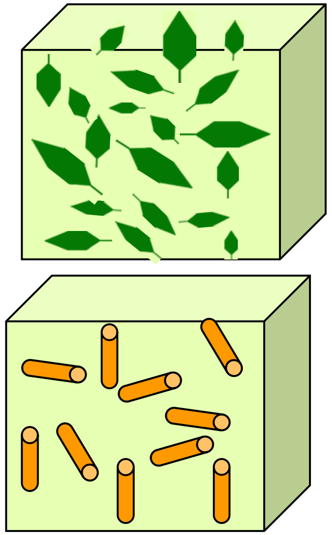
Crop model vs FSPM: a matter of plant representation

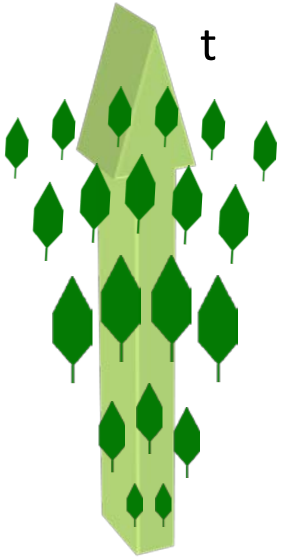
FSPM

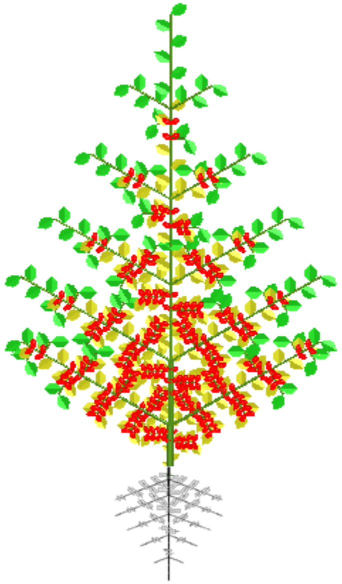
Crop models

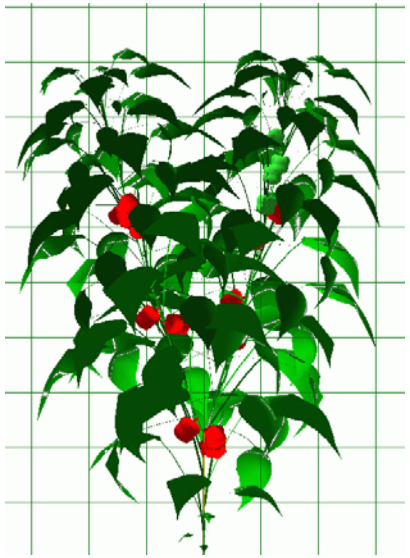
Field | Whole plant | Compartment | Organs | Topology | 3D geometry | Cells, Genes

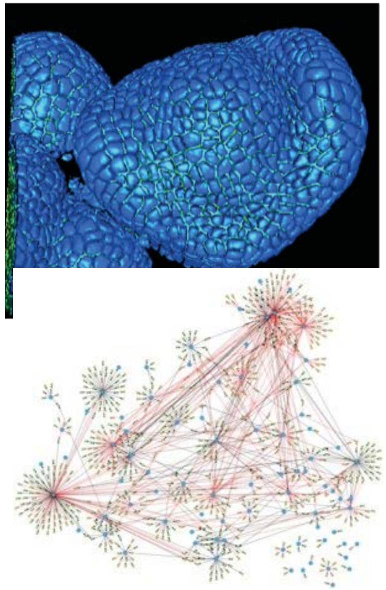












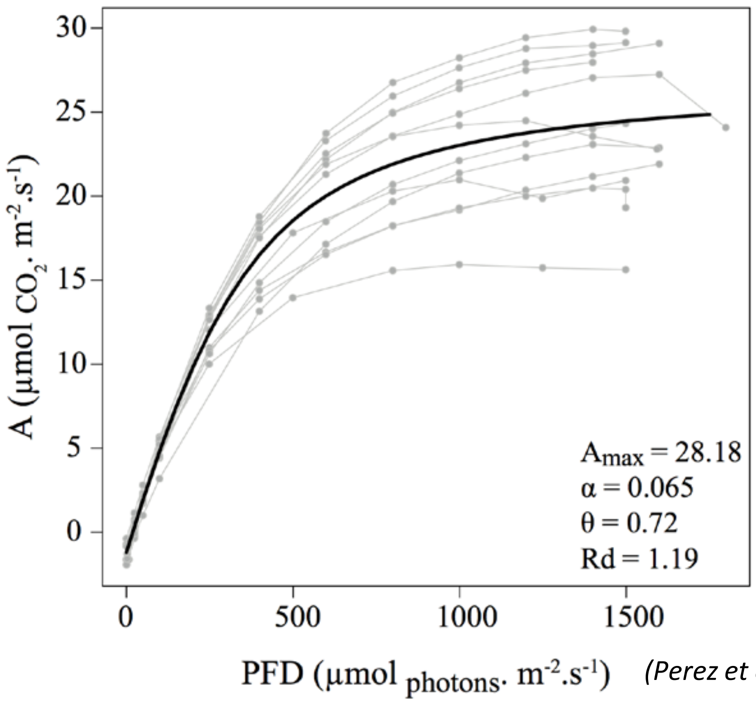
… to simulate quite similar plant/crop functions

Biophysical bases of biomass production

Introduction to crop and functional structural plant models

Introduction – photosynthesis/light

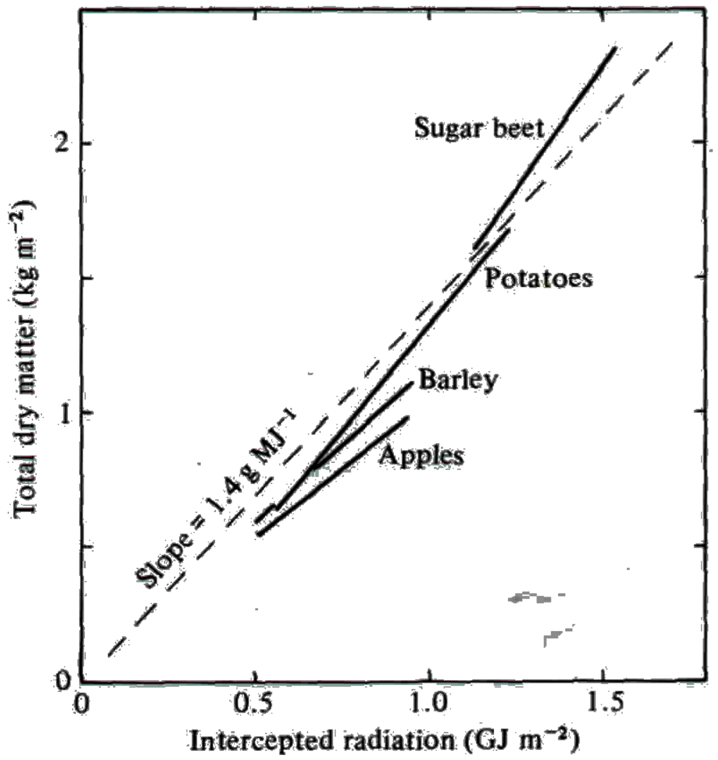
Close relationship between photosynthesis and intercepted light.



(Perez et al. 2018)

At the leaf scale, a radiation « thershold » for maximizing photosynthesis exists.

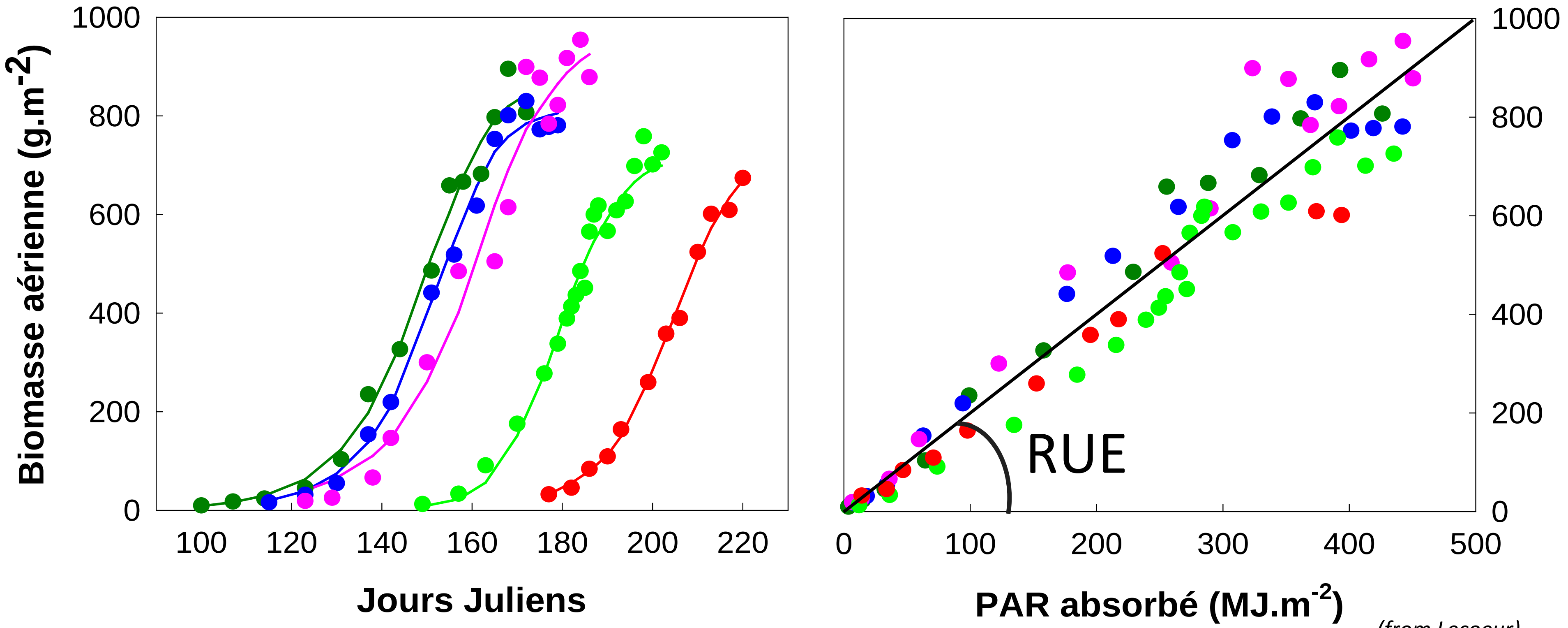
When integrated at the crop scale over long period a linear relation appears



(from Monteith, 1977)

Introduction – intercepted radiation

Intercepted radiation is the meteorological variable explaining variations in biomass production (*under non limiting conditions*)



(from Lecoeur)

The Monteith formalism

A framework to represent the different « efficiencies » involved in biomass production

$$\Delta DM_i = RUEi \times PAR_i$$

$$PAR_{int\,i} = RIEi \times c \times Rs_i$$

$$DM = \sum_{0}^{harvest} RUE_i \times RIE_i \times c \times Rsi$$

ΔDM: daily dry matter production (g)
PAR: incoming photosynthetically active radiation (MJ)
RUE: radiation use efficiency (g MJ^{-1})

PAR_{int}: intercepted PAR (MJ)
RIE: radiation use efficiency
c: climatic efficiency

DM: dry matter produced during the crop cycle
Rs: incoming solar radiation (MJ)

Monteith et al., 1977

The objectives of models dealing with production are to estimate the values of these efficiencies

Different scales are considered when working with crop or FSP models.

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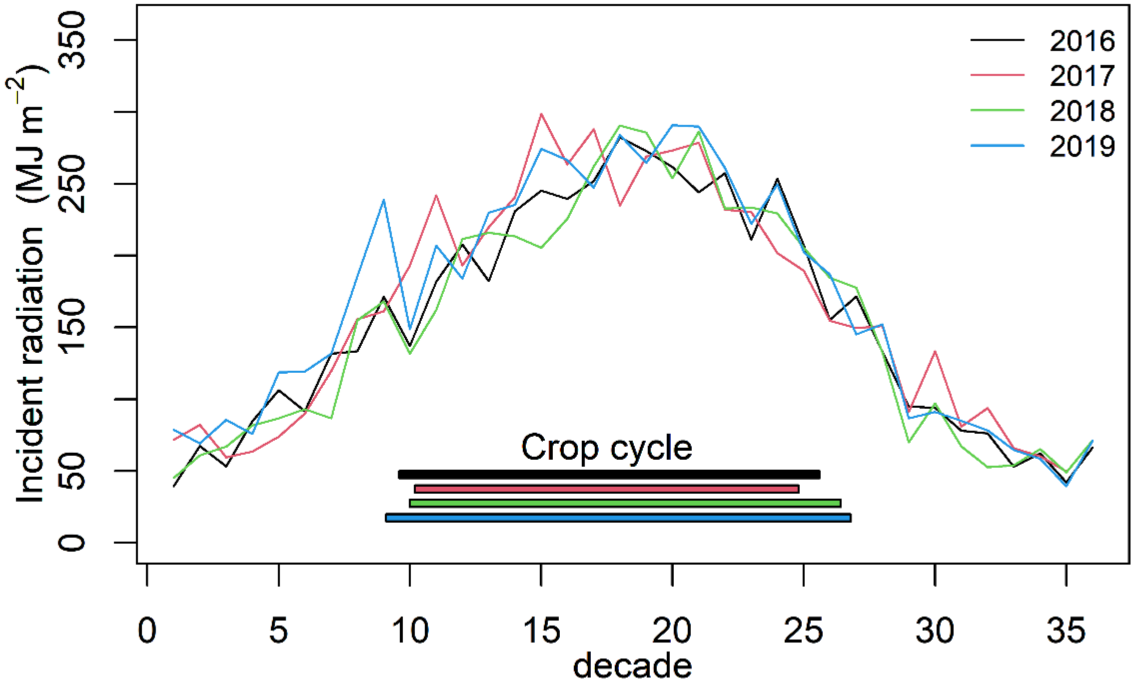
Crop cycle and intercepted light

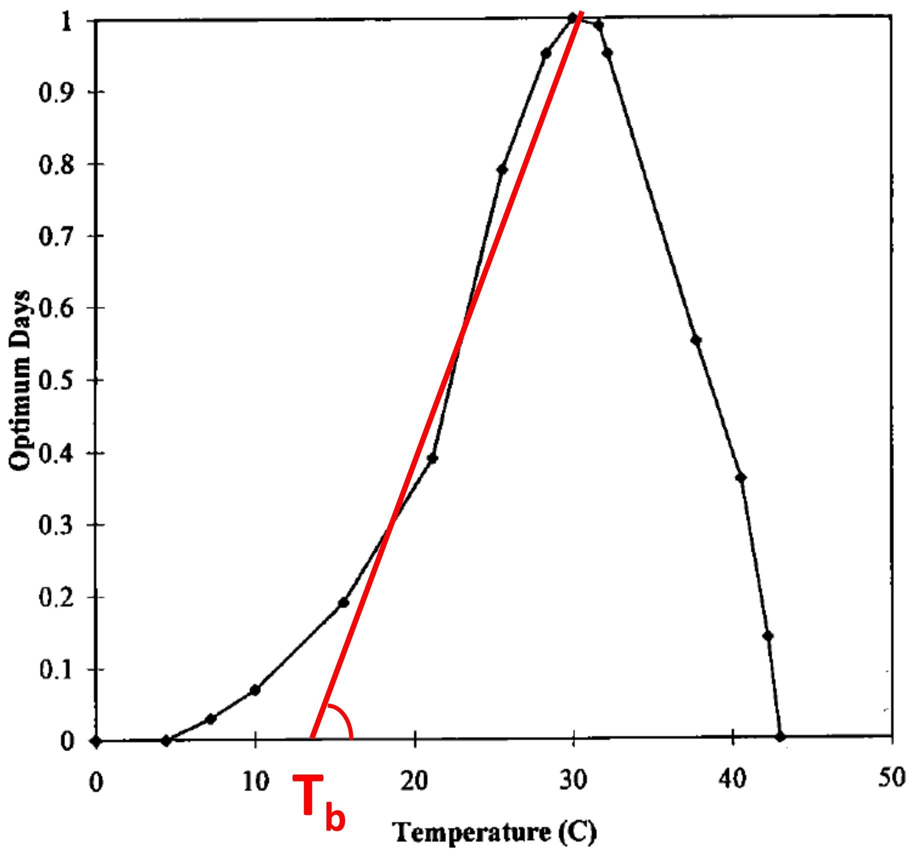


The amount of intercepted light depends on:

- Daily incoming light
- On the plant phenology (duration and positionning of the crop cycle)

Development, phenology and temperature

Old knowledge on the effect of temperature on plant development (Lehenbauer, 1914)



Simplification of this relationship in many models:

- Linear relationship over a wide range of temperatures (constant rate depending on temperature)
- Determination of a base temperature roughly constant in each species (T_b)

Thermal time

Main covariable used to simulate phenological stages and plant development

$$TT_i = \sum_{j=0}^{i} T_{eff,j}$$

With:

$$T_{eff,j} = Tm_{,j} - Tb \text{ if } Tm_{,j} > Tb$$

$$T_{eff,j} = 0 \text{ else}$$

Day	T_m (°C)	T_{eff} (°C)	TT (°Cd)
1	15	5	5
2	3	0	5
3	21	11	16
4	12	2	18

TT: thermal time (°Cd)
T_{eff}: effective temperature (°C)
T_b : base temperature (°C)

Application of thermal time to predict phenology

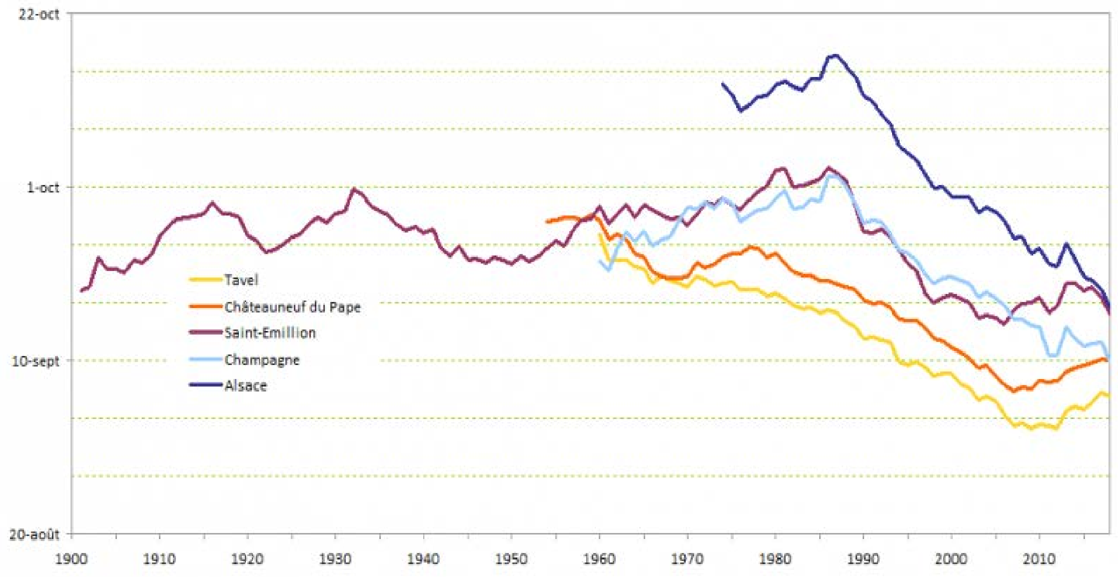
Despite its limitation thermal time is used in many modeling approaches

Estimation of thermal time to reach « véraison » grapevine

Cultivar	Jan 1st			Apr 1st		
	T_b (°C)			T_b (°C)		
	0	10		0	10	
Cabernet Sauvignon	2650	962		2239	950	
Merlot	2712	997		2310	983	
Chardonnay	2637	952		2225	938	
Riesling	2698	975		2295	966	

Zapata et al. 2015

Grapevine harvest date



Source: inter Rhône

Monteith formalism and thermal time

$$TT_i = \sum_{j=0}^{i} T_{eff,\,j}$$

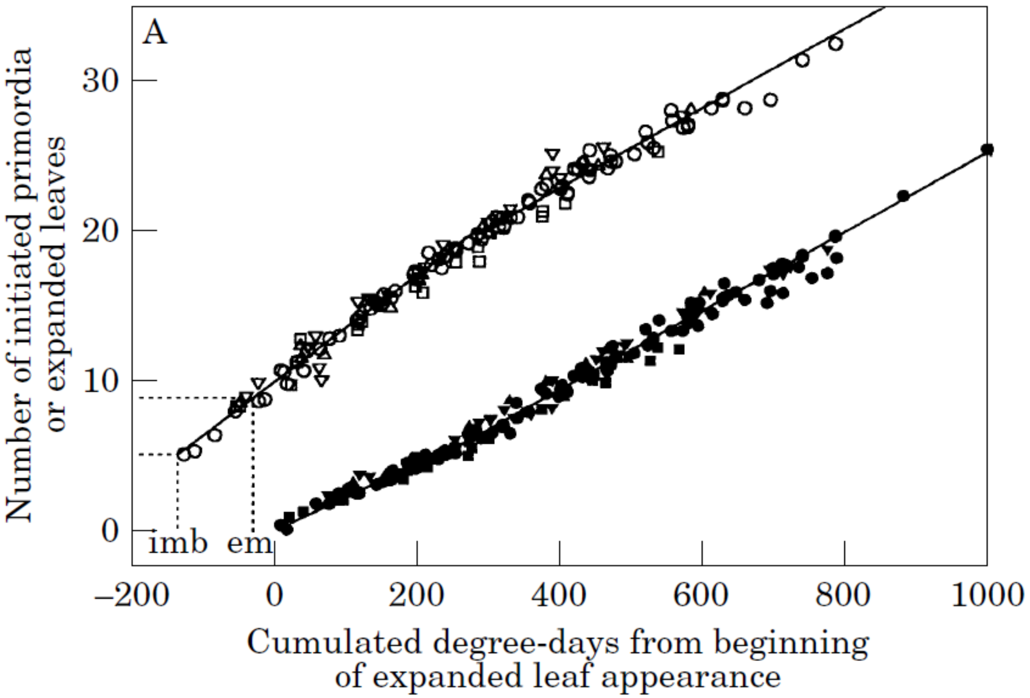
$$DM = \sum_{0}^{harvest} RUE_i \boxed{\times RIE_i \times} c \times Rsi$$

Thermal time is used to simulate developmental and growth processes involved in leaf area development

In both crop and FSPM models.

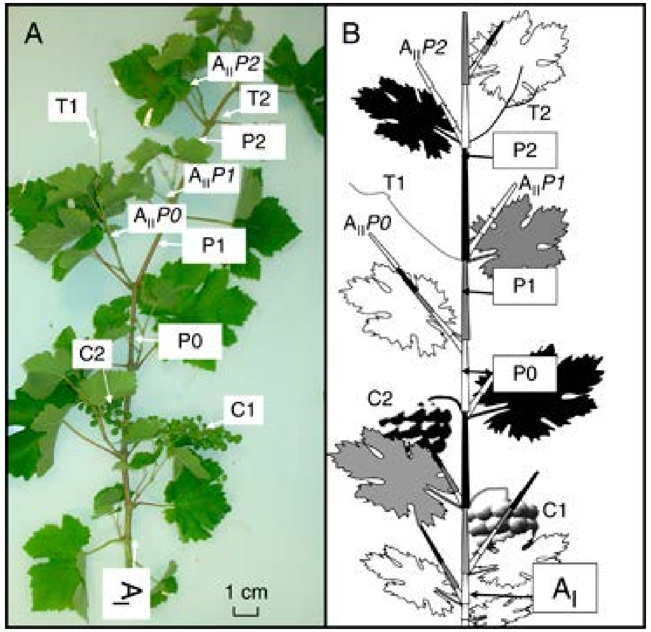
Plant development and meristem activity modeling

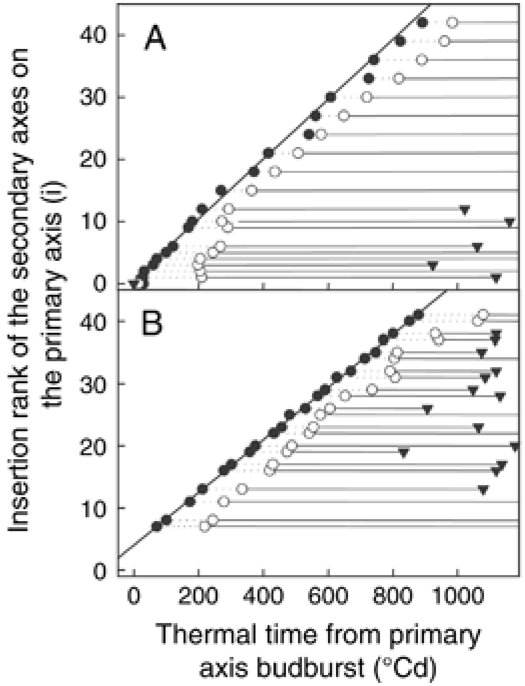
Single stem species (pea)



Turc and Lecoeur, 1997 on pea

Branched plant (grapevine)

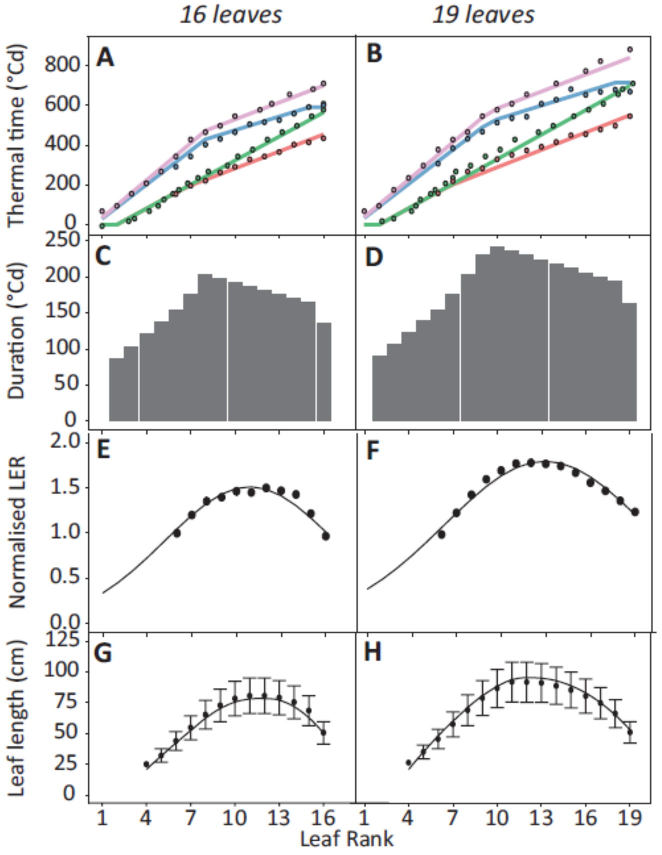




Pallas et al. 2008

Simulation of leaf area establishment

Developmental and growth model
at the leaf scale



Lacube et al. 2000

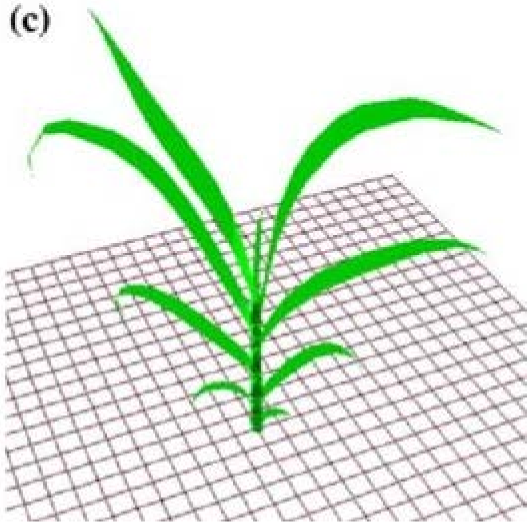
Pseudo 'L-SYSTEM'

```
StartEach:
Teff=compute_Teff(Tmean)

Meristem(t,rank):
 if t>d_leaf_init:
   LER=compute_LER(rank)
   d = compute_duration(rank)
   produce Leaf(0,0,LER,dur)Meristem(Teff,rank+1)
 else:
   produce Meristem(d+Teff, rank)

Leaf(t, area, LER, duration):
 if t<duration:
   t += Teff
   area += LER x Teff
   produce Leaf(t, area, LER, duration)
```

Interpretation:

…

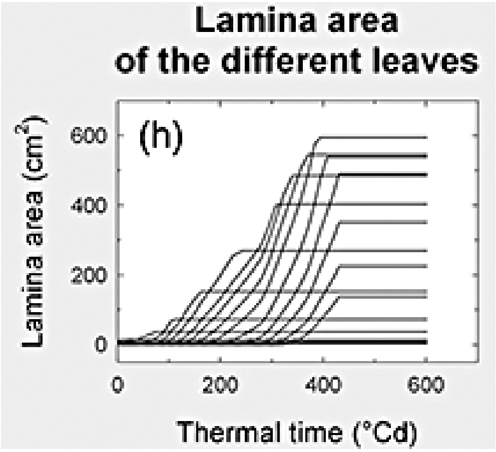
FSPM 3D simulation of leaf development and growth of Maize



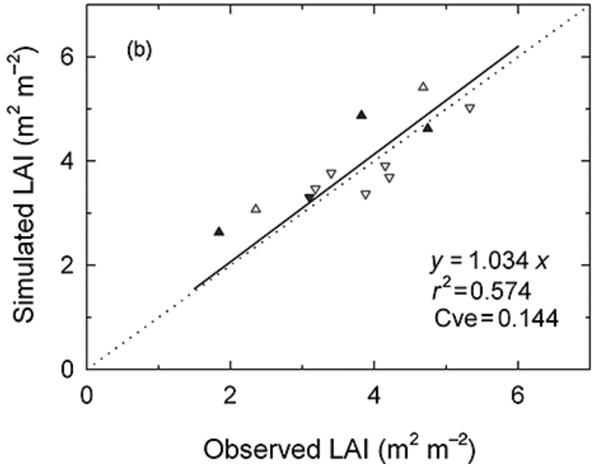
Casa et al. 2020,
From Fournier et al. 1999

Simulation of leaf area establishment – crop model

Developmental models are often included in crop model for predicting leaf area development



Integration at crop scale



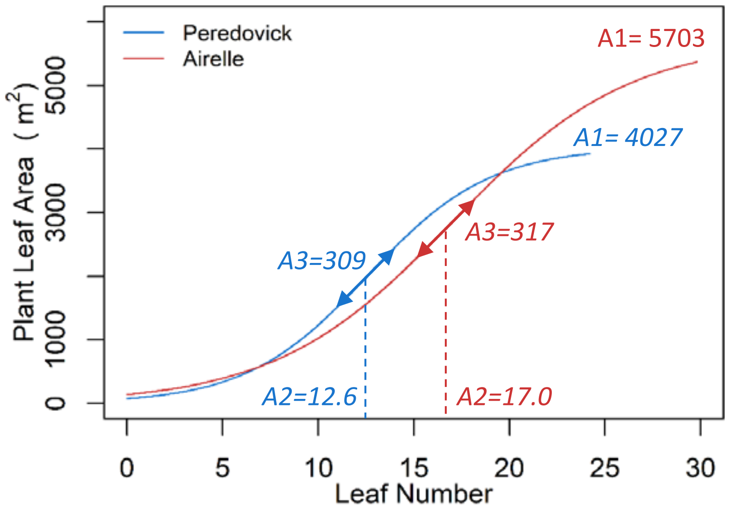
From Chenu et al. 2008, APSIM model

… but more « empirical » formalisms without any representation of individual leaf area exist.

Ex : Sunflo model

$$LA(Ln) = \frac{A_1}{(1 + \exp(\frac{4A_3 \times (A_2 - Ln)}{A_1}))}$$

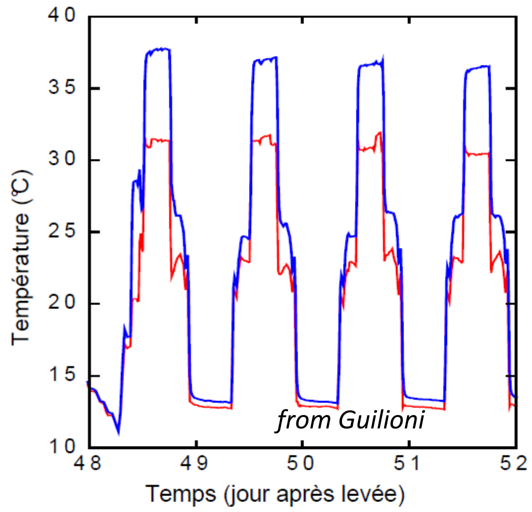
LA: plant leaf area, L_n: leaf number, A1: final leaf area
A2: insertion rank of the biggest leaf, A3: maximal individual leaf area



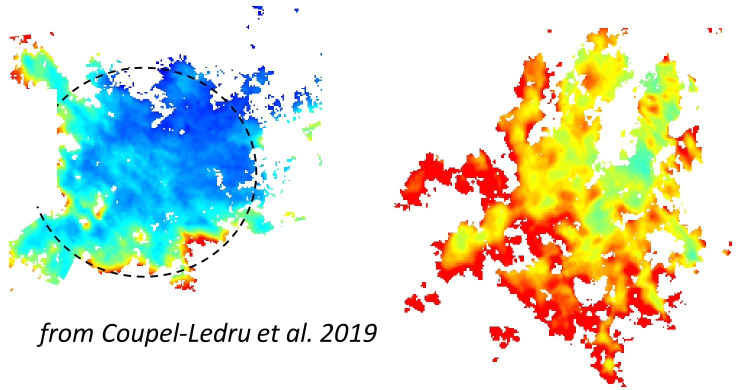
Lecoeur et al. 2011, Casadebaig et al. 2011

Is air temperature the correct variable?

Strong difference between air and meristem temperature

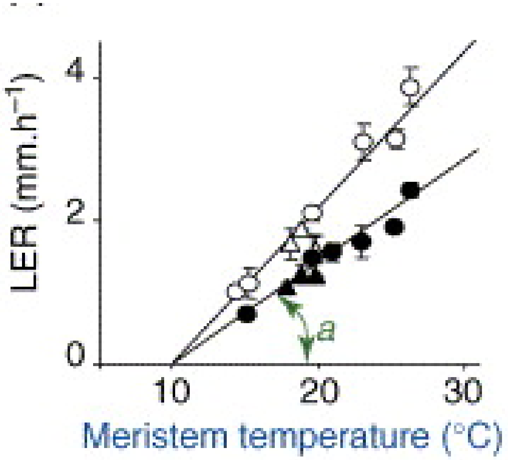


Within tree variation in leaf temperature (ex: apple tree)



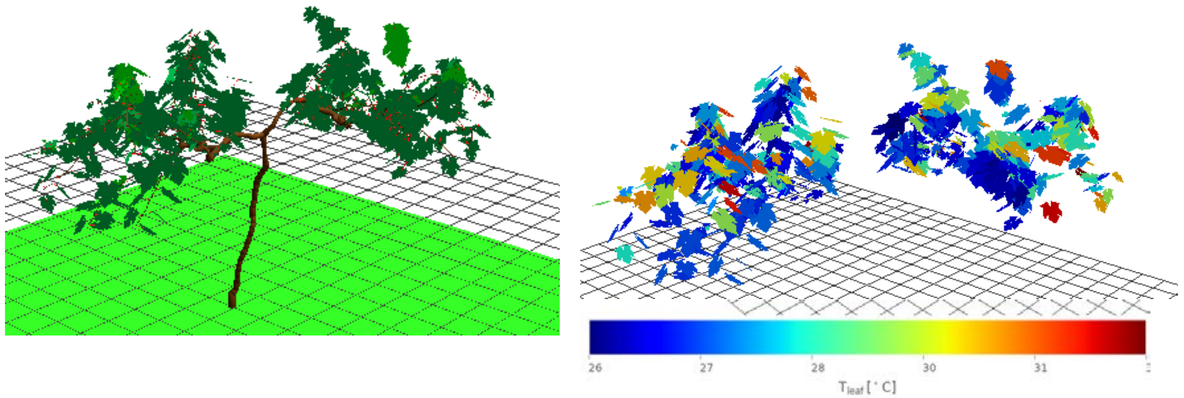
from Coupel-Ledru et al. 2019

Leaf growth is correlated with **meristem temperature**



from Tardieu et al. 2008

Simulation of energy balance at the leaf scale using FSPM

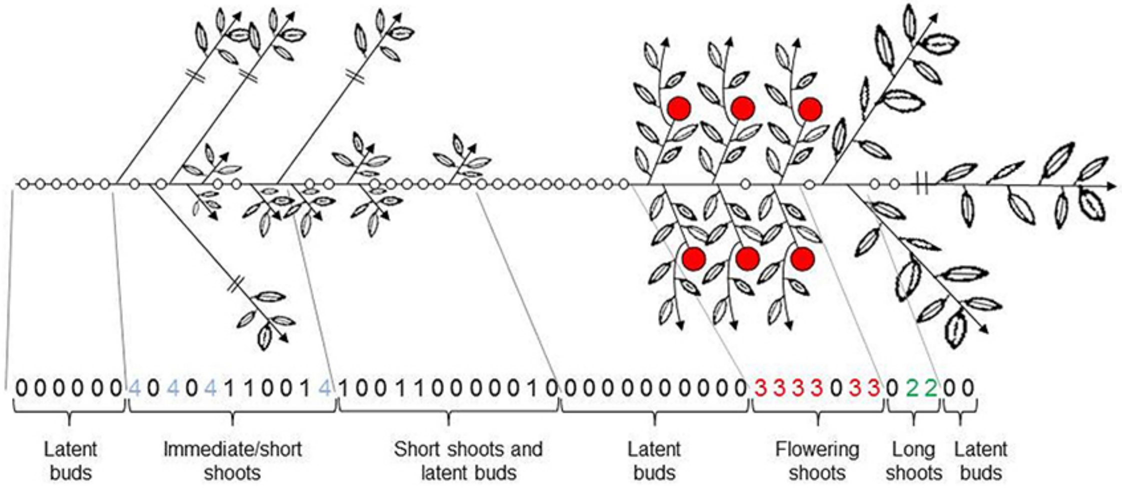


from Albasha et al. 2020

Limits of ecophysiological-based approaches » for the simulation of plant development

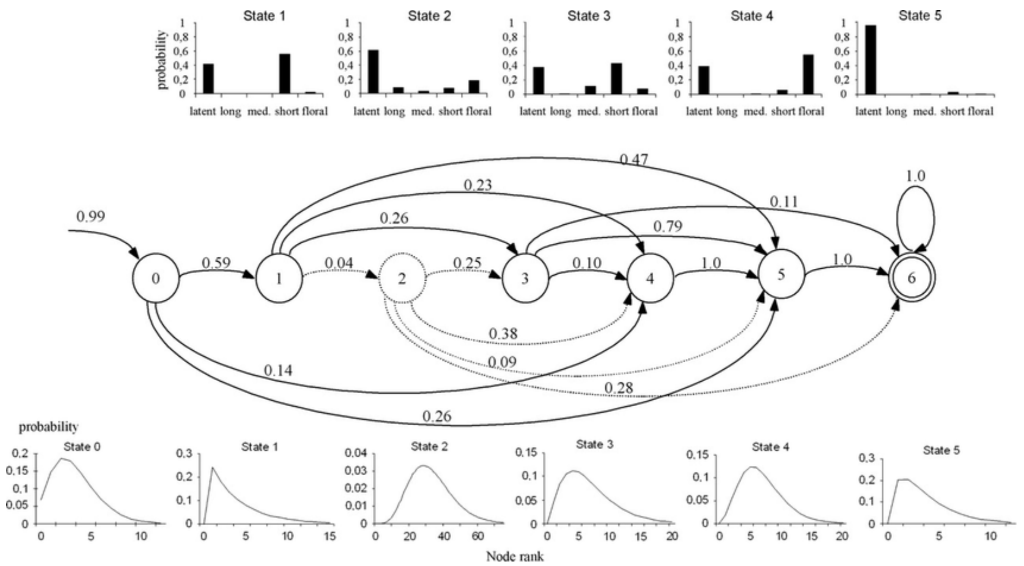
« Botanical » knowledges are needed when dealing with bud fate on perennial plants with complex topology (e.g. fruit trees).

Branching pattern on apple tree

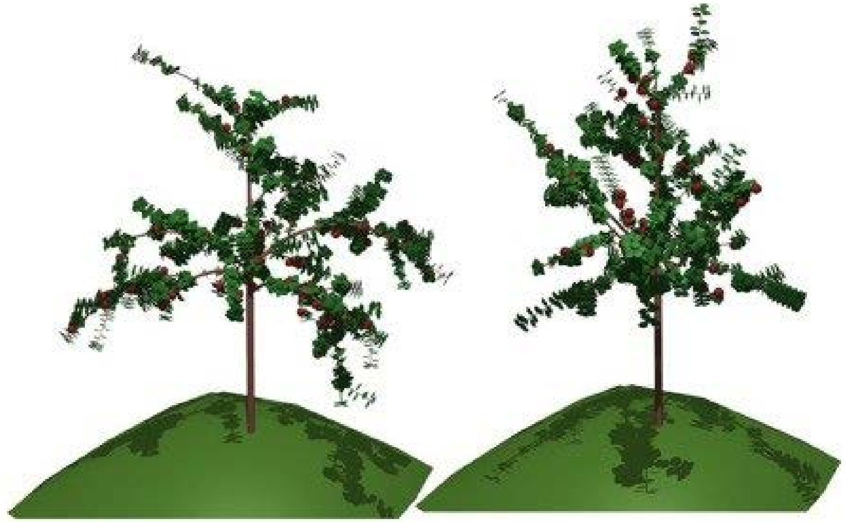


Costes et al. 2014

Hidden Semi Markov model *(Renton et al. 2005)*



Integration at the plant scale *(MAppleT model, Costes et al. 2008)*



Simulation of LAI expansion in crop model

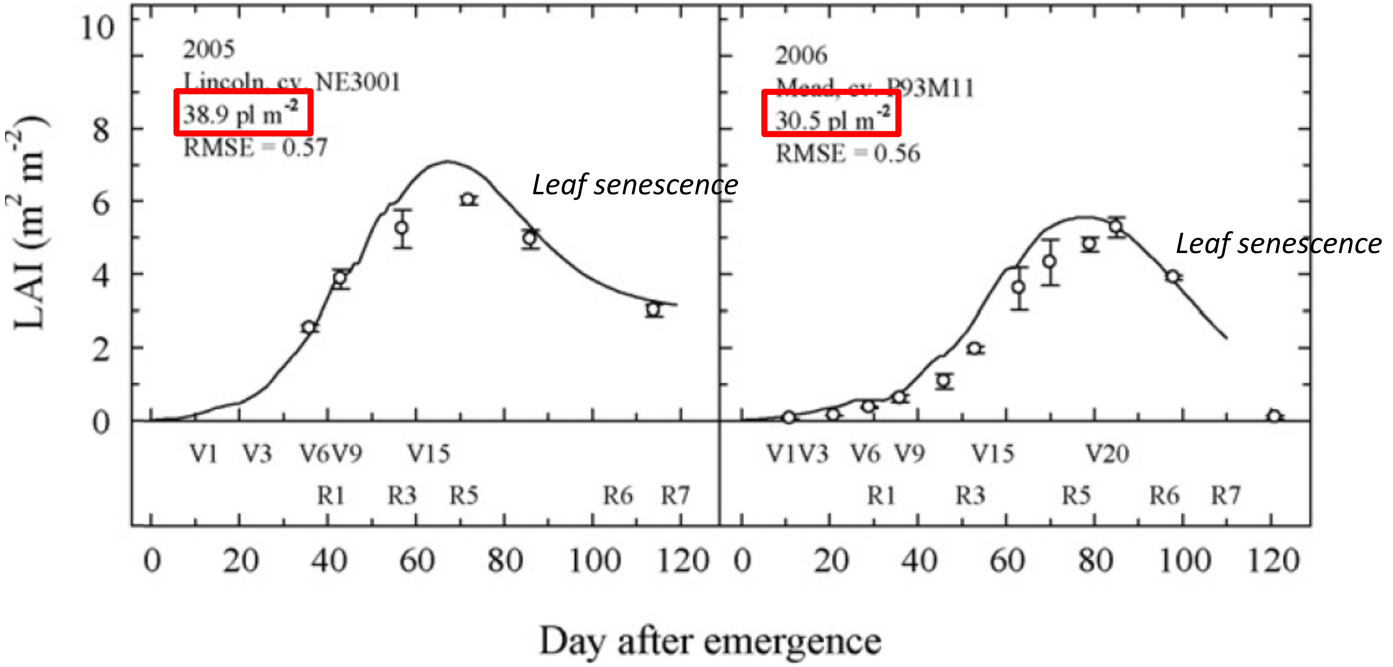
$$\mathrm{LAI} = \mathrm{LA} \times \mathrm{dens}$$

LAI: leaf area index, LA: plant leaf area, dens: plant density

Main assumption:

Homogeneous structure of the field

LAI evolution on soybean *(Setyiono et al. 2008)*



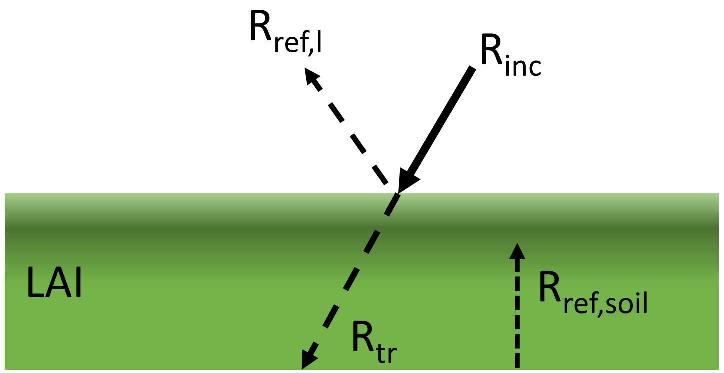
From LAI to light interception at the crop scale

$$\mathrm{LAI} = \mathrm{LA} \times \mathrm{dens}$$

LAI: leaf area index, LA: plant leaf area, dens: plant density

Turbid medium assumption.

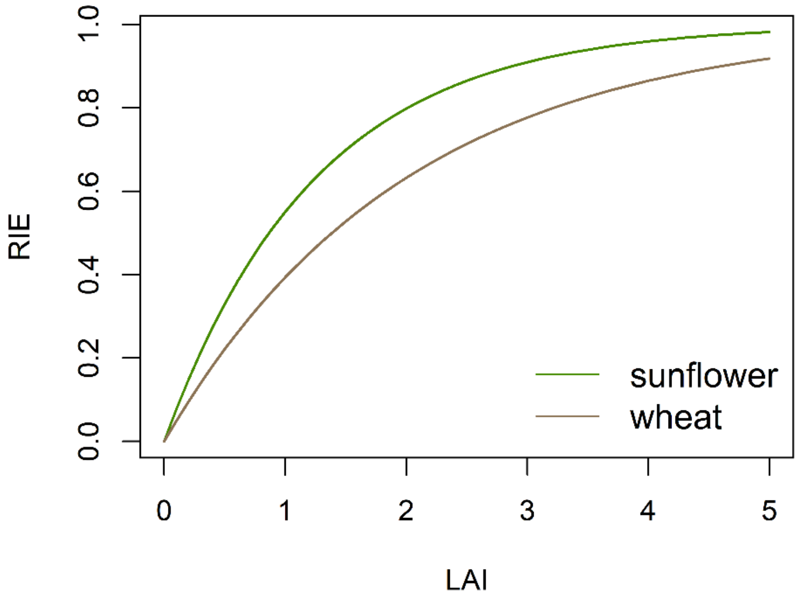
Beer Lambert law, applied to crop



$$1 - \exp(-\color{red}{k}\mathrm{LAI}) = \frac{\mathrm{R_{inc}} - \mathrm{Rtr}}{\mathrm{R_{inc}}}$$

$$RIE \simeq \frac{R_{inc} - Rtr}{R_{inc}}$$

One variable, only used to describe architectural features.



R_{inc} = incident radiation,
R_{tr}:transmitted radiation,
R_{ref} reflected radiation
k: Beer Lambert extinction coefficient

From LAI to light interception at the crop scale

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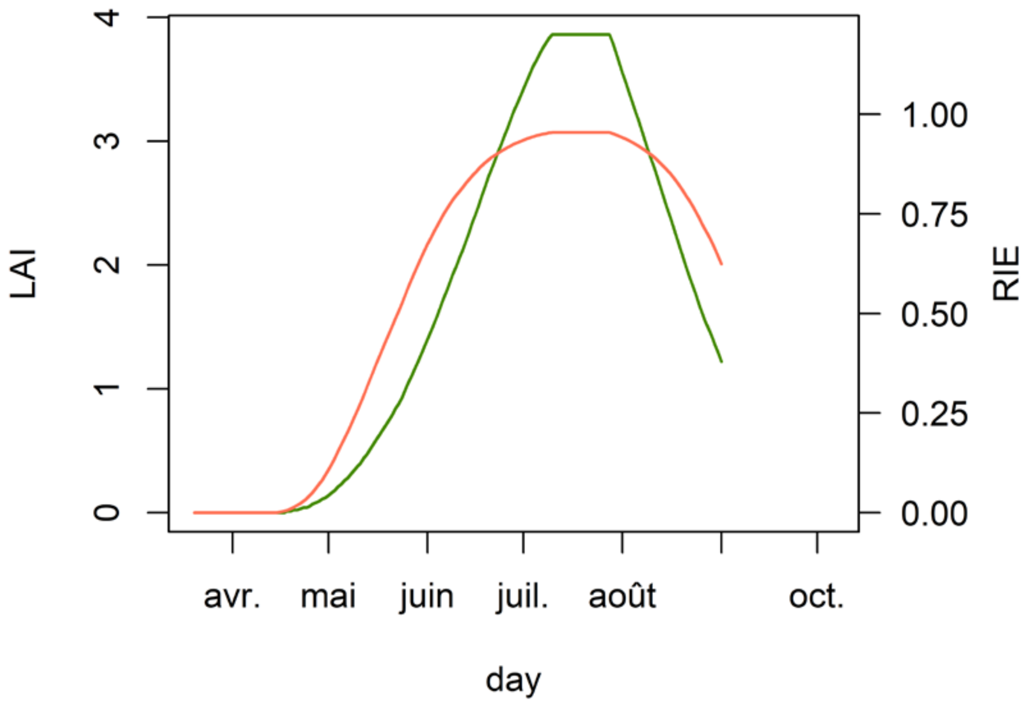


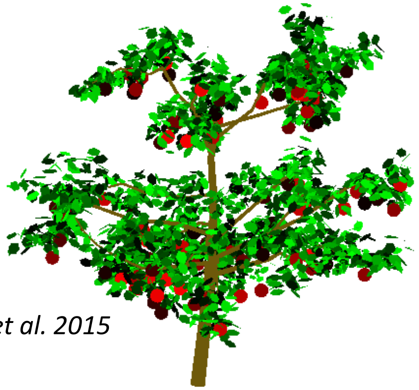
Simulation performed with Sunflo model

3D spatial distribution of light interception *(cf C.Fournier's lesson)*

« Input » architectures

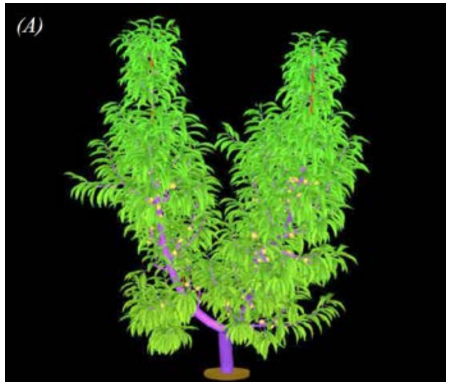
Manual measurements (digitizing/ Lidar)

3D mockups



Pallas et al. 2015

Simulation model

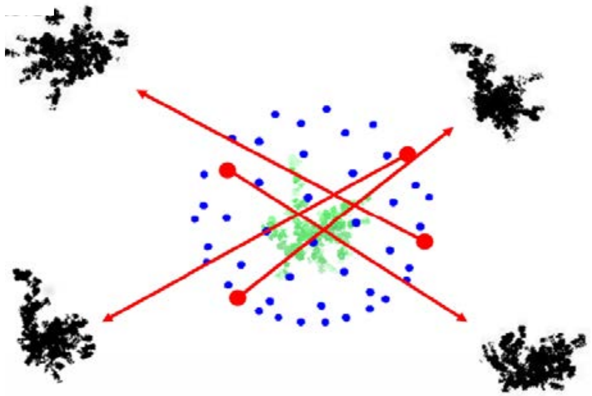


L-Peach model

Lopez et al. 2008

Computation of light interception

e.g STAR computation (raytracing)



$$\mathrm{STAR_d} = \sum_{k=i}^{n} (\omega_i \times Sp_{,i})/ST$$

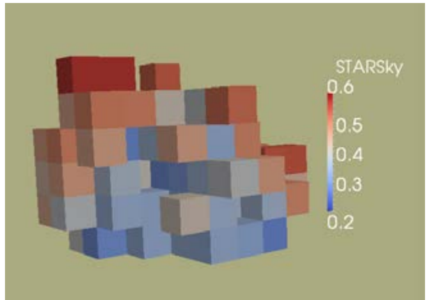
STAR: silhouete to leaf area ratio (diffuse light)

Sp: projected leaf area

ω_i : weighting coefficient

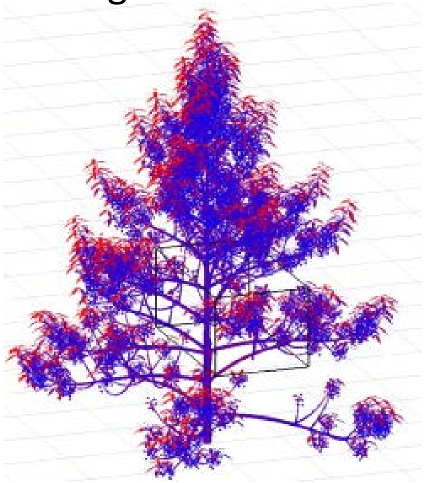
S_T: total leaf area

Light interception per voxel



RATP model (Sinoquet et al. 2001)

At the organ scale



Archimed-MIR model (Dauzat et al. 2008)

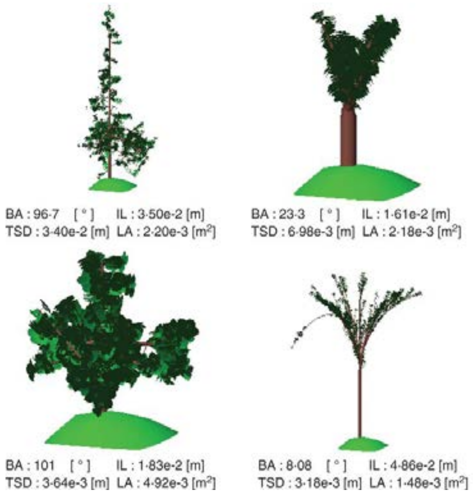
Added values of FSPM for light interception

- Example: **In silico investigation** of the effect of architectural « local traits » on plant performance (→ ideotype definition)

Simulation of contrasted apple tree architecture with the simulation model MAppleT (Costes et al. 2008)

Architectural traits

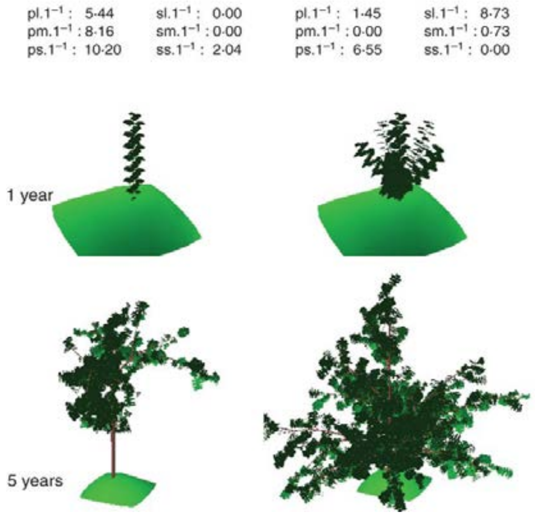
+



Parameter	Lower value	Upper value
Leaf area (m^2)	$3{\cdot}0 \times 10^{-4}$	$9{\cdot}0 \times 10^{-3}$
Internode length (m)	$8{\cdot}0 \times 10^{-3}$	$5{\cdot}0 \times 10^{-2}$
Shoot top diameter (m)	$1{\cdot}0 \times 10^{-3}$	$8{\cdot}5 \times 10^{-3}$
Branching angle (°)	0·0	$1{\cdot}3 \times 10^{-2}$

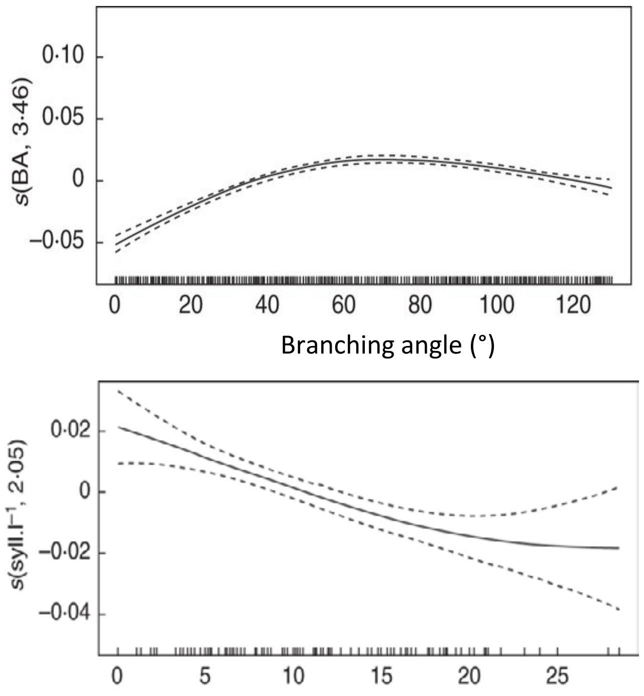
Da Silva et al. 2014

Topological traits



Analysis of the impact of each parameter on STAR values

Sensitivity analysis



Monteith formalism/RUE

$$DM = \sum_{0}^{harvest} \boxed{RUE_i} \times RIE_i \times c \times Rsi$$

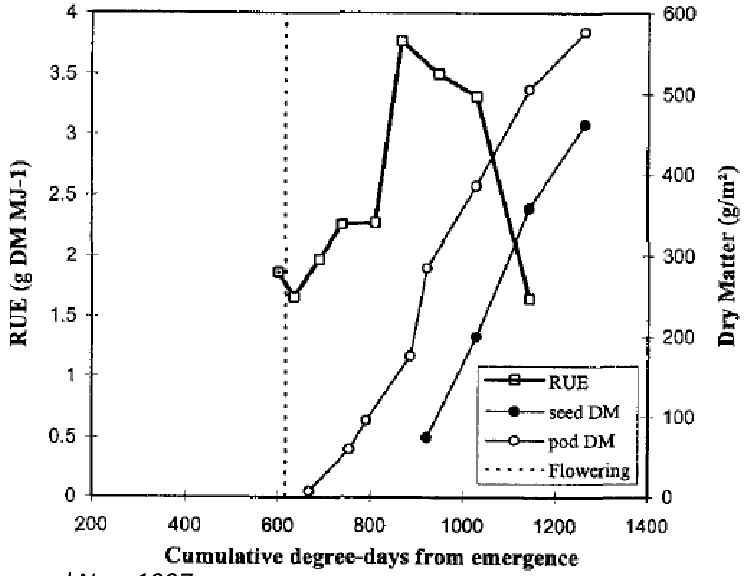
Mean values of RUE depending on the photosynthesis type *(from Sinclair et Horie, 1989)*

C3 plants	1.9 g MS. MJ^{-1}
C3 plants (legume)	1.7
C4 plants	2.5

Radiation use efficiency is an **integrative variable** which strongly depends on:

Leaf photosynthetic activity
On transformation of photoassmilate ($C_6H_{12}O_6$) into biomass (metabolic cost)

Radiation use efficiency at the crop scale



From Jeuffroy and Ney, 1997

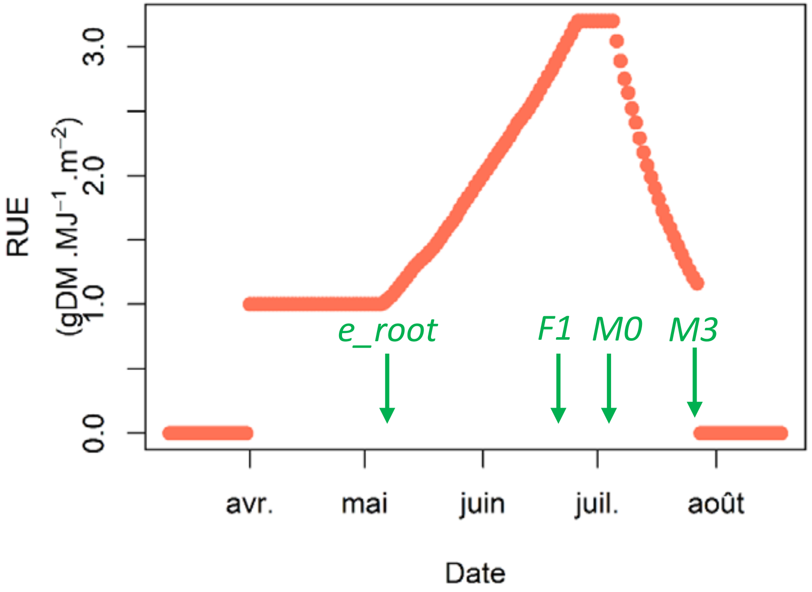
RUE changes during the crop cycle.

- Low values at the beginning (root growth)
- Stimulation of photosynthesis during the seed filling period (high export rate of photoassimilate)
- Decrease at the end due to senescence (N remobilization)

<u>Simulation example with a crop model (SUNFLO, Lecoeur et al. 2011)</u>

Potential values only dependent on phenological stages

```
for (i in (which(data_m$DATE == i_date): dim(data_m)[1]))
{TT[i] = data_m$Teff[i] + TT[i-1]
 if (TT[i] < e_root) {RUE[i] = 1.0}
 if ((TT[i]>= e_root) & (TT[i]<F1))
   {RUE[i] = RUE_max +(TT[i]-F1)/(F1-300) * (RUE_max -1)  }
 if ((TT[i]>=F1) & (TT[i]<M0))
   {RUE[i] = RUE_max}
 if ((TT[i] >=M0) & (TT[i]<M3))
   {RUE[i]= RUE_max*0.36*exp((1-(TT[i]-M0)/(M3-M0)))}}
```



Simulation of photosynthesis activity (leaf scale)

In FSPM, photosynthesis is simulated at the leaf scale to account for microclimate conditions

« Biochemical » approach

(Farquahr, 1980)

$$A_{net} = \min(A_c, Aj, Aw) - Rd$$

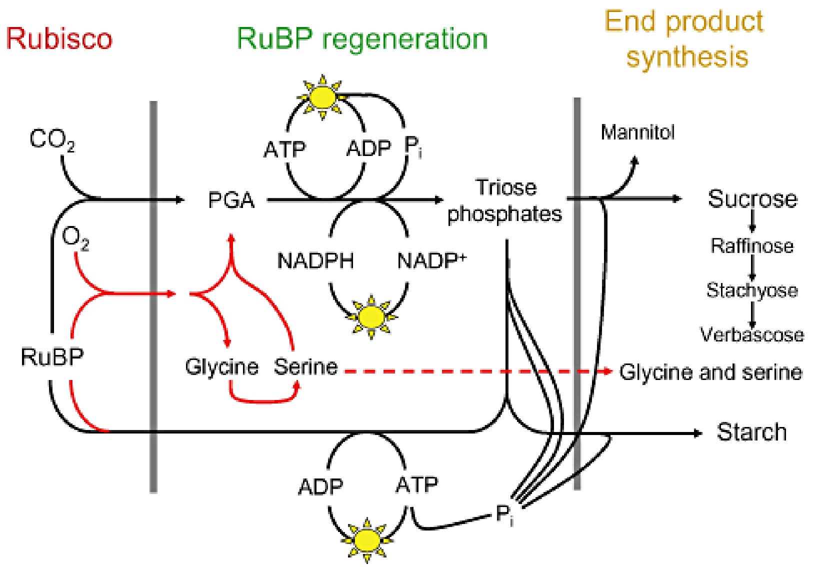
$$A_c = Vcmax\left[\frac{(Cc - \Gamma^*)}{(C_c + Kc(1 + \frac{O}{Ko}))}\right] - Rd$$

$$A_j = J\left[\frac{(Cc - \Gamma^*)}{(4C_c + 8\Gamma^*)}\right] - Rd$$

$$J = \frac{\alpha PAR}{\sqrt{1 + \alpha PAR^2/Jmax^2}}$$

Anet, Net photosynthesis (µmol/m2/s), A_c Limitation by Rubisco activity, A_j Limitation by electron transfert rate, A_w limitation by TPU, Cc partial pression of CO2, J electron transfert rate, Γ* compensation point for photorespiration, Rd dark respiration

Processes affecting photosynthesis activity



Sharkey et al. 2007

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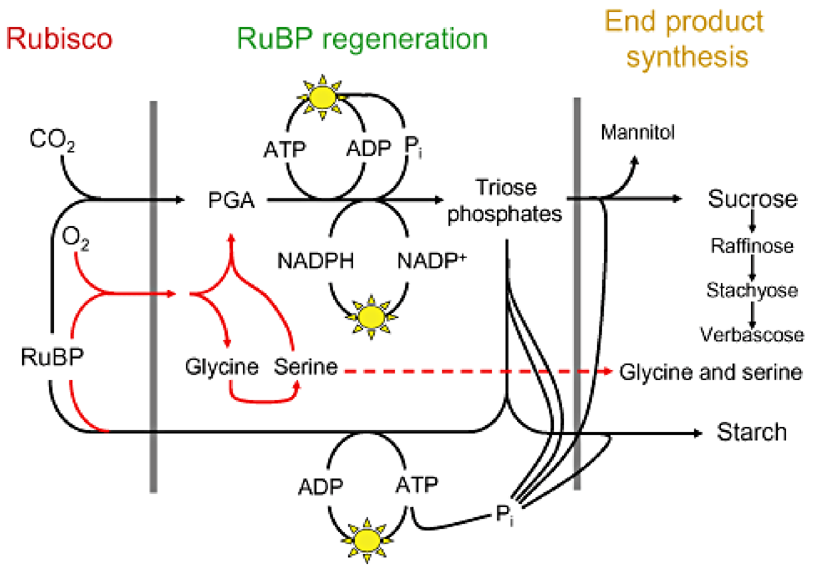
Processes affecting photosynthesis activity



Sharkey et al. 2007

Photosynthesis activity depends on:

. Internal CO_2 concentration (C_c)

. Incident radiation (PAR)

Simulation of photosynthesis activity (leaf scale)

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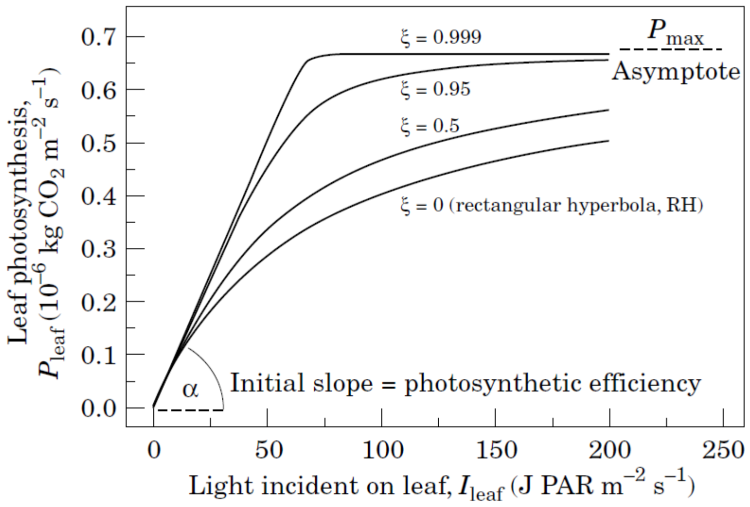
«Semi-empirical » formalisms

(e.g Thornley 1998)

Non rectangular hyperbola

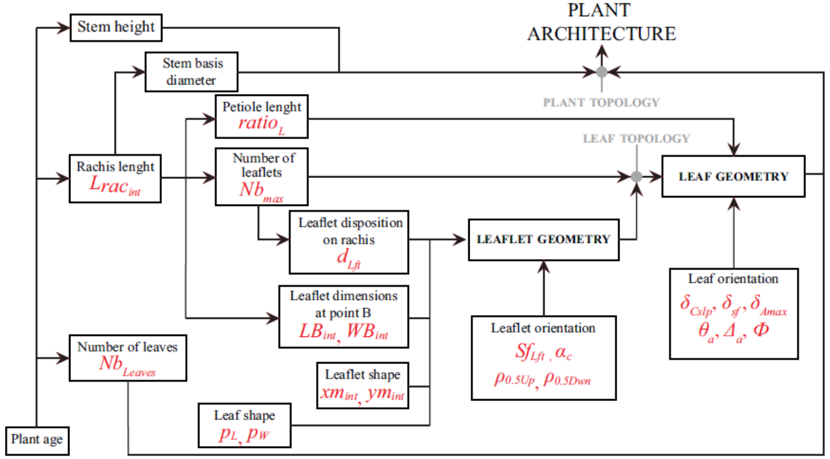
$$P_{leaf} = \frac{\alpha I_{leaf} + Pmax - \sqrt{[(\alpha I_{leaf} + Pmax)^2 - 4\xi\alpha I_{leaf}P_{max}]}}{\xi}$$



Simulation of photosynthesis activity-application

1. Architectural model

Allometric relationships describing ontogenetic and morphogenetic gradients.

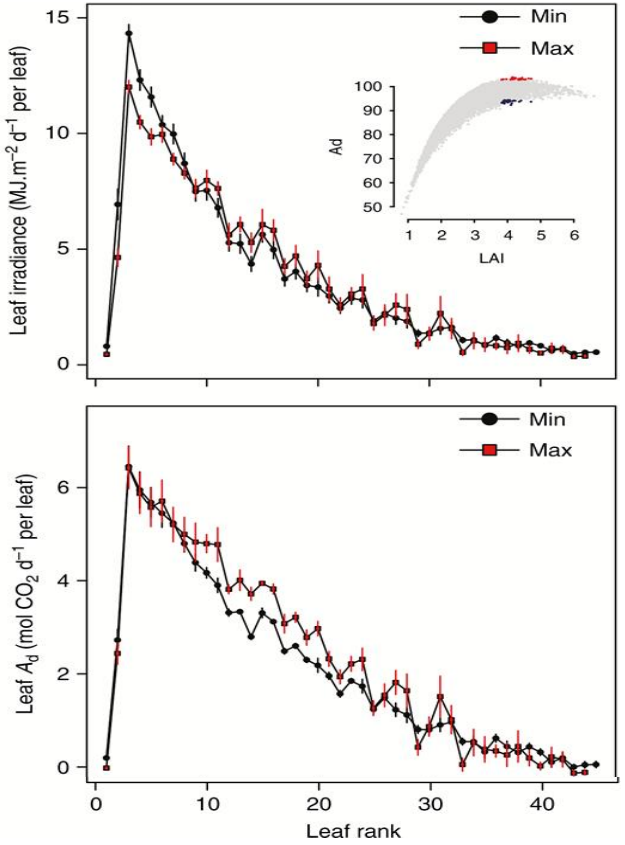


2. Modeling of light interception and photosynthesis

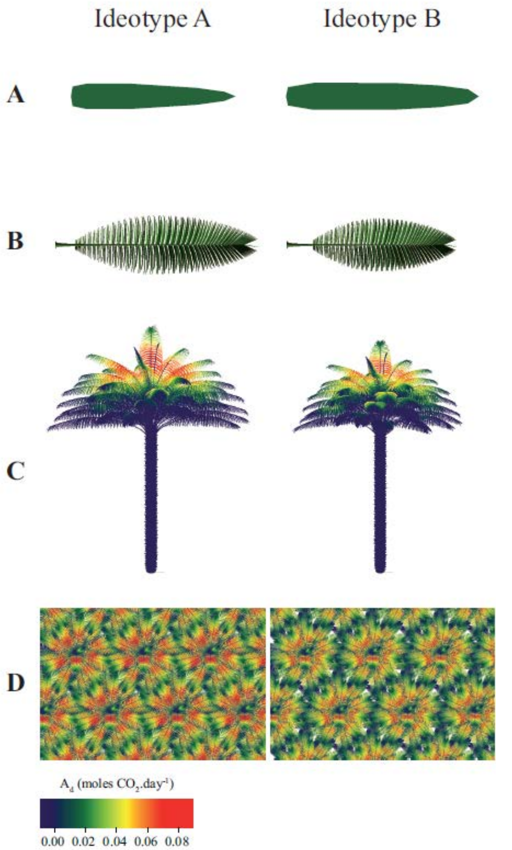
Light effect as the only explaining variable

$$P_{leaf} = \frac{\alpha I_{leaf} + Pmax - \sqrt{[(\alpha I_{leaf} + Pmax)^2 - 4\xi \alpha I_{leaf} P_{max}]}}{\xi}$$

3. Simulation at the leaf scale



4. Determination of different types of ideotypes maximizing photosynthesis



(Perez et al., 2017)

Simulation of leaf gas exchange

Coupling photosynthesis, stomatal conductance and leaf energy balance

1. Photosynthesis model

$$A_{net} = f_1(Ci)$$

2. Stomatal model (e.g Leuning 1995)

$$C_i = Ca - \frac{A}{gs}$$

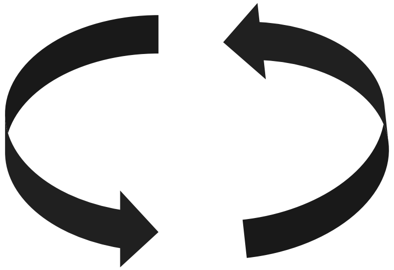
$$g_s = go + a_1 \times \frac{f_2(VPD) \times A}{(Cs - \Gamma)}$$

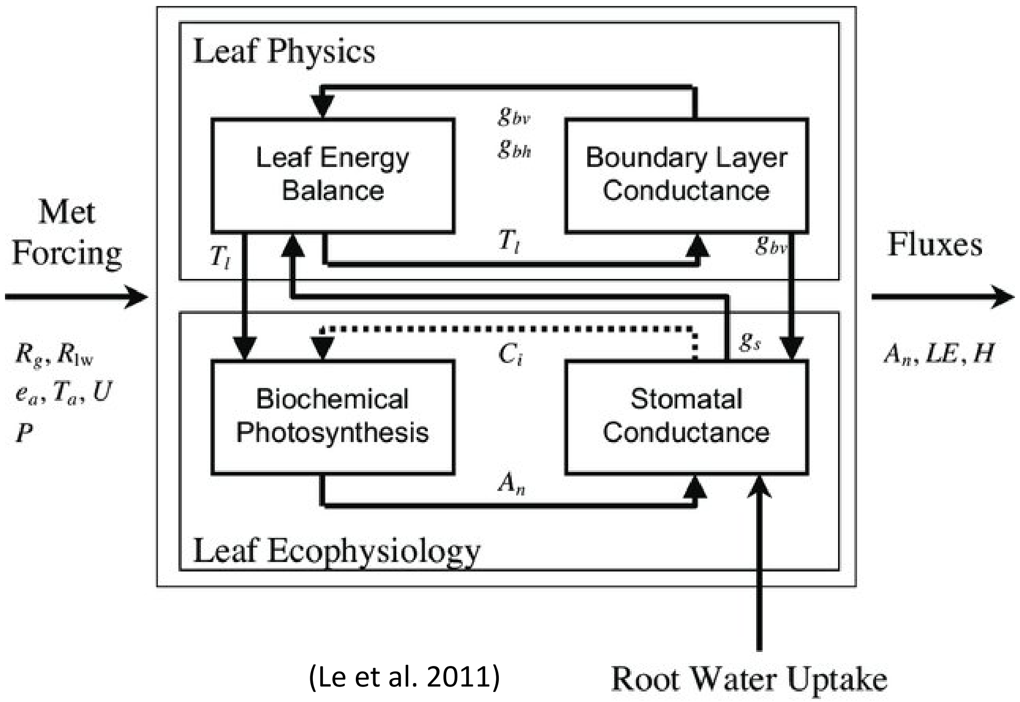
3. Energy balance

$$VPD = f(Tleaf)$$

$$T_{leaf} = f(gs, Rn, \dots)$$

Recursive algorithms



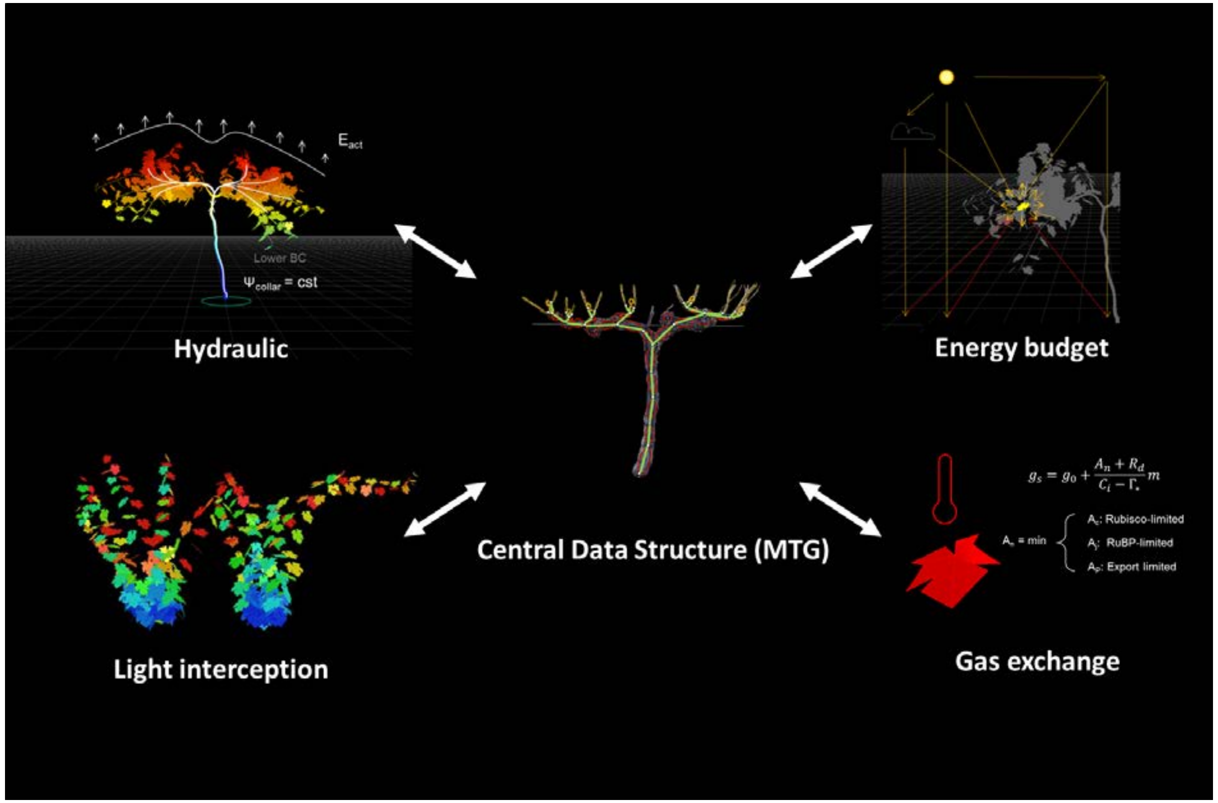


(Le et al. 2011)

Anet, Net photosynthesis (µmol/m2/s), C_i internal partial pression of CO2, C_a external pression of CO_2, g_s stomatal conductance, g_0 conductance of the boundary layer, VPD vapor pressure deficit, R_n net radiation

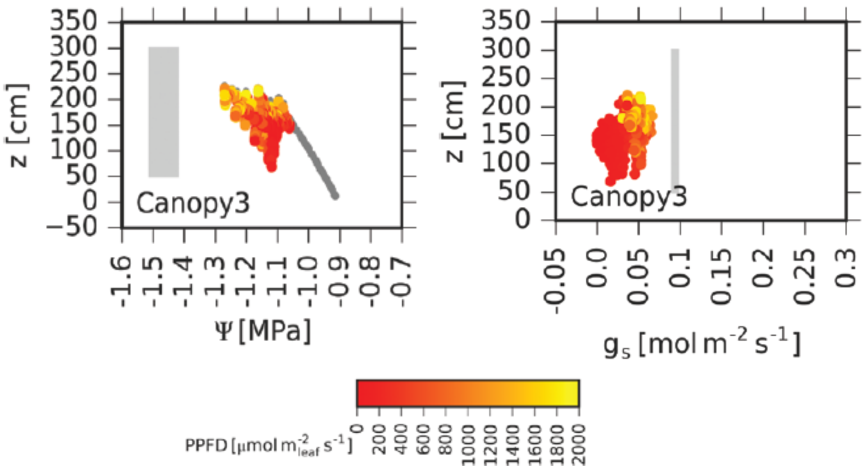
Simulation of leaf gas exchange - application

Coupling photosynthesis, stomatal conductance, leaf energy balance and leaf hydraulic properties

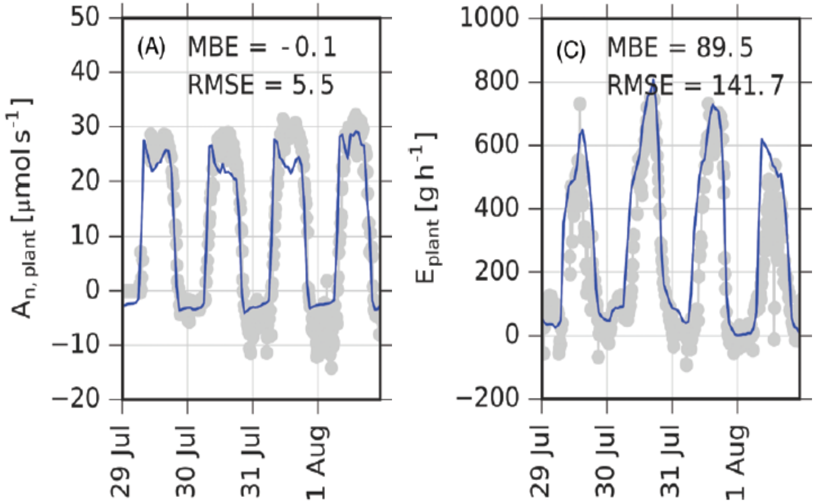


(Albasha et al. 2020)

Leaf scale simulations



Diurnal variation at the plant scale



From dry weight to harvest weight

A matter of biomass allocation and seed/fruit formation

$$DM = \sum_{0}^{harvest} RUE_i \times RIE_i \times c \times Rsi$$

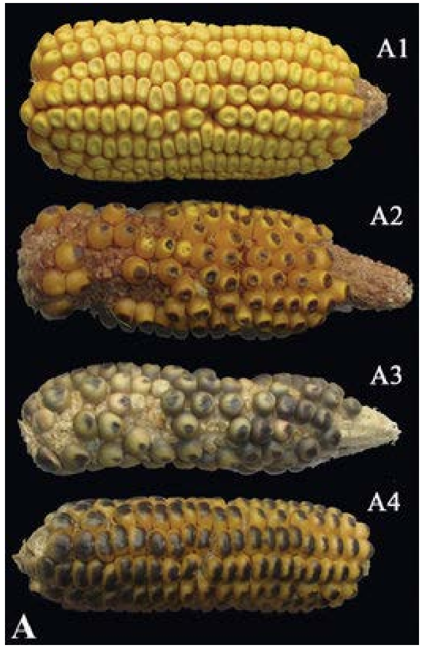
$$W_{harv} = \boxed{HI \times} DM$$

HI : harvest index

Just a coefficient ! The problem is to estimate it !

➡ *Dependent on many processes*
(seed formation/fruit set/floral induction/seed-fruit filling)

Morphological in maize ears from many progenies (Xu et al. 2013)



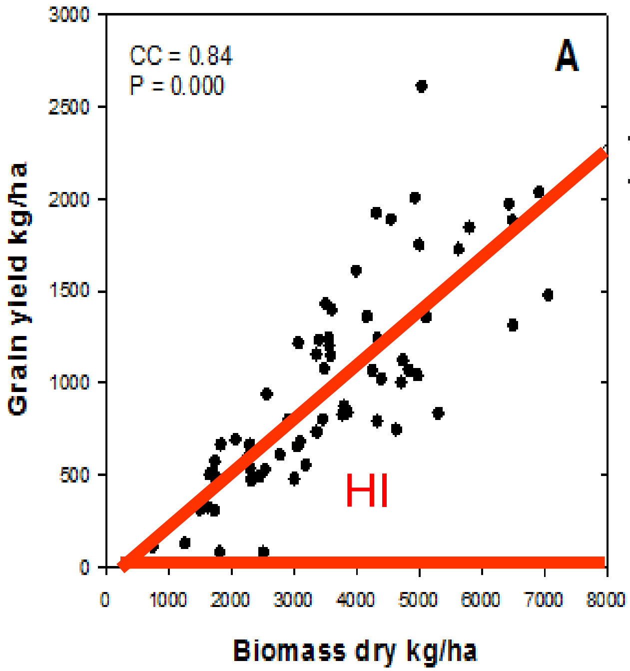
Harvest characteristics apple tree

Crop load	Yield (kg/tree)	Nb_fruit	MFW (g)
High	57.3	306	187
Medium	35.1	117	300
Low	18.2	52	345

Harvest characteristics apple tree
(from Wünsche et al. 2005)

Simulation of HI in crop models

« Static approach » (Use of a "final value")



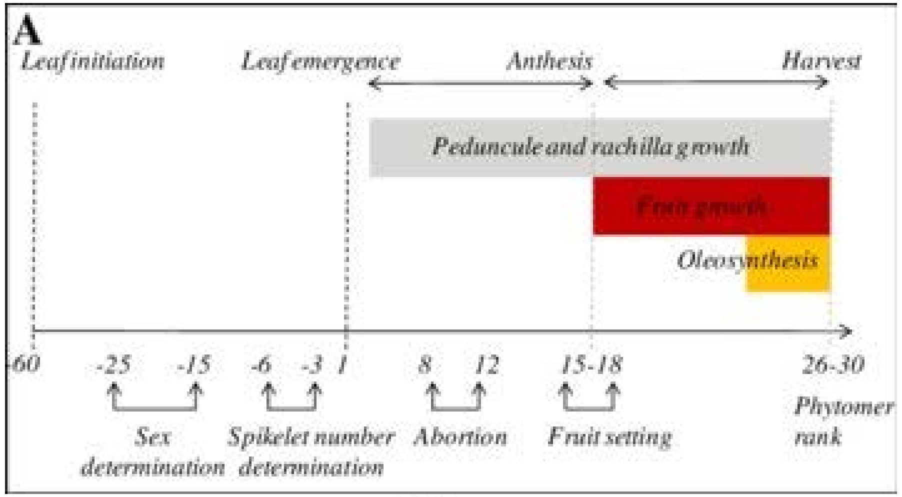
HI values for sunflower cultivar

(Lecoeur et al. 2011)

Genotype name	$HIcapi_{max}$	HIseed
Peredovick	0.52 (6)	0.52 (22)
INRA6501	0.52 (6)	0.51 (23)
Rémil	0.53 (3)	0.55 (21)
Airelle	0.51 (17)	0.57 (19)
Relax	0.52 (6)	0.59 (15)
Mirasol	0.52 (6)	0.57 (19)
Primasol	0.50 (23)	0.63 (10)
Cargisol	0.52 (6)	0.61 (13)
Viki	0.53 (3)	0.58 (18)
VAQ × PAR6	0.52 (6)	0.65 (6)
Ha × Hm16	0.50 (25)	0.40 (24)
Ha × Hm23	0.50 (24)	0.40 (24)
Ha × HmC7	0.50 (26)	0.40 (24)

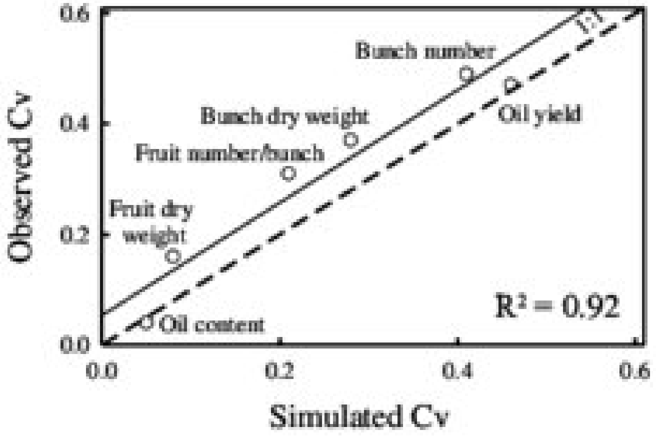
«Dynamic approach »

Yield component elaboration of oil palm bunches



Simulated plasticity of each yield component

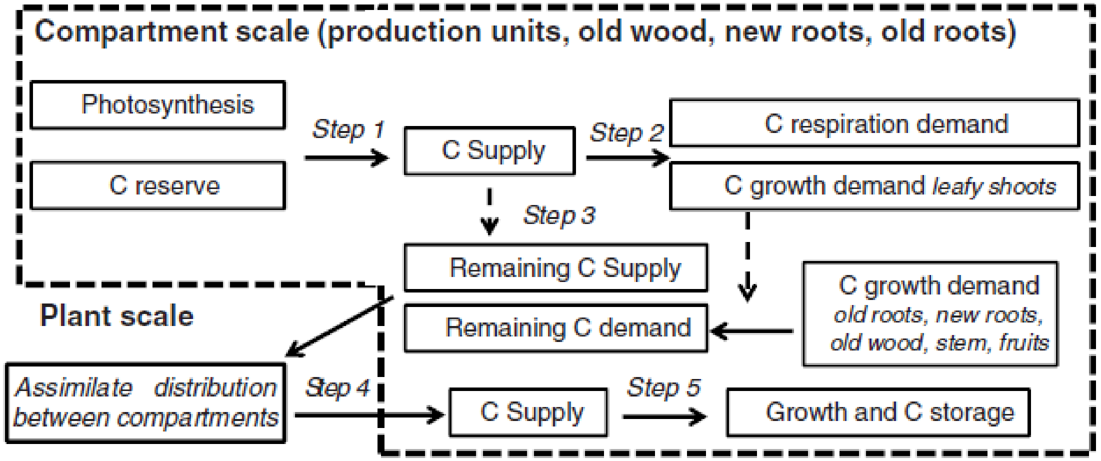
Pallas et al. 2013



Simulation of HI in crop models

A special focus is often made on biomass allocation in FSPM

Workflow of biomass allocation in Qualitree (peach, apple).
Specification of the different C sinks.

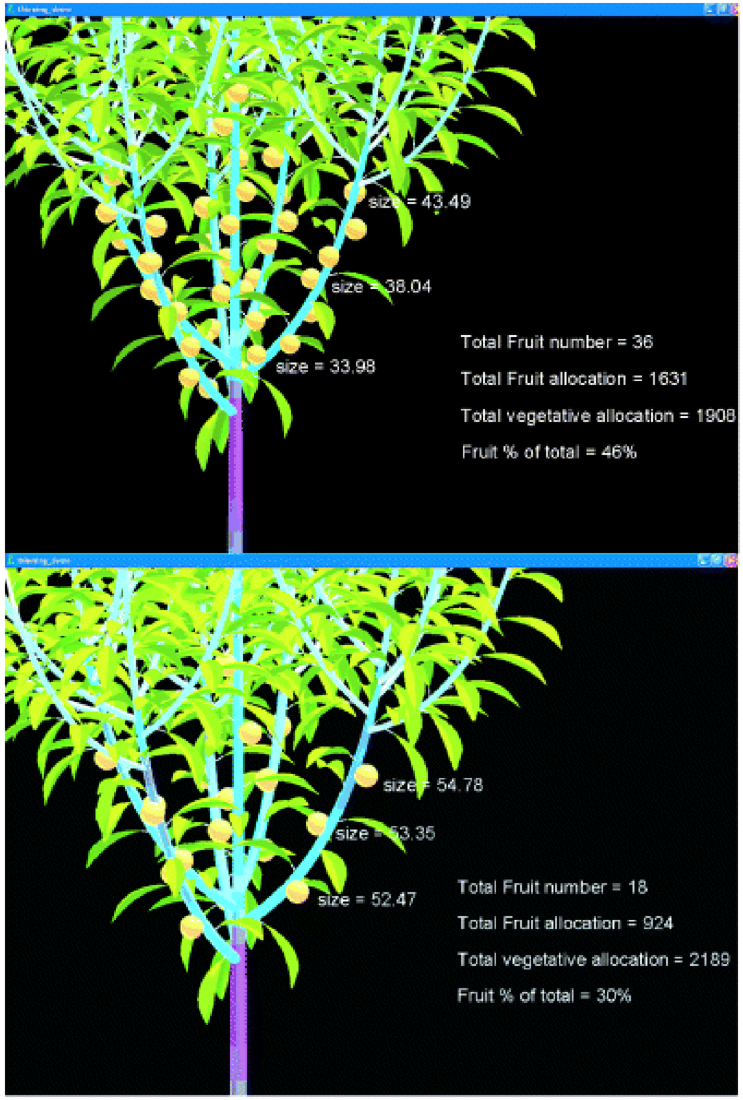


Allocation depending on **distances between source and sinks**

$$F_{ij} = \frac{S_i \times Di}{\sum_1^n D_j} (d_{ij})^a$$

F_{ij}: carbon flux from source i to sink j, D_i , carbon demand of sink j, S_i, carbon supply of source i, d_{ij}, distance between between source i and sink j.

Simulation with LPeach



Integration of limiting factors

$$\Delta DM_i = RUEi \times PARint_i$$

$$PAR_{int\,i} = RIEi \times c \times Rs_i$$

$$DM = \sum_{0}^{harvest} RUE_i \times RIE_i \times c \times Rsi$$

$$W_{harv} = HI \times DM$$

Monteith et al., 1977

Limiting factors (water stress, nitrogen deficiency, diseases…) could act on all the terms of the ‘Monteith formalism’.

Specific case of water stress:

RUE:
Stomatal closure/damage on photosynthesis system

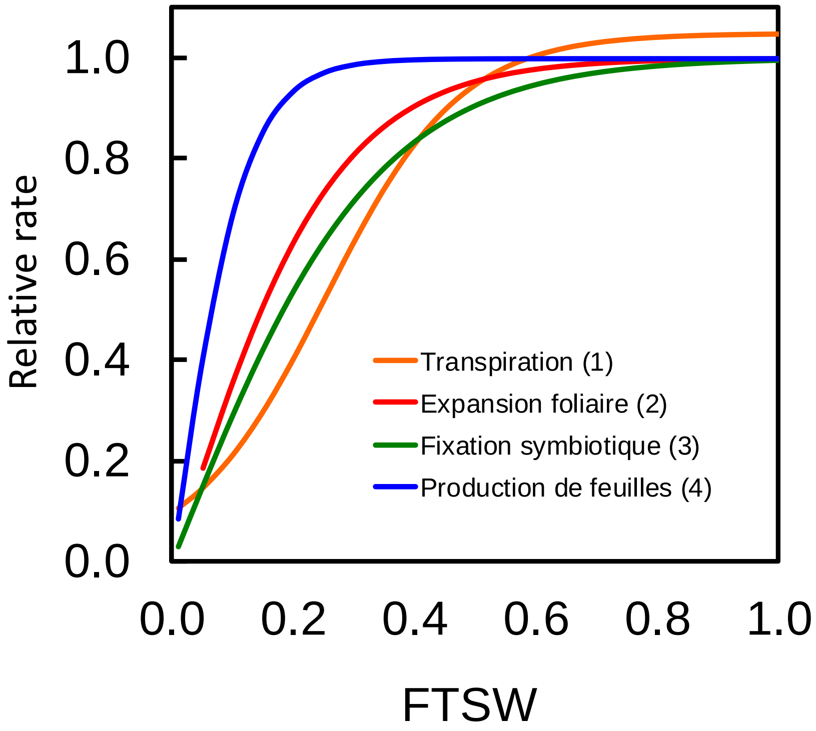
RIE:
Decrease in leaf expansion/phyllochron/leaf fall and senescence.

Growth cycle duration:
Enhance flowering

HI:
fruit/seed set, flower initiation

Integration of limiting factors – response curve

A general framework used in crop model



From *Lecoeur and Sinclair (1996) (1, 2) ; Sinclair (1986) (3) ; Lecoeur and Guilioni (1998) (4))*

Response curve:

- Impact of a specific « constraint » (C) on a specific variable (X)

$$X_i = f(Ci) \times X_{pot,\ i}$$

With X_i the real value of the variable (leaf expansion rate, RUE, transpiration…)
$X_{pot,i}$ the potential value of the variable at day i (driven by phenology, thermal time…)
C_i : the intensity of the constraint.

Challenges:

1. Quantifying the intensity of C (easy for climatic variable, more tedious for nitrogen or water availability)
2. Building these responses curves for a large set of environment.
3. Integrating the effect of multiple stresses

Estimation of soil water availability

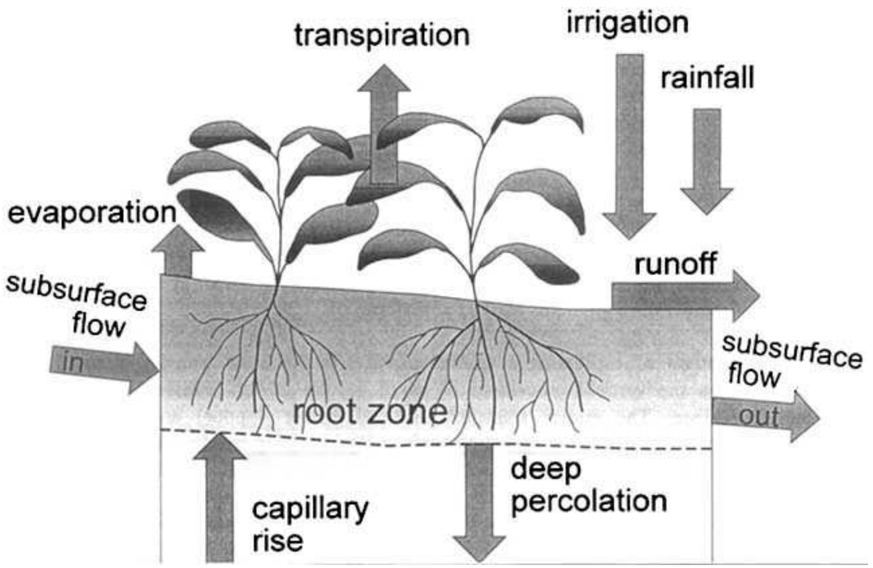
The water balance

$$ASW_i = ASWi_{-1} + Raini + Wati - Tri - Evi + \cdots$$

$$FTSW_i = ASWi/TTSWi$$

ASW_i: available soil water content, Wat_i watering, Rain rainfall, Tr plant transpiration, Ev soil evaporation, TTSW the total soil water available at field capacity.

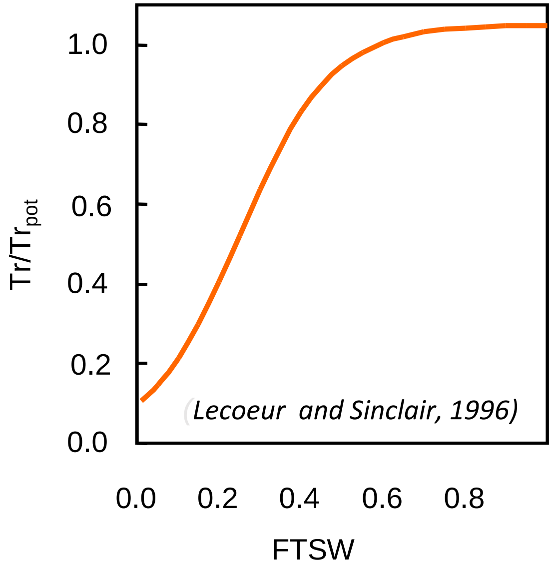
FTSW [0,1], the fraction of soil water available (**state variable** representing the intensity of soil water deficit)



Complex system with feedback loop between plant behavior and soil water content

$$FTSW_i = f(Tr_i)$$

$$Tr_i = f(FTSWi)$$



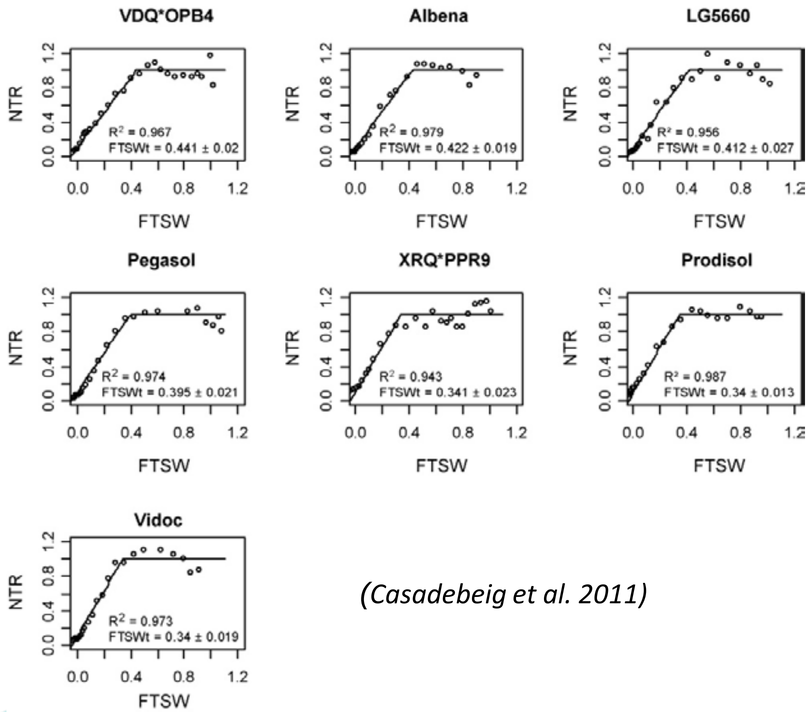
Phenotyping for the response to climate

Estimation of response curve for a set of genotypes.

$$\mathrm{NTR} = 1 \text{ if } \mathrm{FTSW} > \mathrm{FTSWth}$$

$$\mathrm{NTR} = \mathrm{FTSW}/\mathrm{FTSWth} \text{ else}$$

NTR: normalized transpiration rate, $FTSW_{th}$ FTSW threshold



(Casadebeig et al. 2011)

Use of dedicated experimental platform

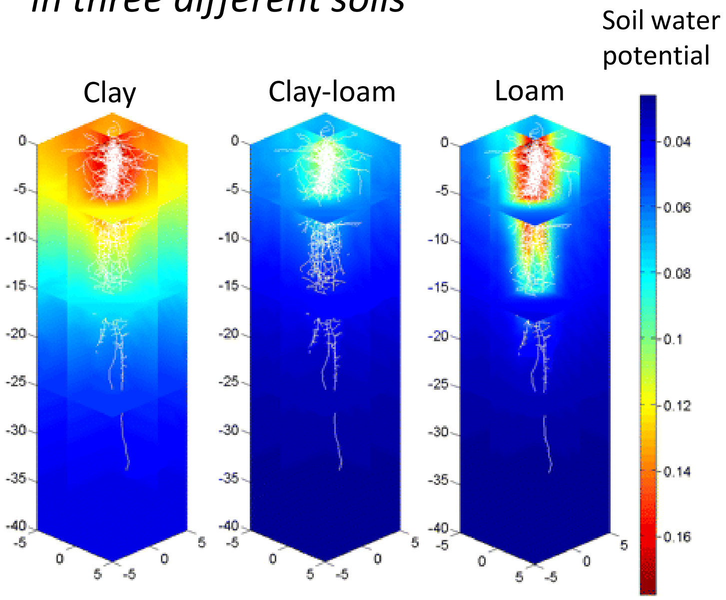
Opportunity for a rapid quantification of genotype responses over a wide range of growing conditions/

Simulation of the effect of microclimate with FSPM

Thanks to its 3D representation FSPM are highly relevant for assessing **organ** functionning in response to environmental or biotic variable. → upscaling at the crop scale for a better accuracy?

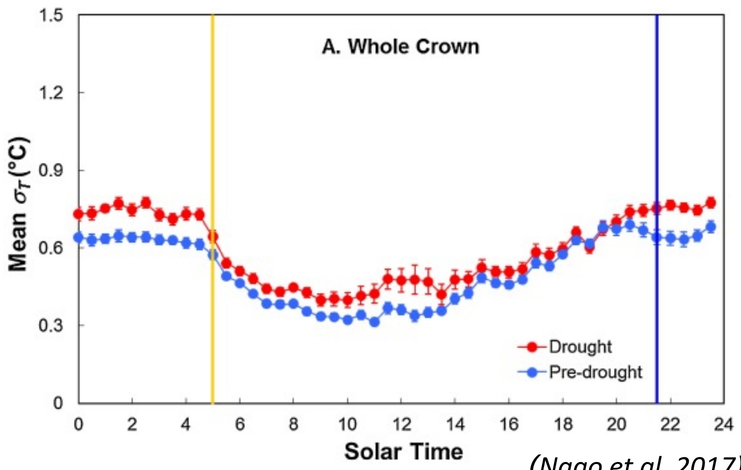
<u>Some examples:</u>

Soil water potential and root water uptake in three different soils



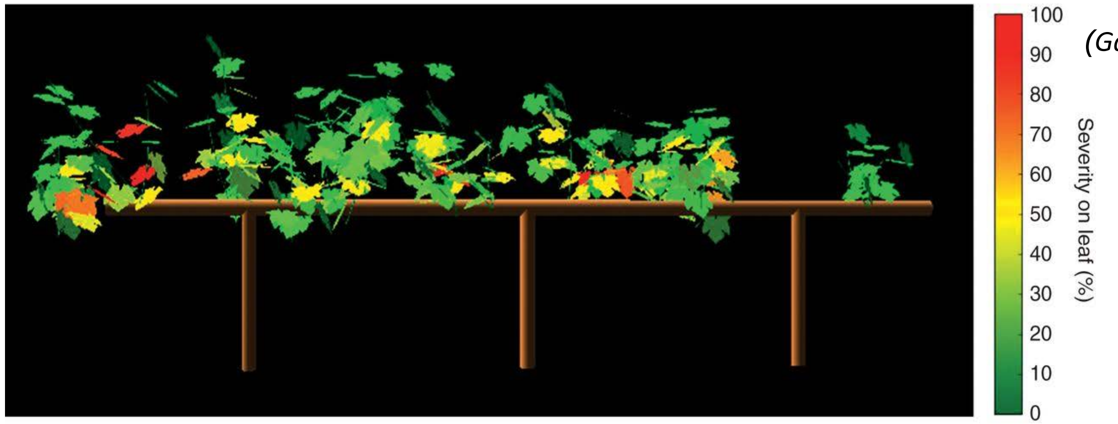
(Draye et al. 2010)

Simulation of within-tree variability in leaf temperature under WW and WS (apple tree)



(Ngao et al. 2017)

Simulation of foliar infection by powdery mildew in grapevine.

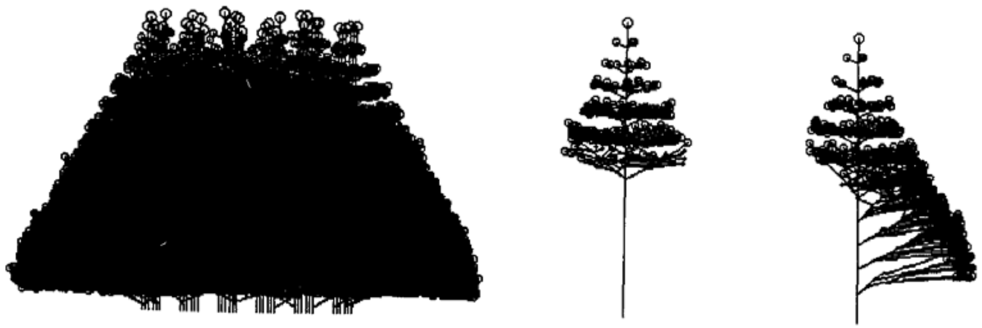


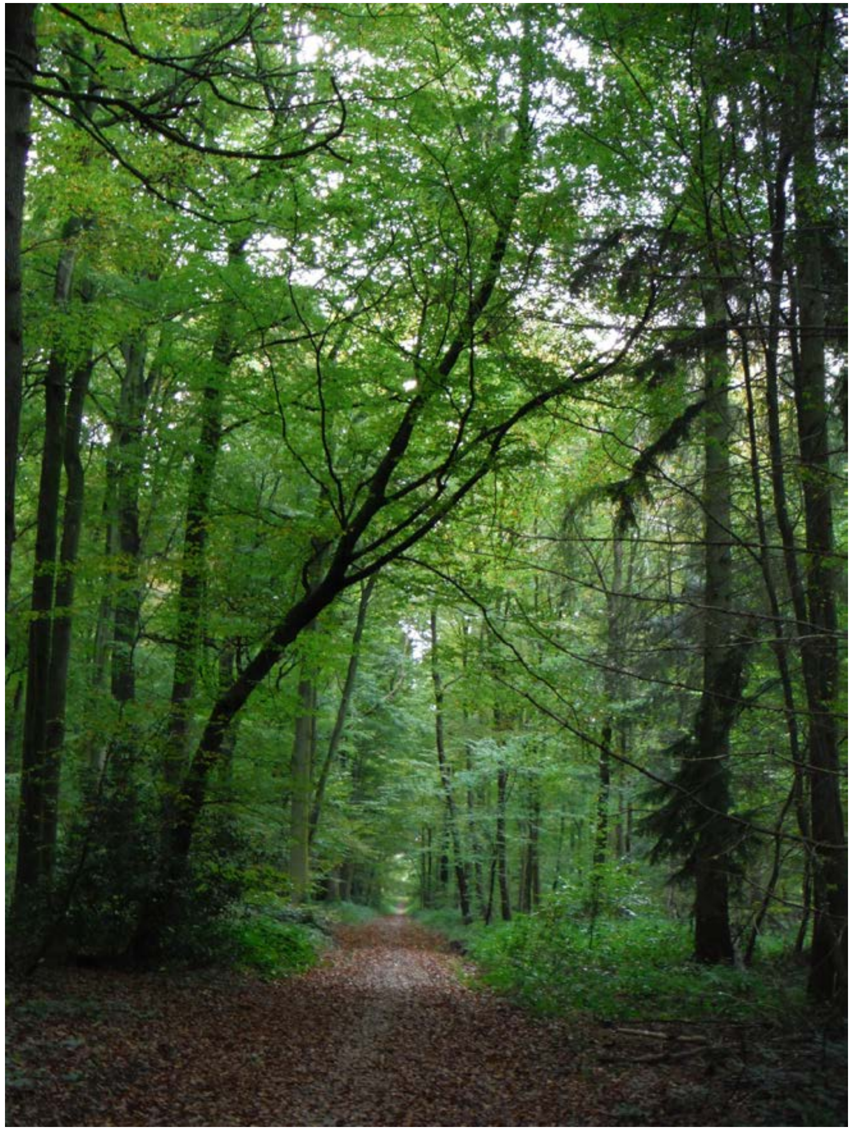
(Garin et al. 2014)

Retroactions between environment, development and growth

Huge challenge to integrate retroaction between local environment and development

Simulation of branch growth in a stand depending on light availability (Takenaka et al. 1994)





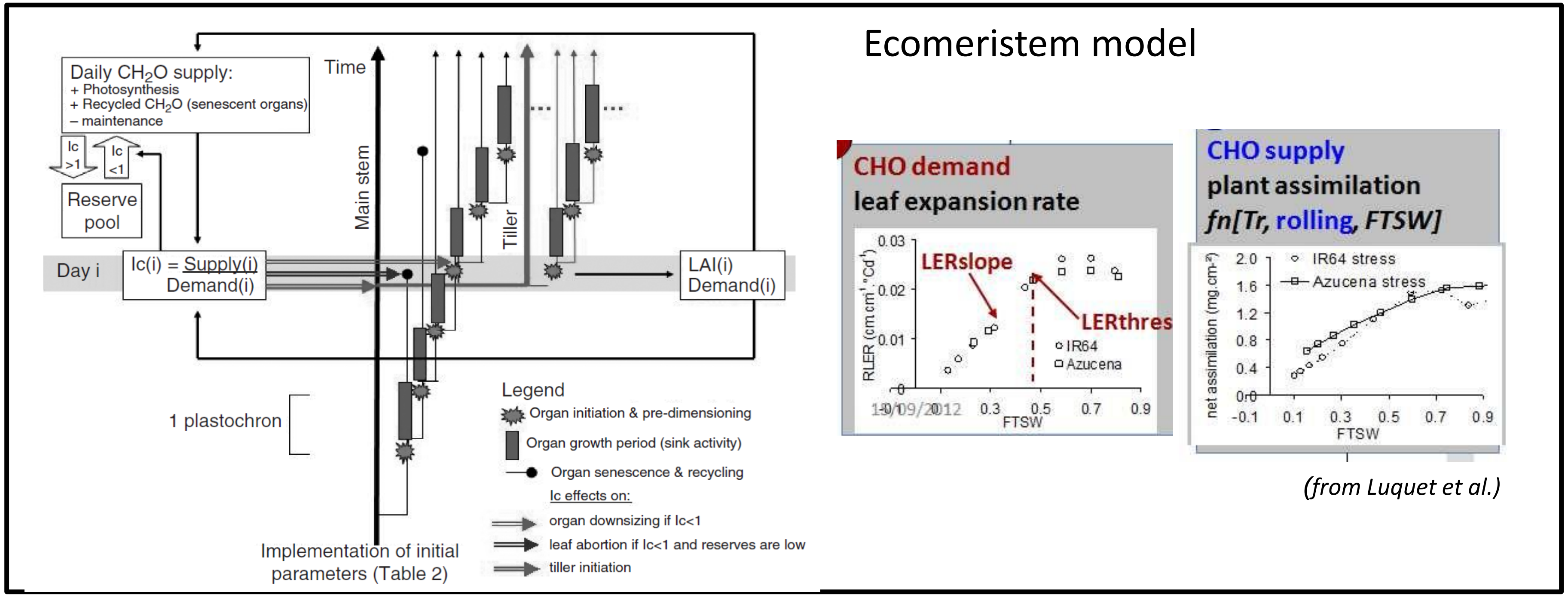
https://saulecauseur.org

Integration of multiple stresses and plant ontogeny

Use of a **metavariable**, driving plant development

$$Ic = \frac{Supply_i}{Demand_i}$$

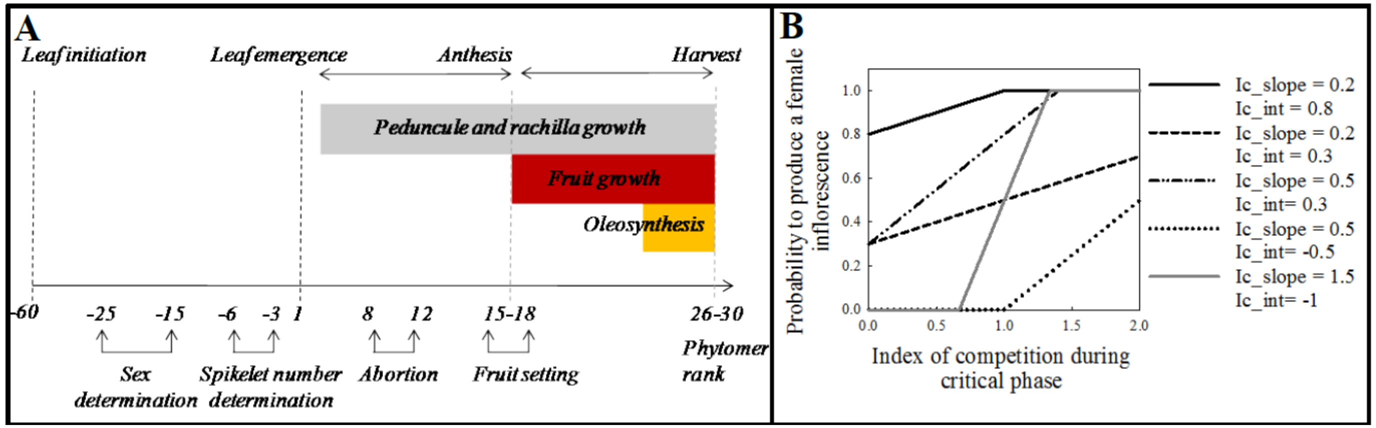
$Supply_i$, plant assimilate supply
$Demand_i$: plant assimilate demand



(from Luquet et al.)

The competition index affects in turn many developmental processes

Limit: no 'local' effect of this variable



(Pallas et al. 2013)

Concluding remarks

Crop and FSP model simulates almost the same processes but at different scales.

Crop models due to their simplicity and flexibility are routinely used for assessing crop potential yield under contrasted environnements

Upscaling of simulation results at the organ scale by FSPM are needed to estimate whole plant behavior.

FSPM model are necessary for the simulation of some growth, development and functionning variables.

Both type of approaches could include genotypic variability in order to analyze GxE interaction and define new ideotypes.

Two forthcoming lessons : (1) light interception modeling, (2) biomass allocation.