Introduction to plant architecture

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Outline

- Concepts of architectural analysis

Terminology

Architectural models

Analysis of the dynamics of plant development

    Repetitions and regularities)

    Ontogenetic gradients

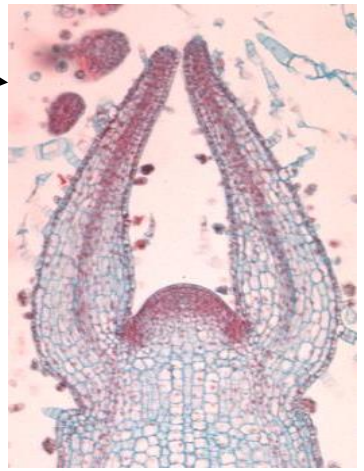
- Genetic control of plant architecture

Between species

Within species

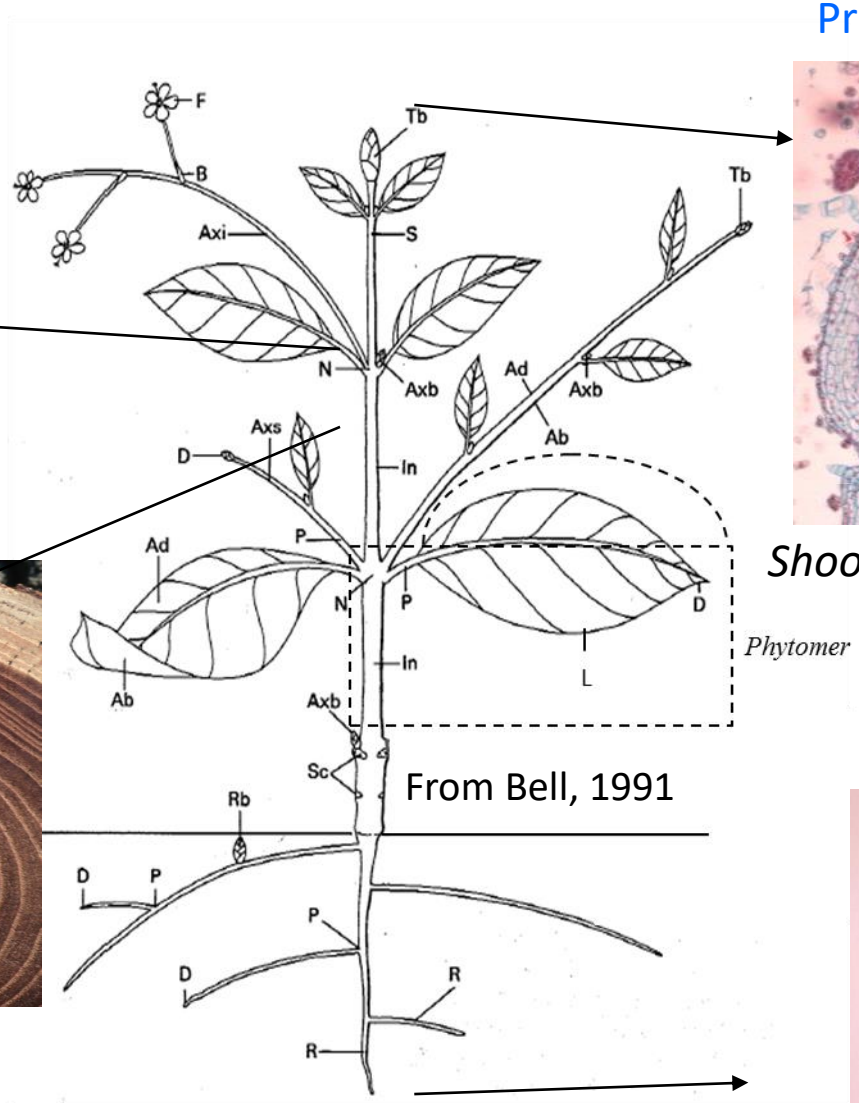
Plant organisation: stem, leaves, roots

Primary growth



Shoot apical meristem

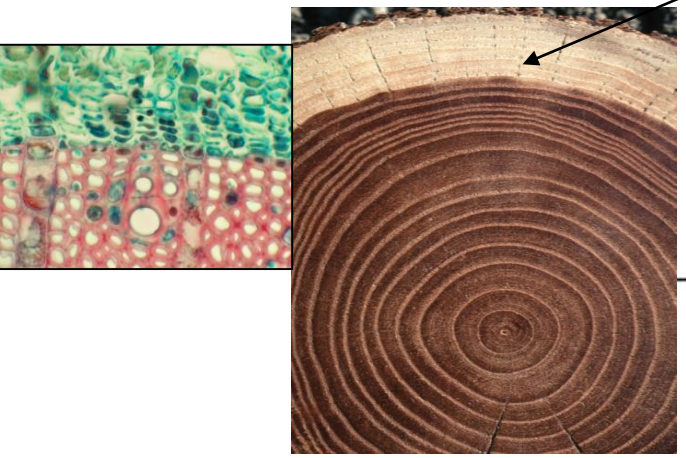
Axillary meristems
Branching

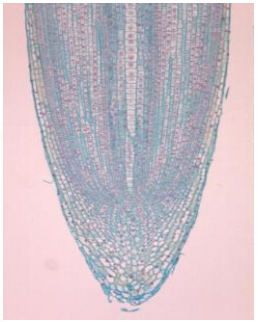


Phytomer

From Bell, 1991

Secondary growth





Root apical meristem

Growth from extremities, bipolarity
Immobilism, Undefined embryogenesis

Main process involved in plant architecture development

1- Growth:

phyllotaxy
growth continuous / rhythmic
direction plagiotropic / orthotropic
life span

2 - Branching

timing: monopodial / sympodial branching
position: Basitonic / mesotonic / acrotpnic

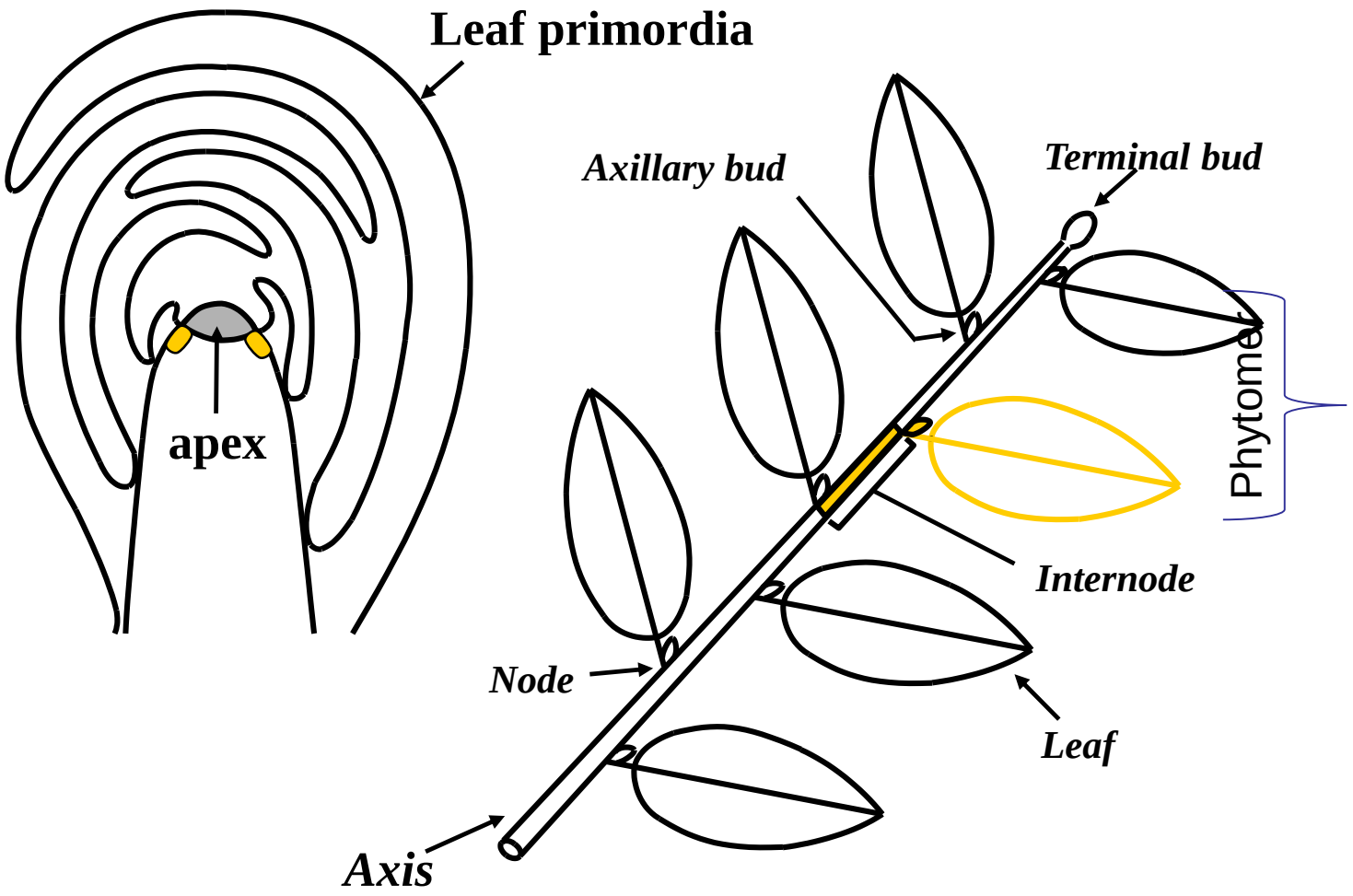
3 – Flowering

4 - Axes differenciation:

equivalents / differenciated / mixed

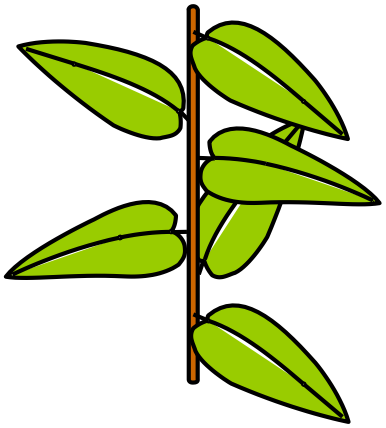
Leafy stem

Growth = Organogenesis + lengthning

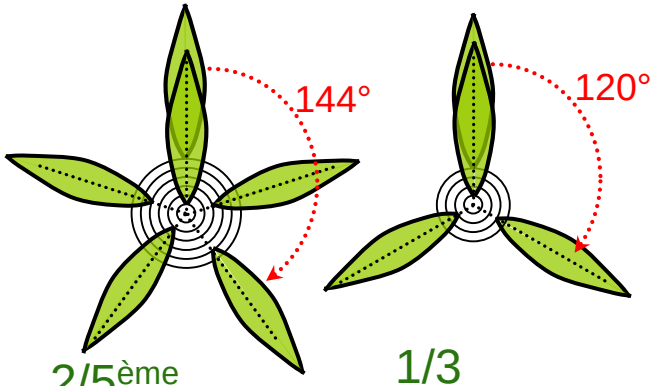


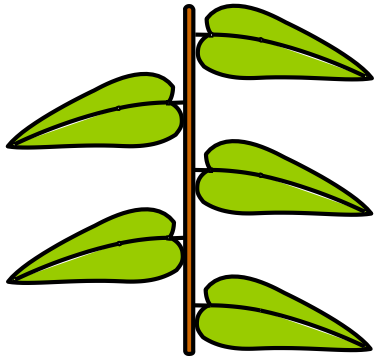
Phyllotaxy: leaf insertion along the stem

1 leaf per node

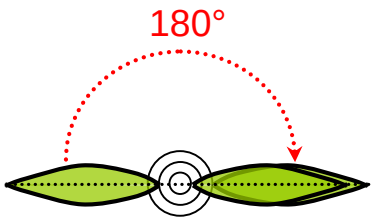


Alternate spiral

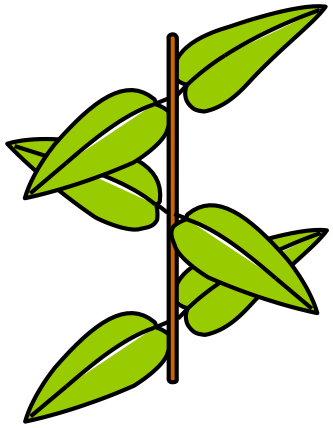




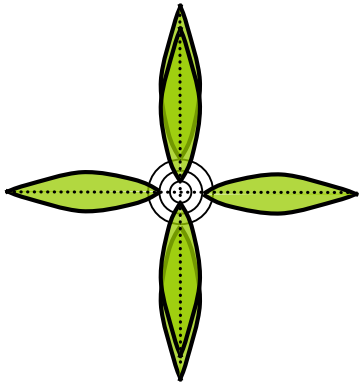
Alternate disticus

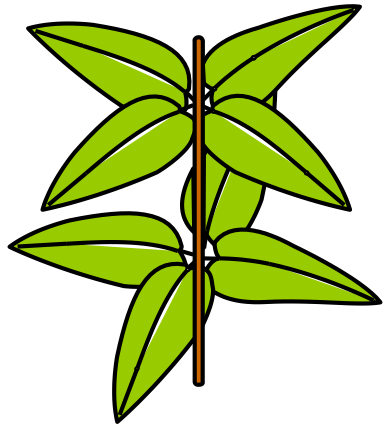


Several leaves per node

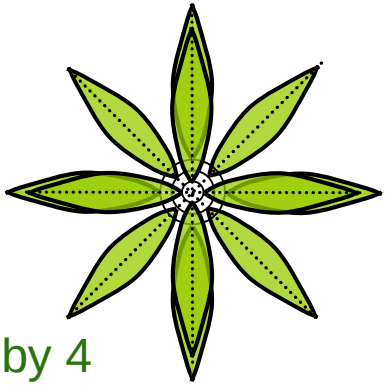


Opposate-décussate





Verticillate



by 4

Schéma P. Heuret

Phyllotaxy alternate distichous

Phyllotaxy alternate and spiral

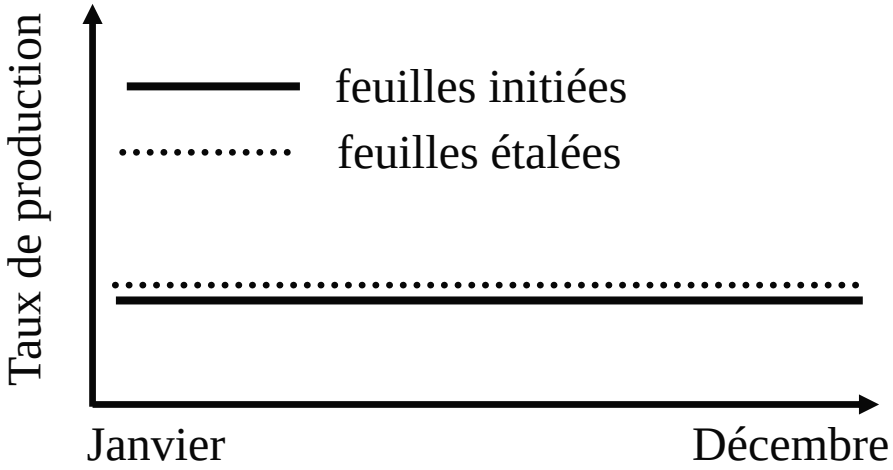
Rosaceae fruit trees

Peach tree

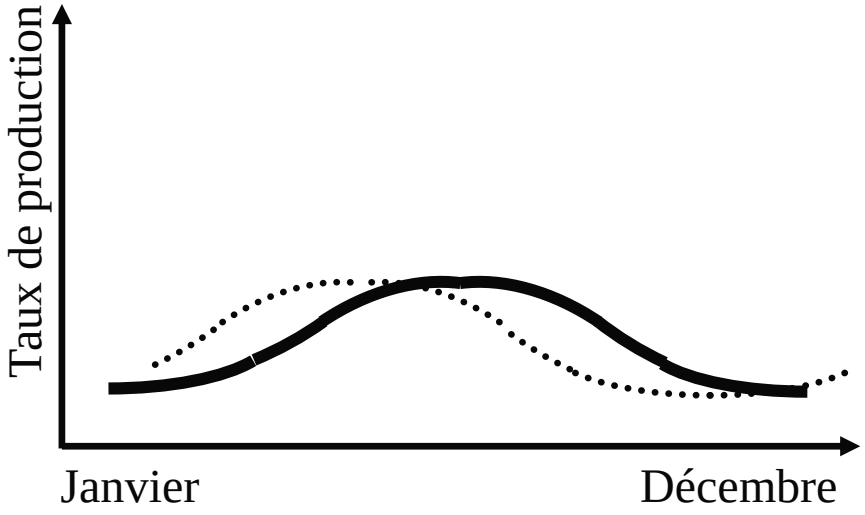
Apple tree

Phyllotaxy verticillate by 2 : opposate-decussate

Primary growth : temporal leaf emission
Continuous growth

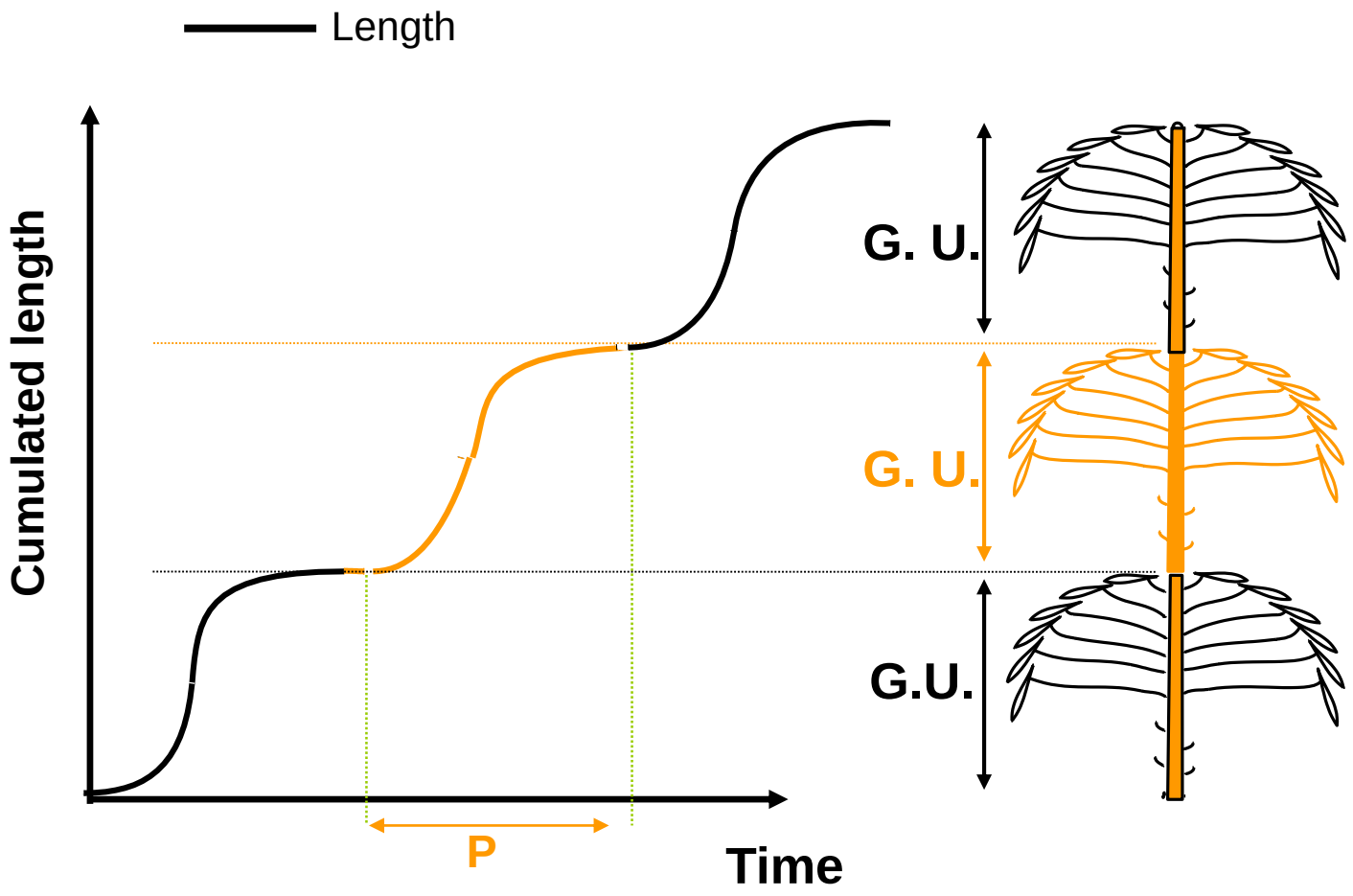


Cocos nucifera (Arecaceae)



Rhizophora mangle (Rhizophoraceae)

Stem growth : temporal leaf emission
Rhythmic growth



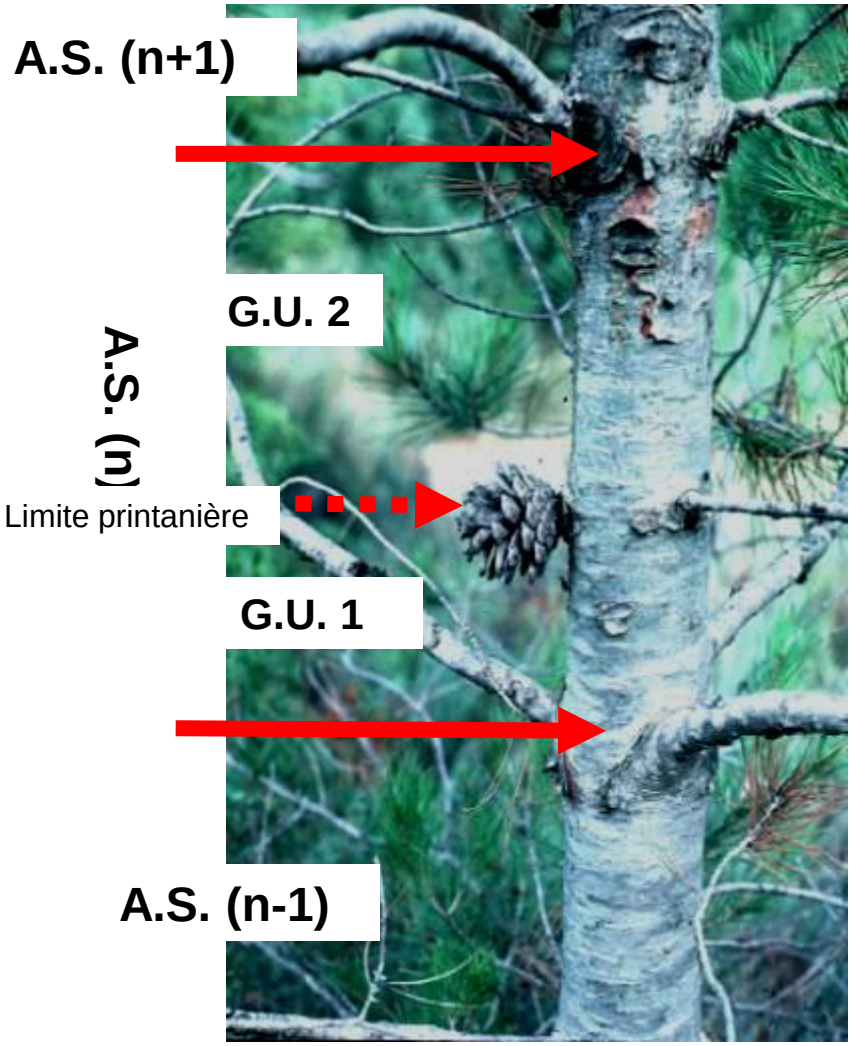
Growth unit (G.U.)

Hevea brasilensis
Hallé and Martin (1968)

Growth unit and annual shoot

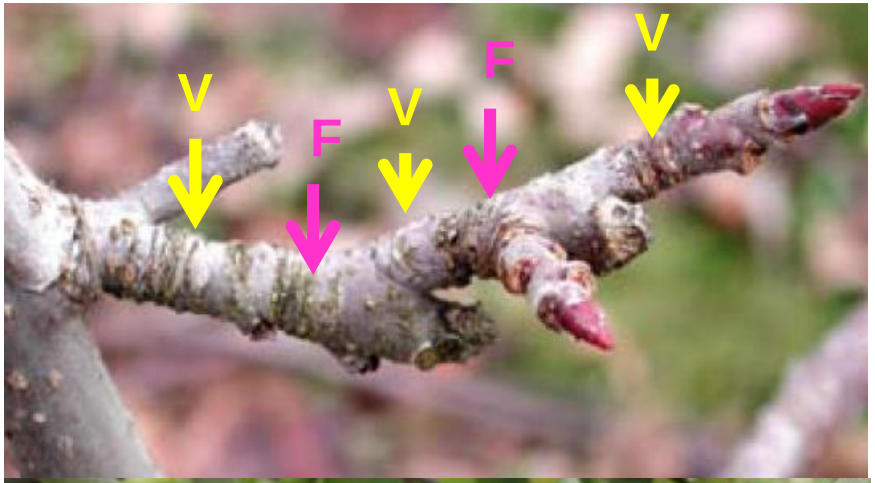
An annual shoot can be made of one, two or more growth units

Polycyclism: when several growth cycles occur in a same year

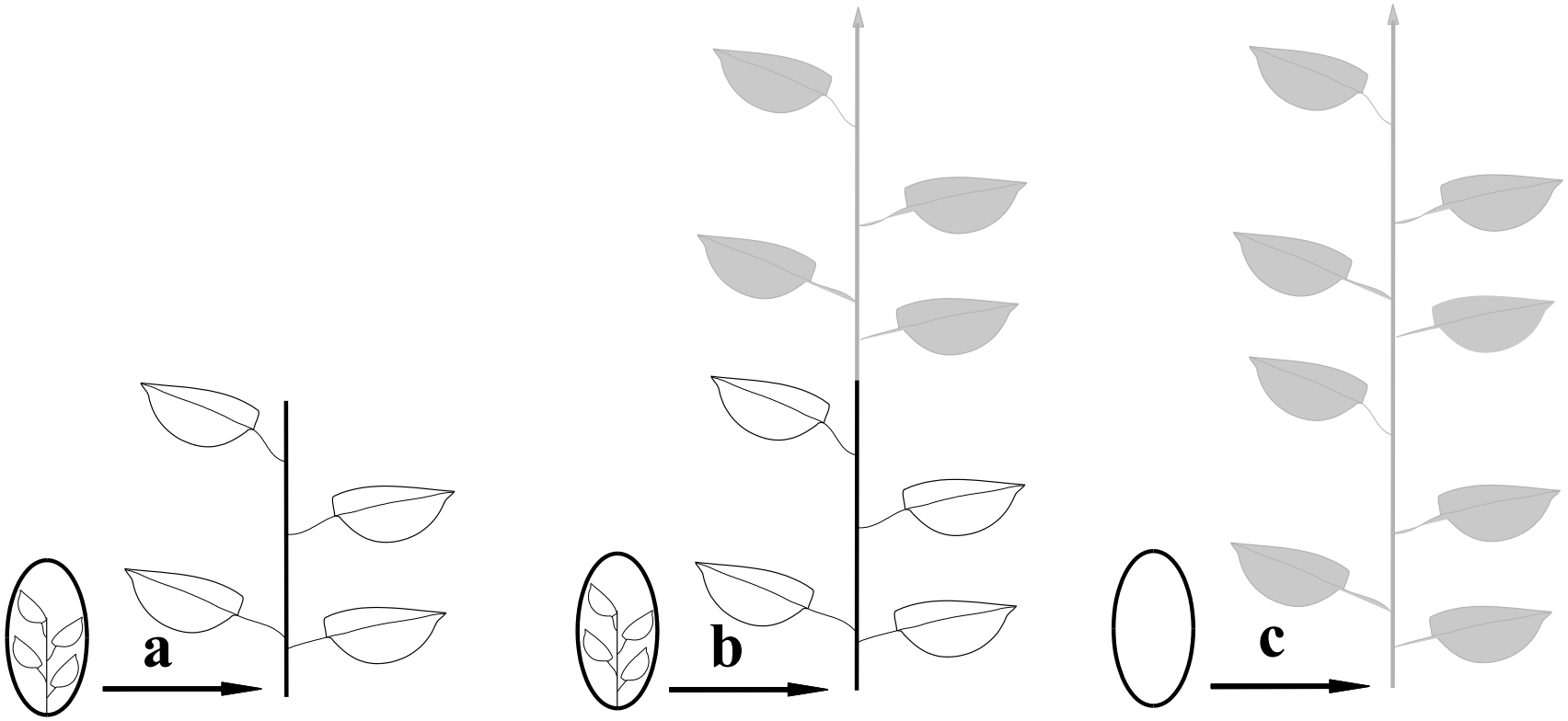


Alep Pine

Apple tree : a floral GU is followed by a vegetative GU (bourse shoot) in the samz year

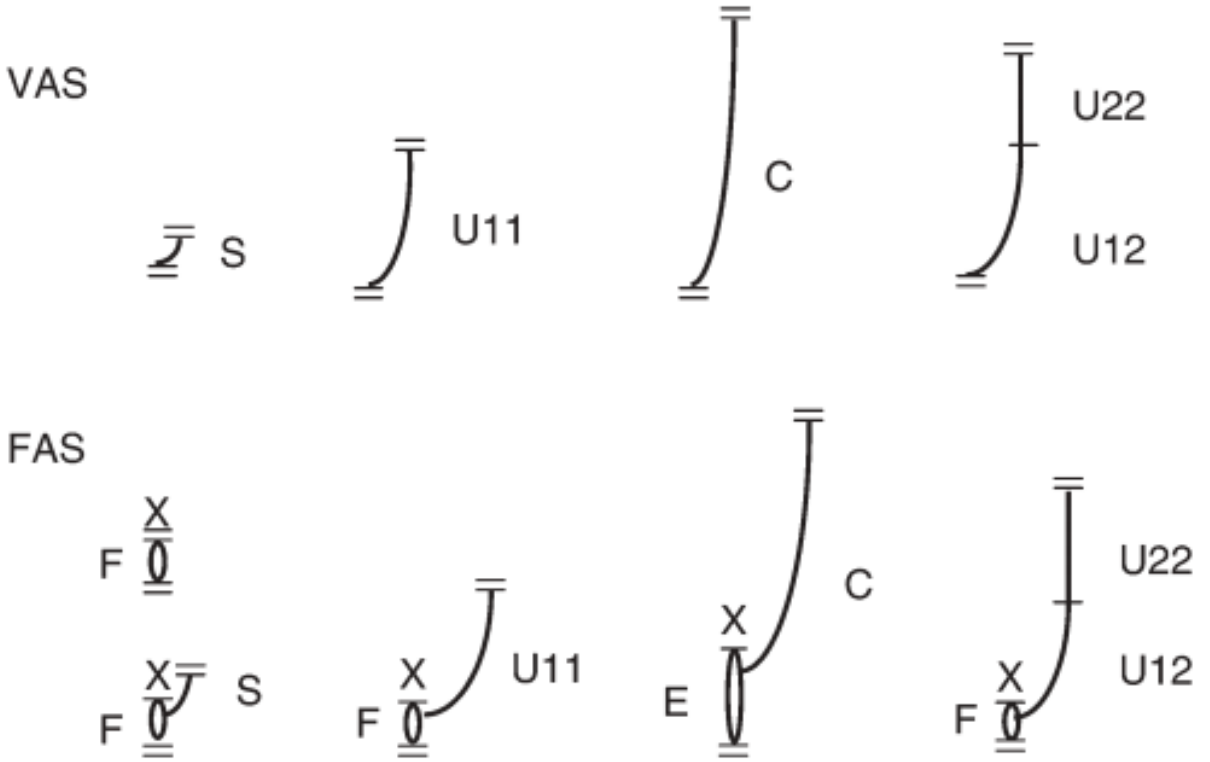


The winter bud:
Preformed and neoformed organs



Dessins Y. Caraglio

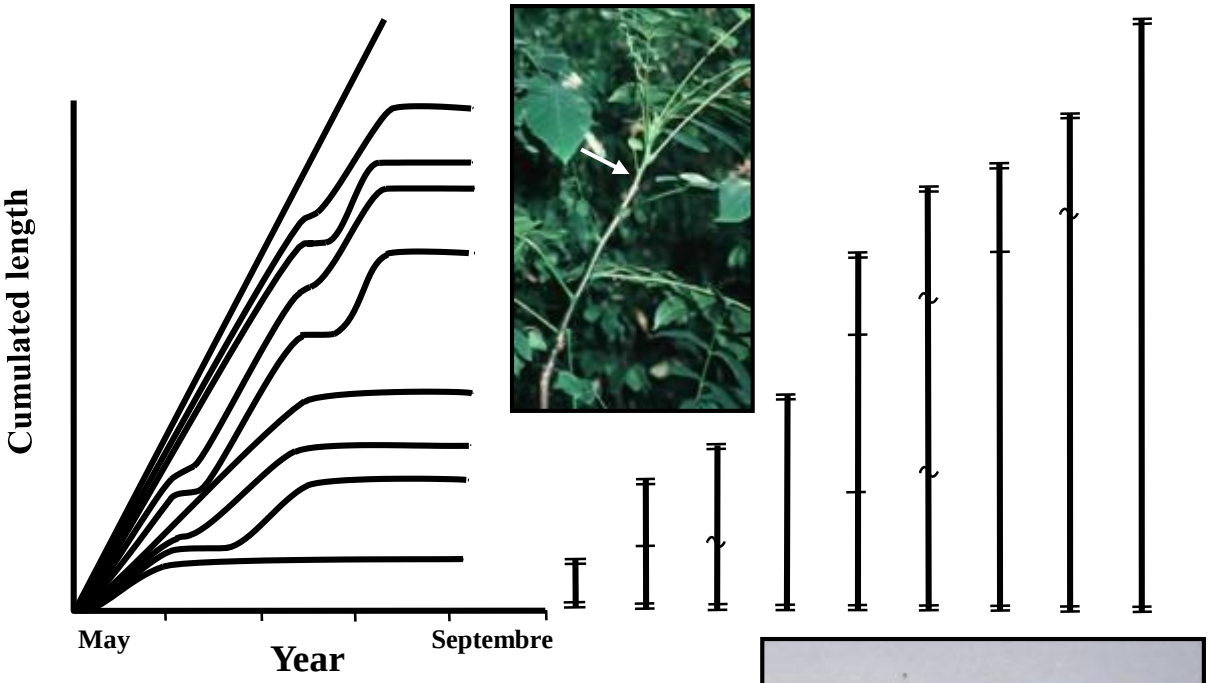
Neoformation and axis polymorphism

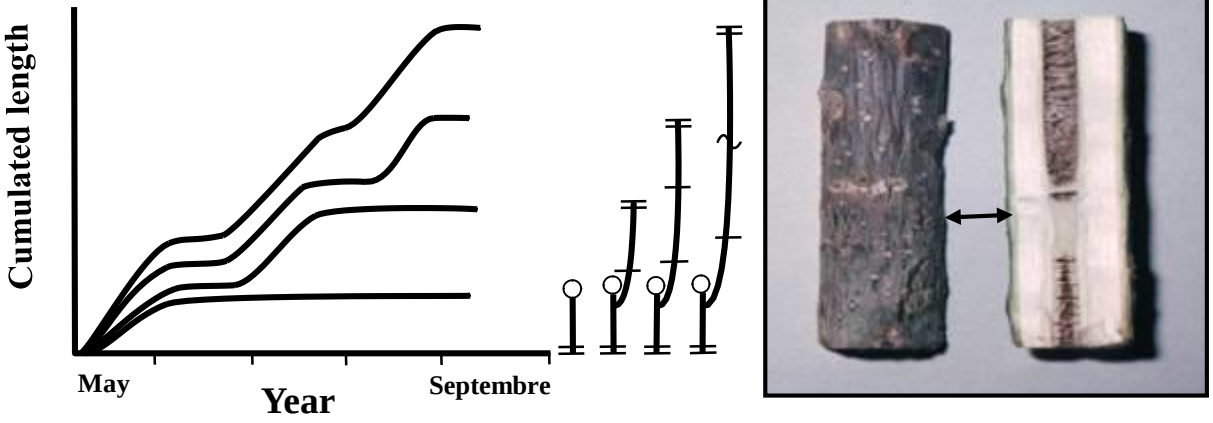


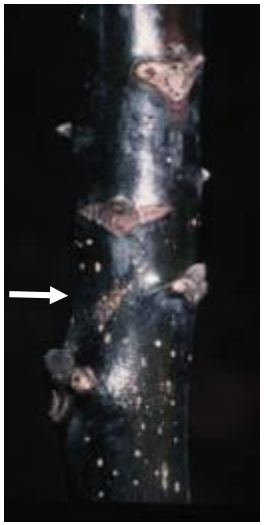
Seleznyova et al. (2008)

FIG. 1. Examples of composition of vegetative (VAS) and floral (FAS) annual shoots in apple. F, Floral growth unit, bourse (represented by an oval); E, extended bourse (represented by elongated oval); S, vegetative spur; U, extension growth unit; C, uninterrupted growth unit. Index indicates growth unit type, e.g. U12, first of two growth units of annual shoot. =, Limit of annual growth; –, limit of growth unit (flush); X, termination of apical meristem. In floral annual shoots, the first growth unit is always F or E and subsequent vegetative growth can occur from an axillary meristem.

Growth modalities: cinetic and … morphological markers







The walnut case, *Juglans regia* (from Sabatier and Barthélémy)

Axis orientation des axes in space: Orthotropy and Plagiotropy

Orthotropic axis

- Vertical growth
- Phyllotaxy alternate spiral
- Axial symetry
- Exploration of space

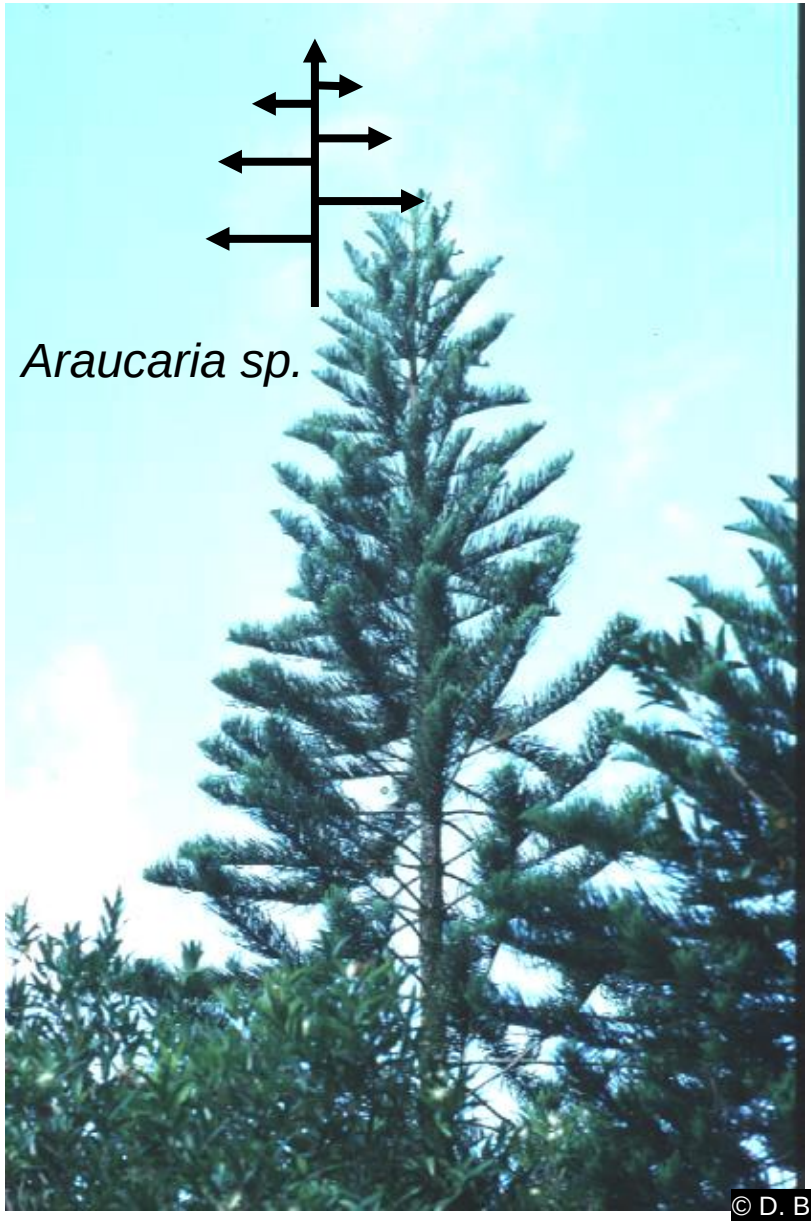
Axis orientation des axes in space: Orthotropy and Plagiotropy

Plagiotropic axis

Coffea arabica

- Horzontal growth
- Phyllotaxy alternate distichous
- Symetry bilateral
- Sexuality
- Exploitation of space

Ulmus rubra
(from phytotheque.wordpress.com



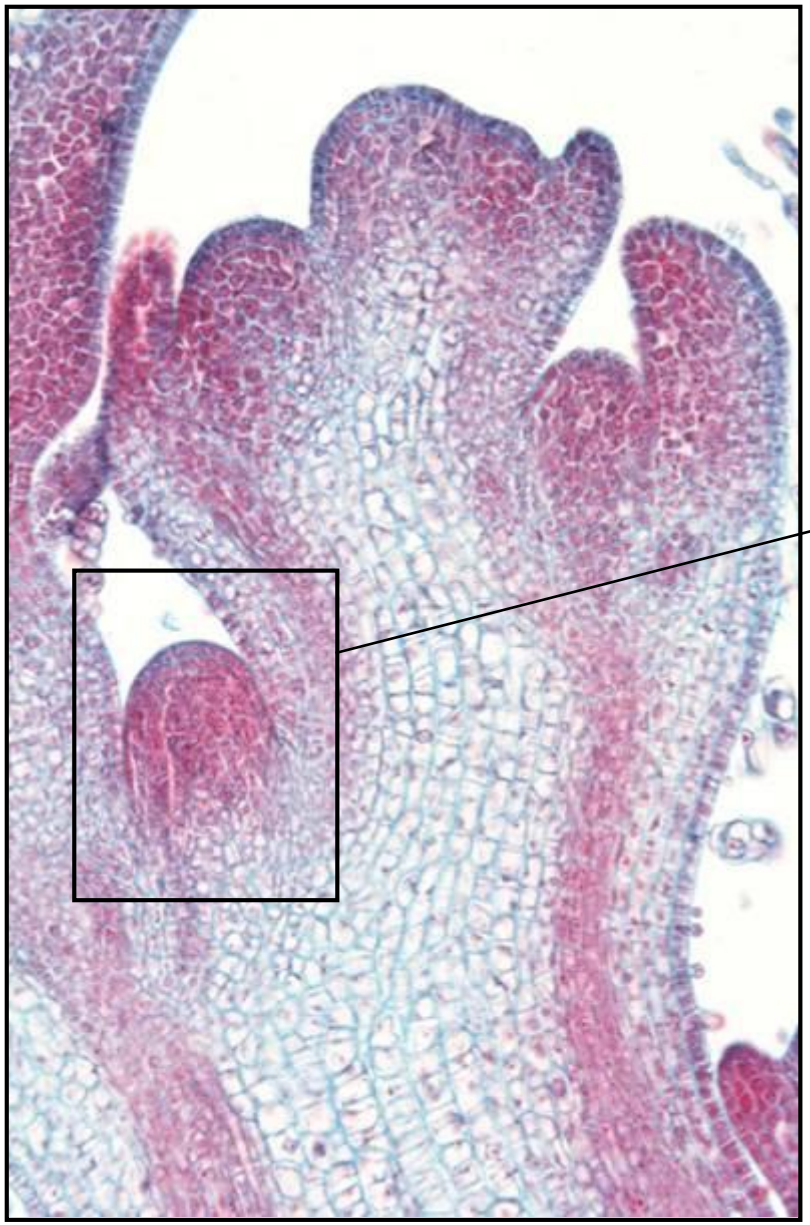
All axes are orthotropic or …..

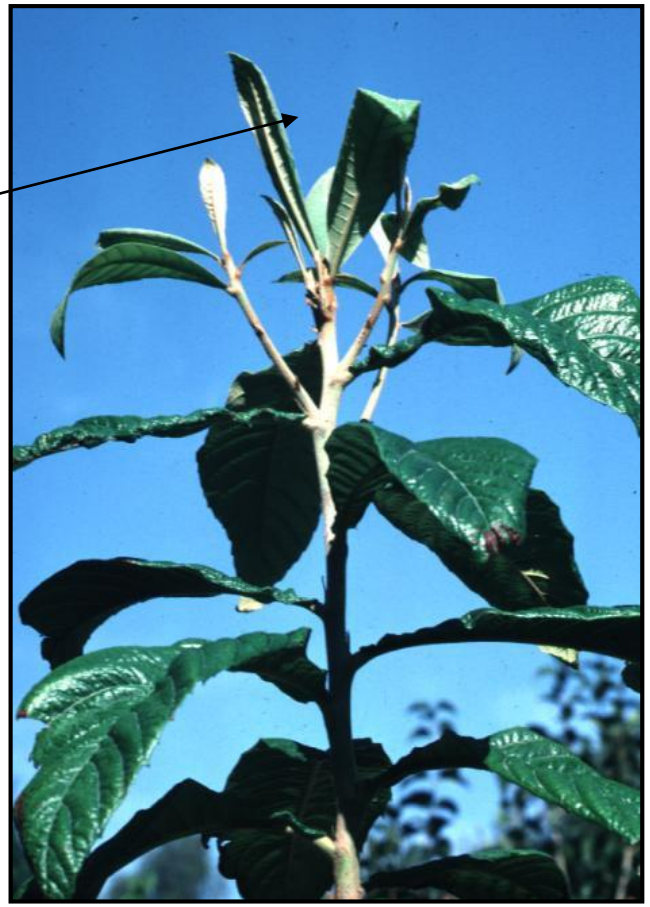
one axis is orthotropic and the others are plagiotropic

Mixed axes

A same apical meristem builds an axis first orthotropic then plagiotropic
With change in phyllotaxy and symetry

Branching





Medlar (Eryobotria japonica)

Branching in time: immediate or delayed

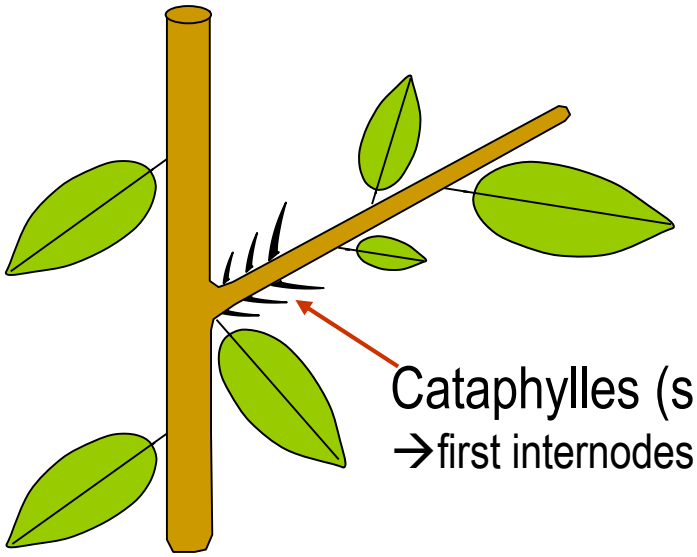
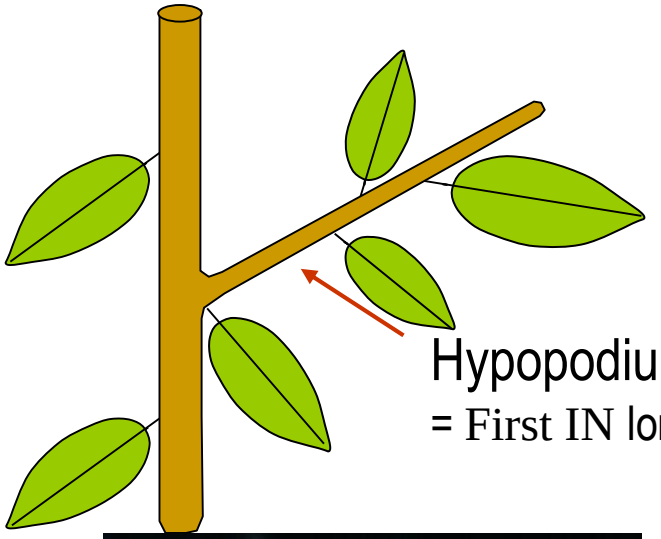


Schéma
P. Heuret

Cataphylles (small leaves
→first internodes are very shorts

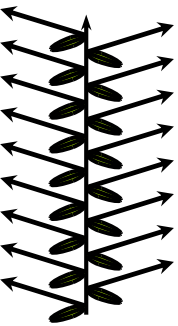


Hypopodium
= First IN long

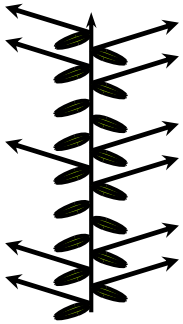
Lateral with delayed branching
(phase with axillary bud before outgrowth)

Lateral with immediate branching

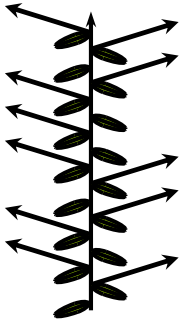
Branching in space – continuous, rhythmic or diffuse



continuous

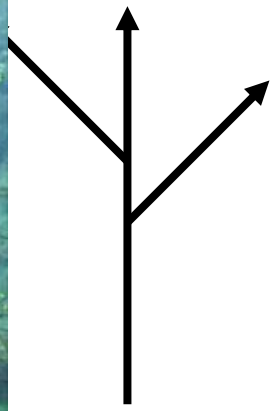


rhythmic

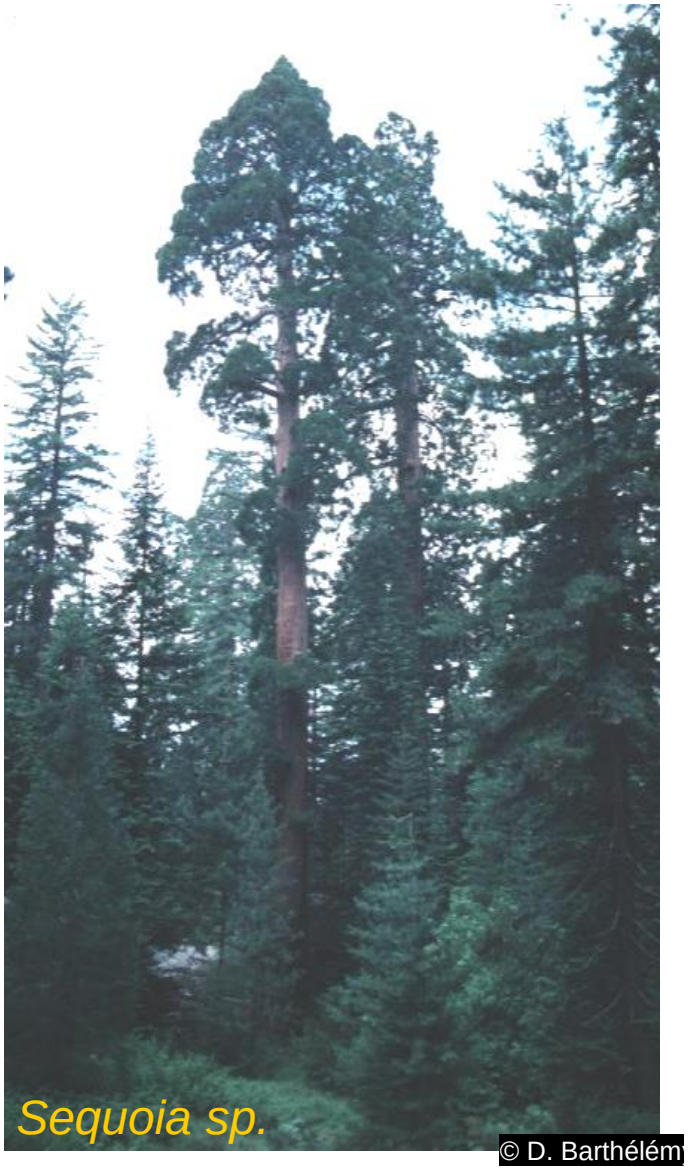


diffuse

Monopodial branching



Monopode



Meristeme has a undeterminate growth

Determinate growth: stop of stem construction

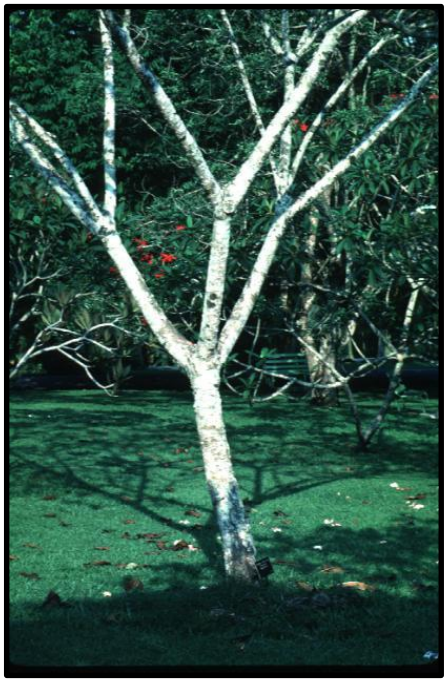
Terminal flowering

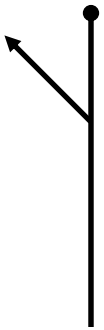
Transformation in spine…
Parenchymatisation of apical meristem

Death of apical meristem

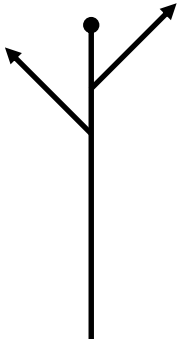
Meristem has a determinate growth

Sympodial branching

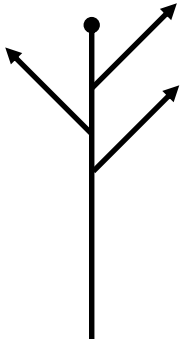




Sympode



Sympode



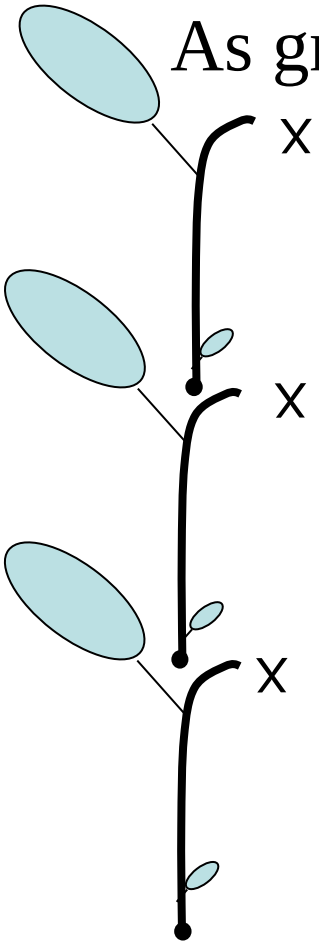
monochasial

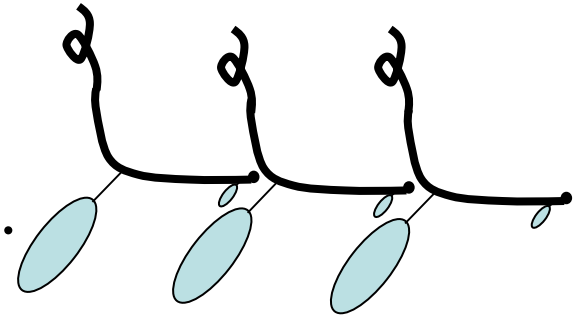
dichasial

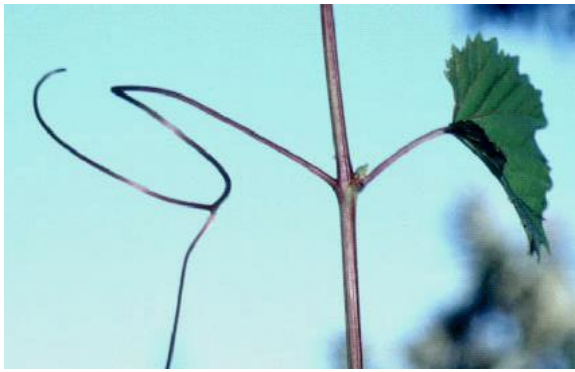
polychasial

Axis built as succession of sympodes

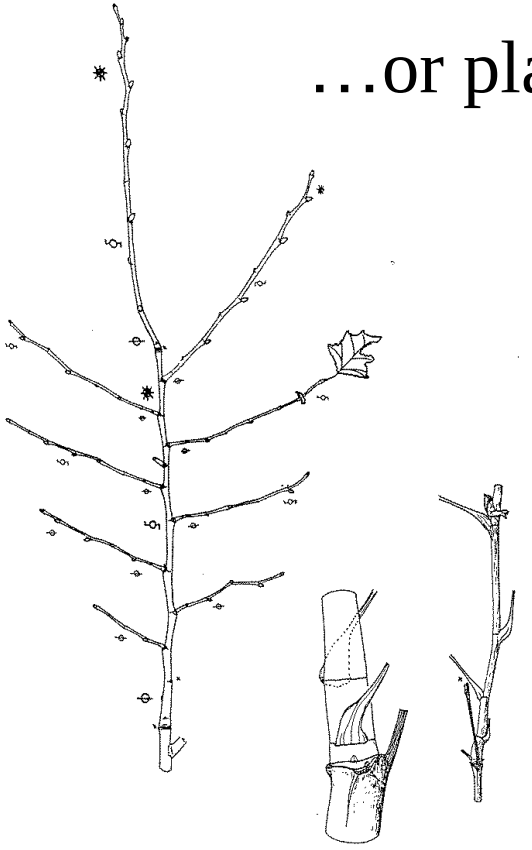
As grape vine…







…or platanus

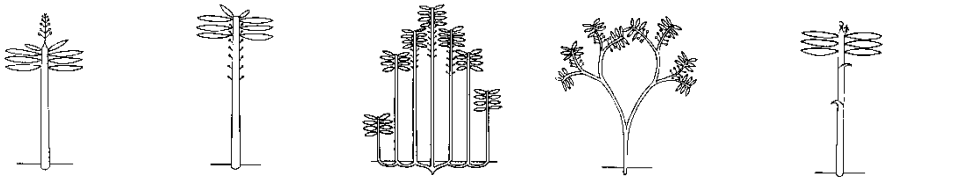


Architectural analysis and dynamics of plant developpement

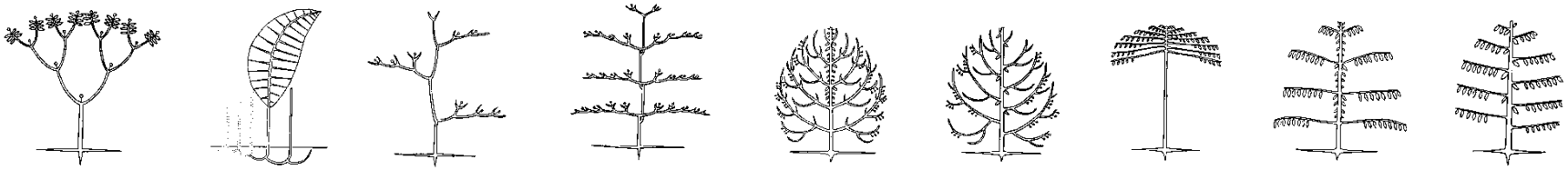
23 architectural models (Hallé et al., 1970; 1978)
corresponding to specific combinations of traits

1 – Unbranched plants
2 – Branched plants
- Axes are all equivalents and orthotropic
- Axes are differenciated :
  - growth continuous / rhythmic
  - monopodial / sympodial branching
  - direction plagiotropic / orthotropic
  - life span
  - able to flower and position of flowers
- Axes are mixed

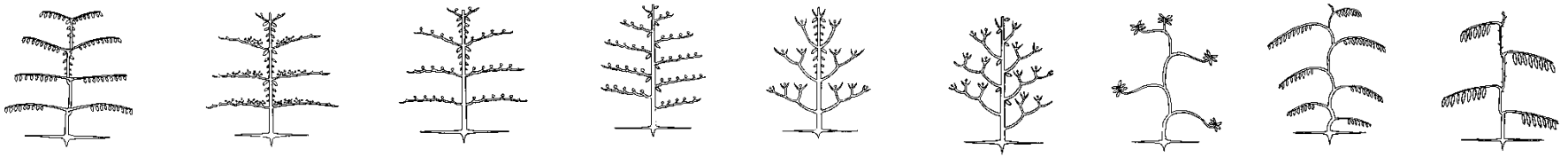
Stability of plant architecture for a given species: A framework for organizing plant architecture diversity



Modèle de **HOLTTUM** | Modèle de **CORNER** | Modèle de **TOMLINSON** | Modèle de **SCHOUTE** | Modèle de **CHAMBERLAIN**



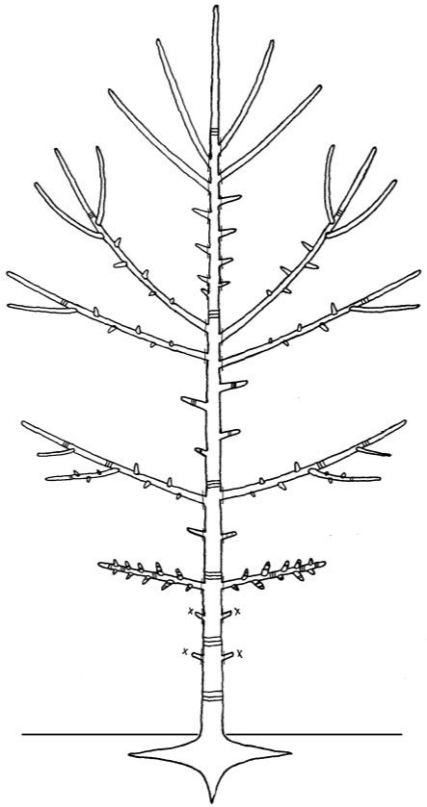
Modèle de **LEUWENBERG** | Modèle de **Mc CLURE** | Modèle de **KORIBA** | Modèle de **PREVOST** | Modèle de **RAUH** | Modèle de **ATTIMS** | Modèle de **COOK** | Modèle de **MASSART** | Modèle de **ROUX**



Modèle de **NOZERAN** | Modèle de **AUBREVILLE** | Modèle de **FAGERLIND** | Modèle de **PETIT** | Modèle de **SCARRONE** | Modèle de **STONE** | Modèle de **CHAMPAGNAT** | Modèle de **TROLL** | Modèle de **MANGENOT**

Hallé et al. (1970; 1978)

The architectural unit

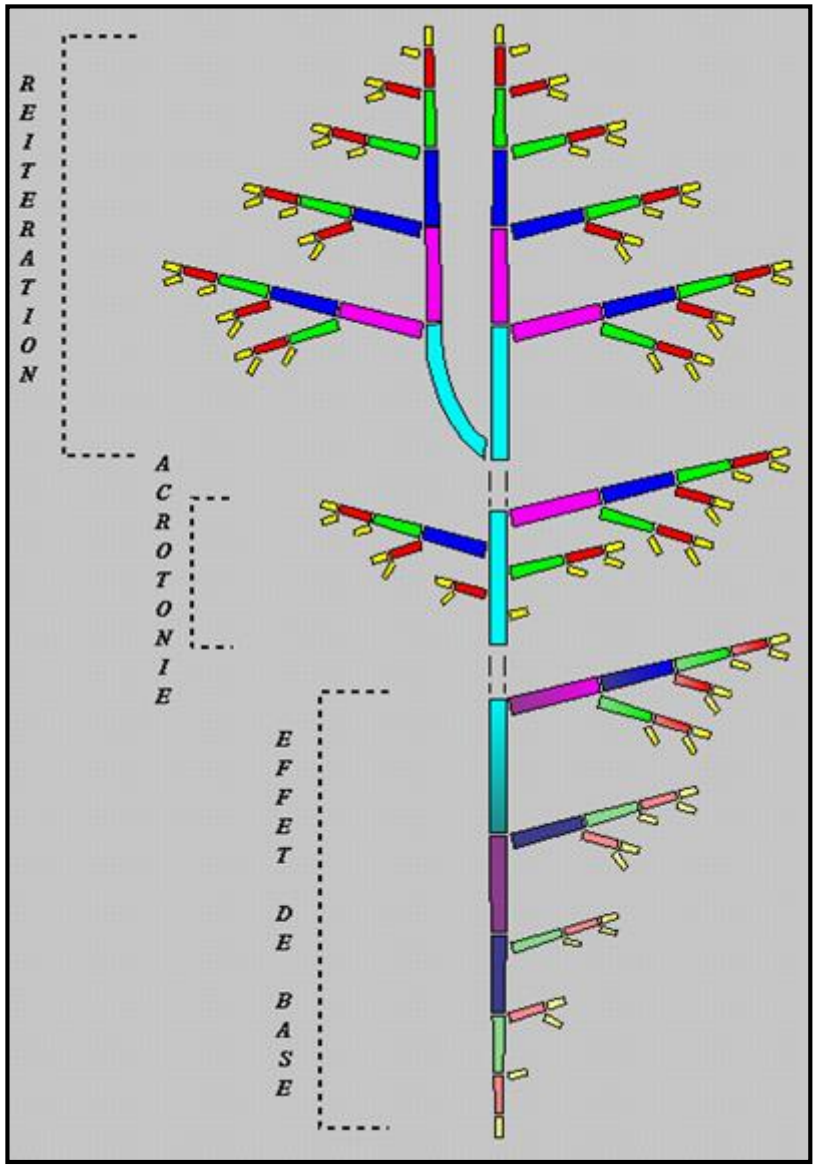


	Tronc	Branche	Rameau	Rameau court
Ramification	Porte tous les autres éléments architecturaux	Porte des rameaux et des rameaux courts	Porte des rameaux courts	Non ramifié
Nombre de rameaux longs	En moyenne entre 4 et 6	En moyenne entre 2 et 4	Aucun	Aucun
Sexualité	Seules les premières feuilles de l'unité de croissance porte des fleurs	Seules les premières feuilles de l'unité de croissance porte des fleurs	seules les premières feuilles de l'unité de croissance porte des fleurs	Toutes les aisselles sont florifères sauf les écailles de chaque unité de croissance
Nombre de feuilles par unité de croissance	Très variable de 8 à 50 et plus	Assez varible, de 8 à 30	Peu variable autour d'une dizaine	Très stable entre 3 et 7
Direction de coissance	Verticale	Oblique	Horizontale	Sans préférence (agéotrope)

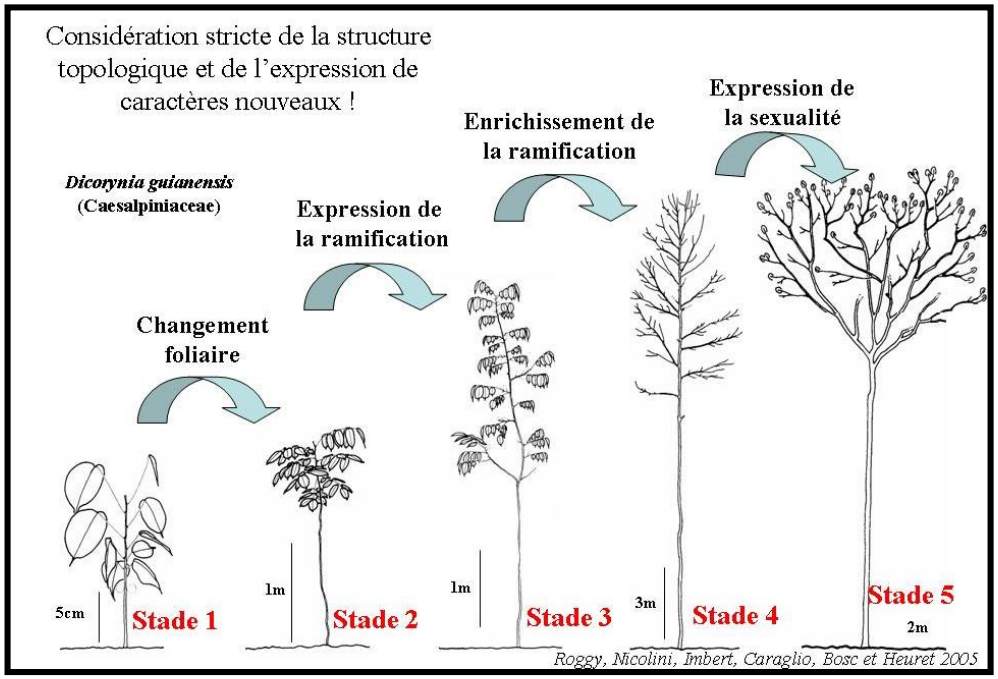
(Barthélémy et al. 1989)

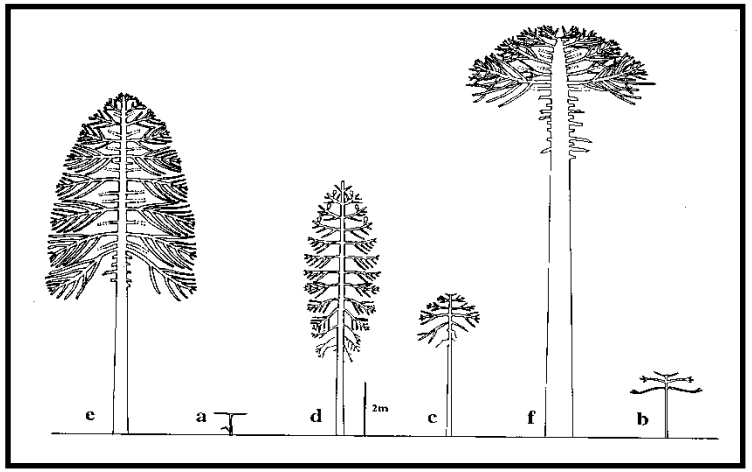
- Specific stage where all axis categories are developped
- Diagnostic on all axis categories for a given species.

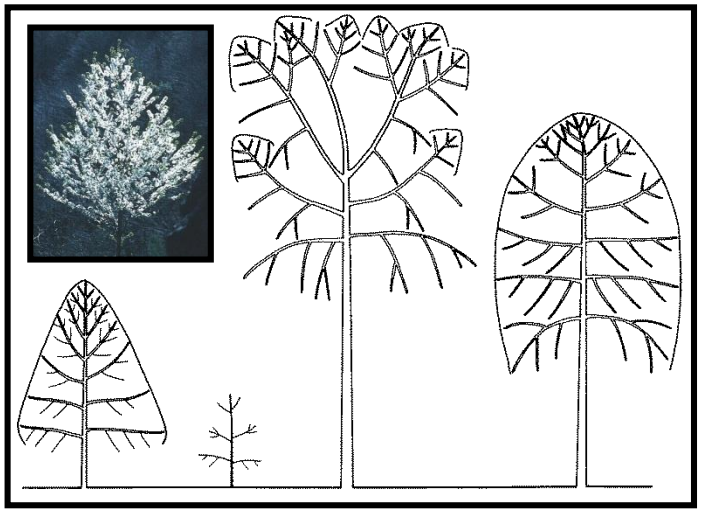
Plants are organised in time and space: Morphogenetic gradients



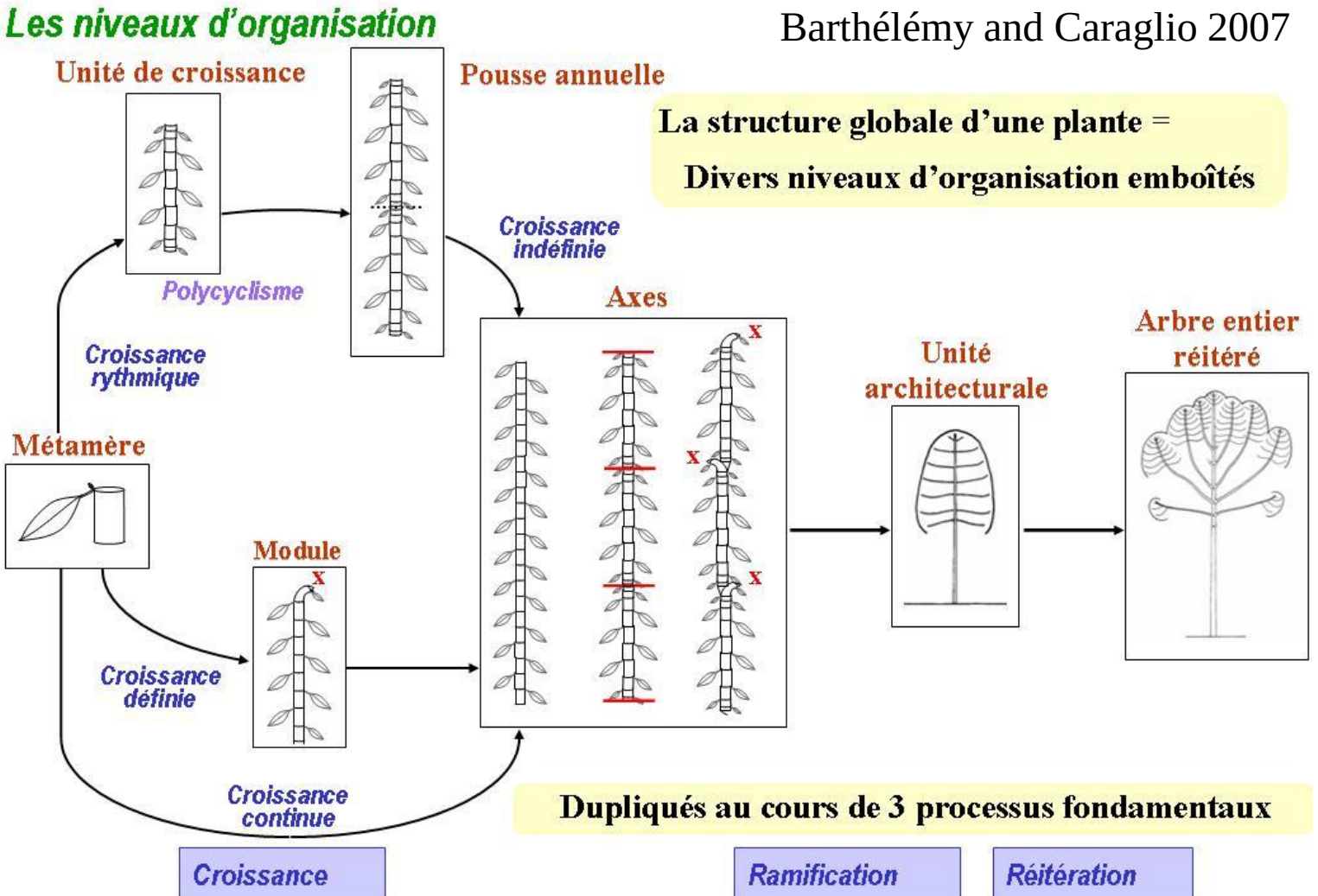
Plants are organised in time and space: Morphogenetic gradients





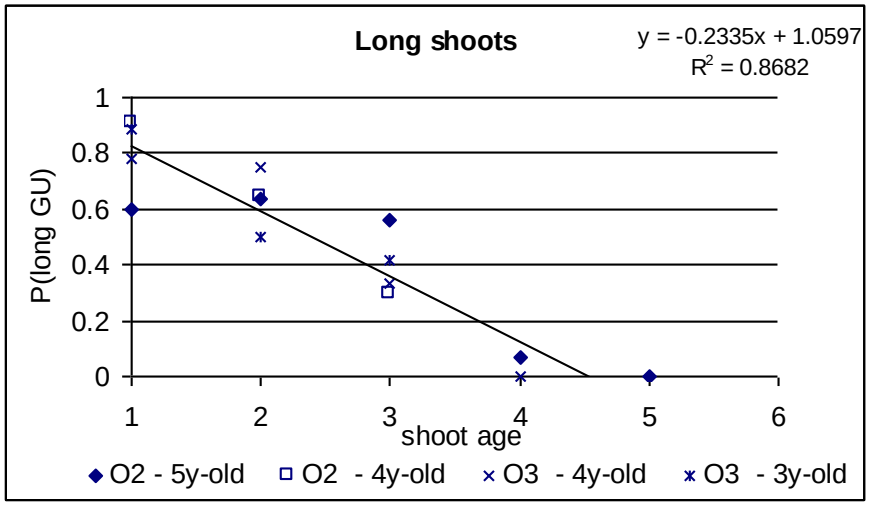


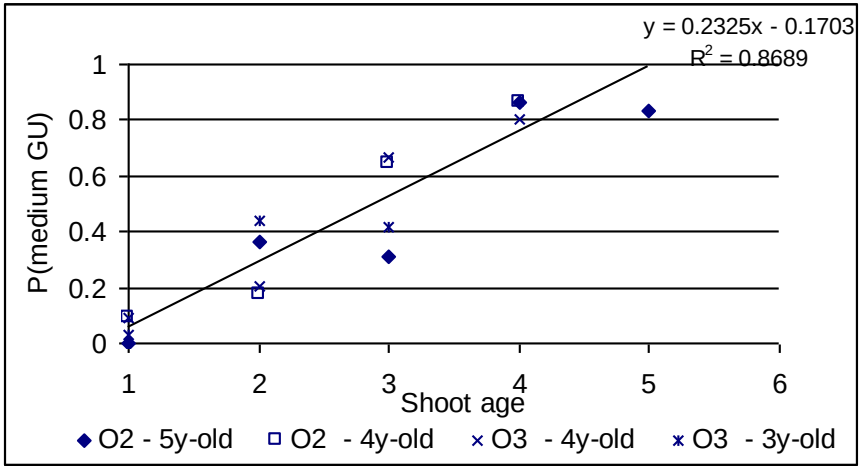
Identifying organisation levels in the plants
➔ identifying spatial and temporal regularities



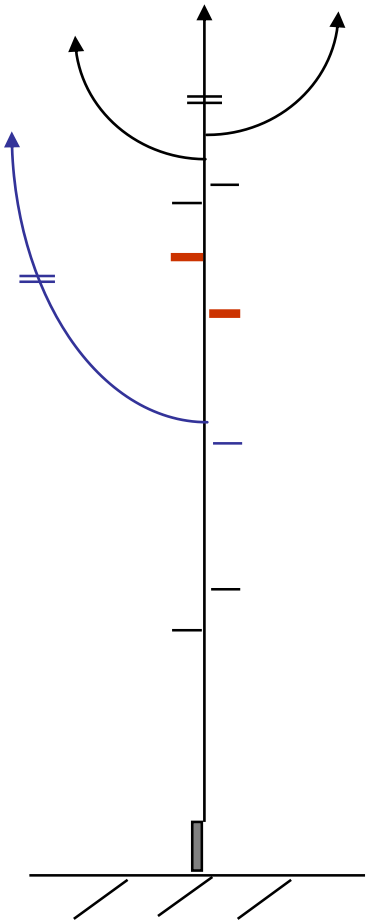
The example of the apple tree

Phyllotaxy spiral
Preformation : short axes (spurs)
Neoformation : medium to long axes
Rhythmic growth





The example of the apple tree
Branching in space

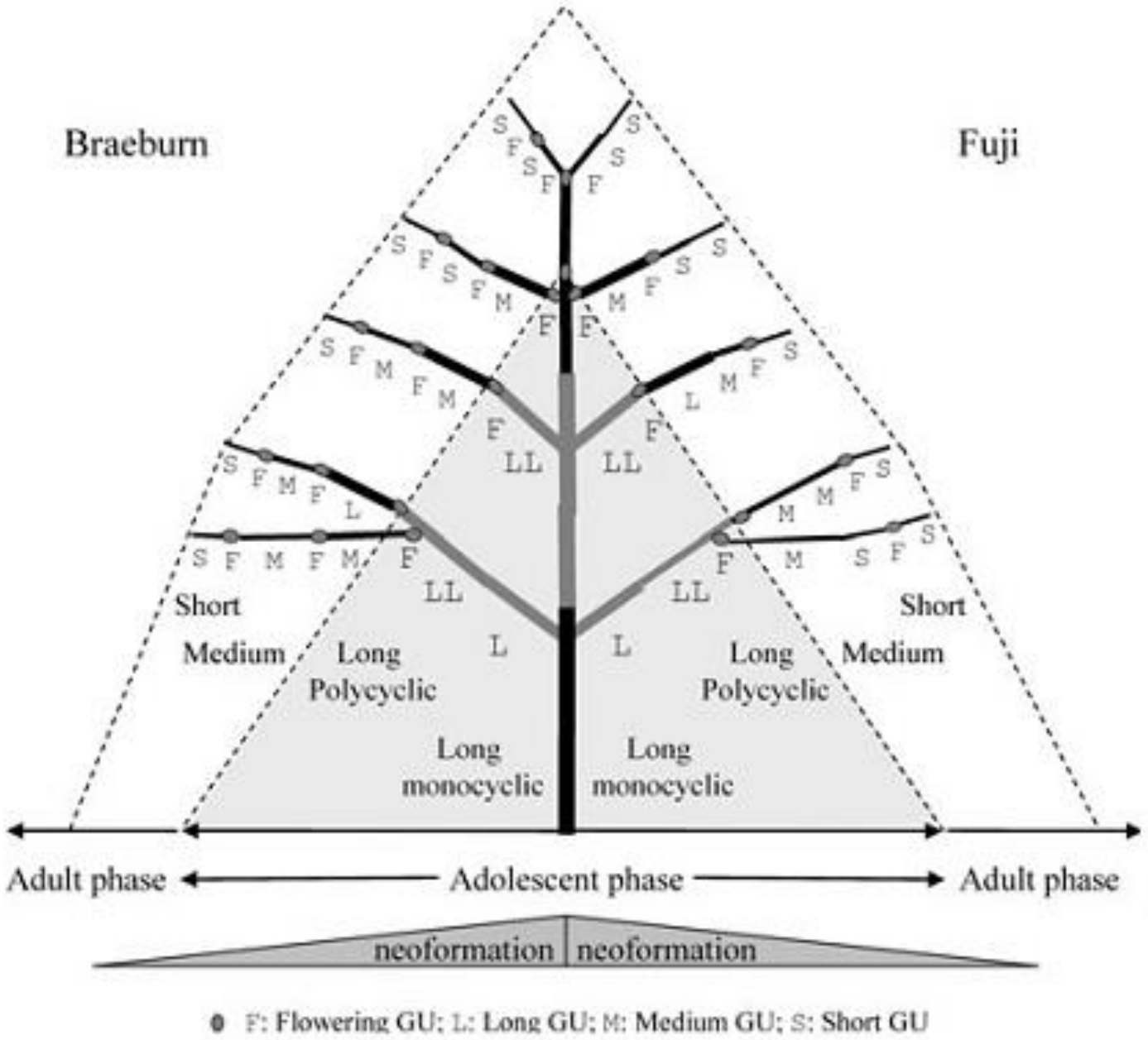


During vegetative phase :
- Immediate and monopodial
- Delayed and monopodiale

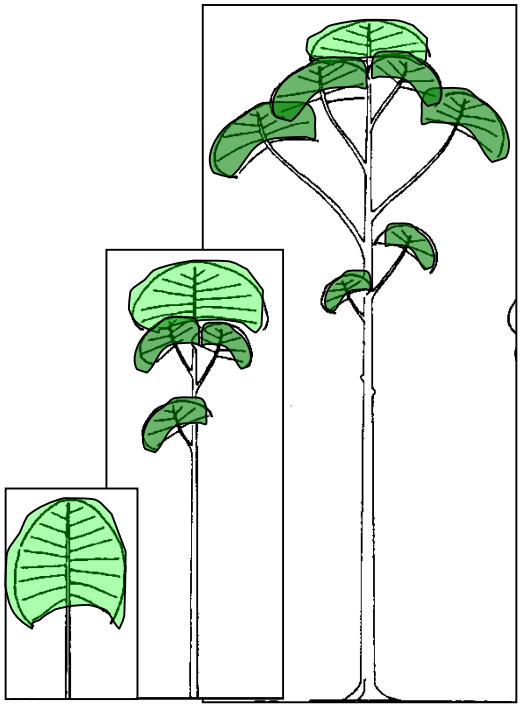
Photo P.E. Lauri

After flowering:
Immediate and sympodial
Delayed and monopodiale
(on long axes)

Guedon and Costes (2012)



Reiteration



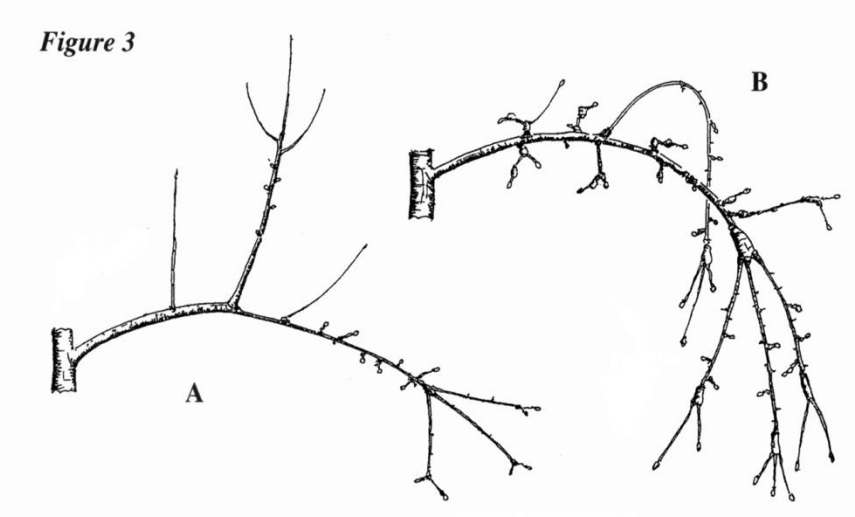
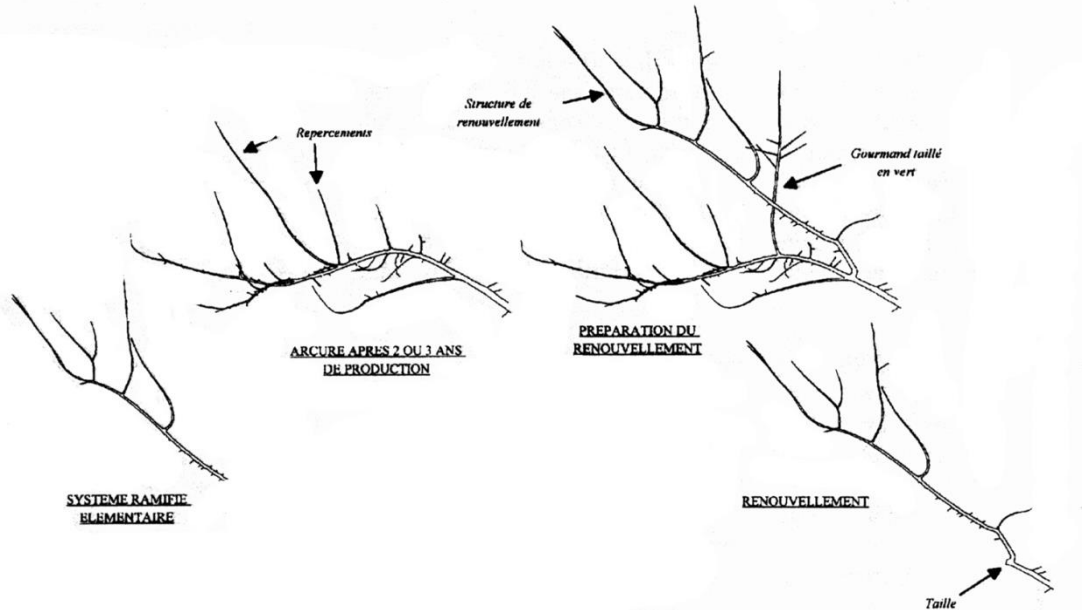


Figure 1 - Chronologie du renouvellement (exemple de "Modesto")



Traumatic reiteration

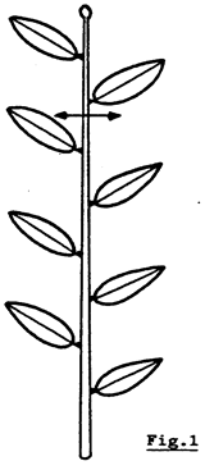


Fig.1

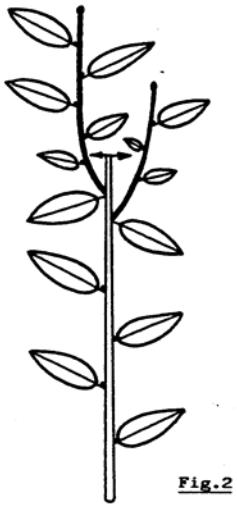


Fig.2

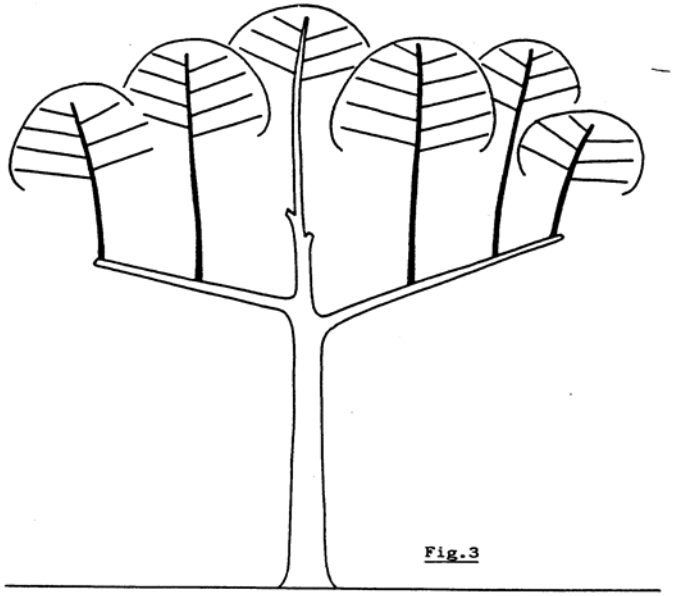
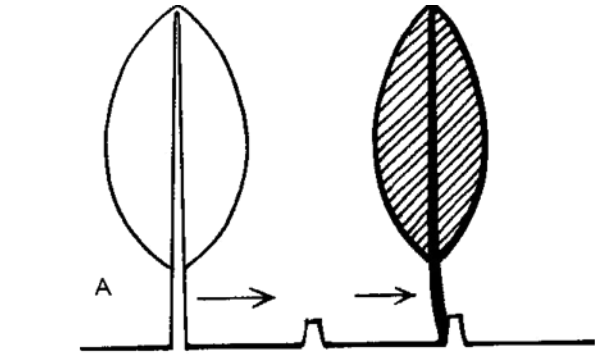
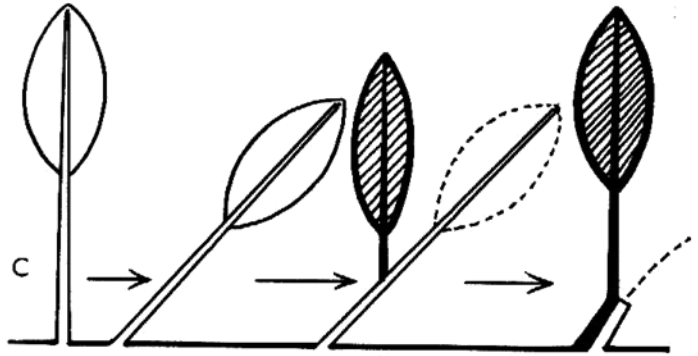
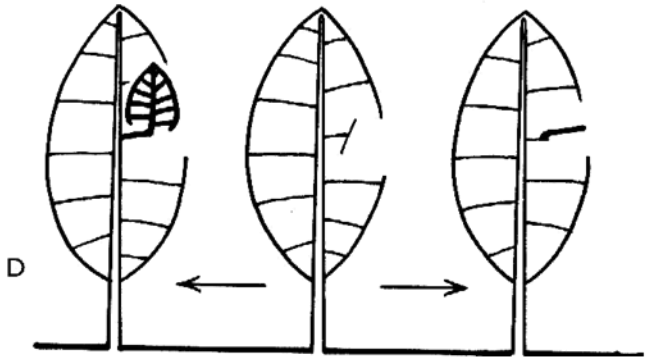


Fig.3







Take home messages

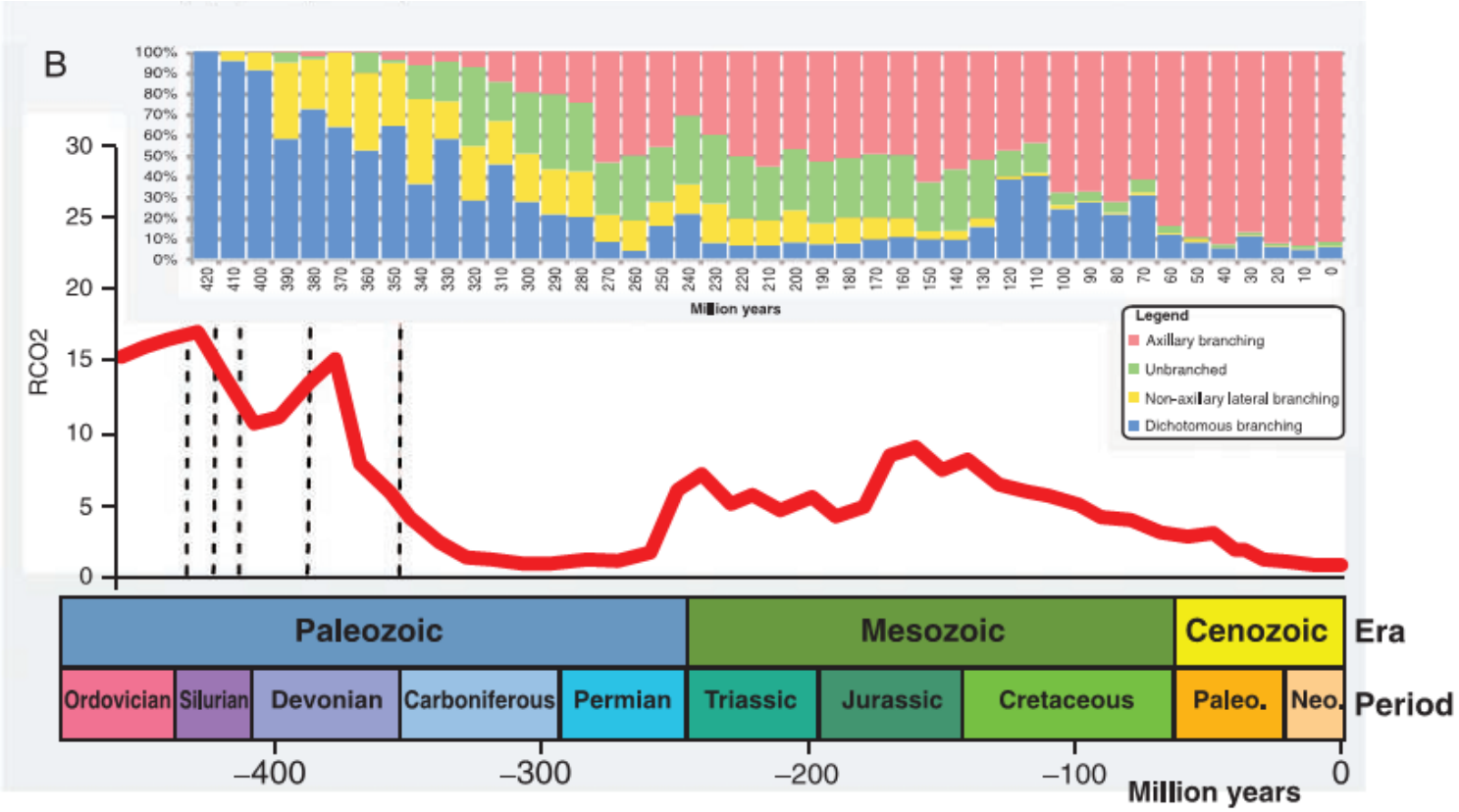
- Plant architecture results from a defined set of rules that can be enumerated (limited number) and combined
- Each species is build according to a specific combination
- The dynamics of plant development is driven by repetitions
- Those repetitions are highly organized in time and space

Genetics of plant architecture

Evidence for genetic control of plant architecture

- Long history of observations on the diversity of plant morphology and its evolution

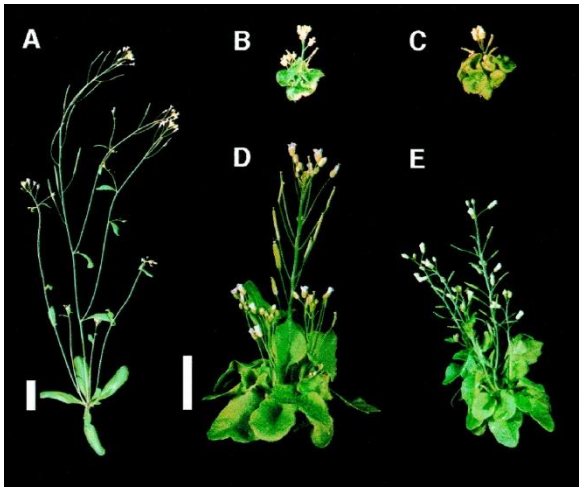
Plant metamorphose *(Goethe, 1790) ; Raunkiaer (1934);*
Niklas (2000): Developmental constraints and biomechanics ;
Benitez et al. (2017) or Harrison et al. (2017): eco-devo point of view of plant body evolution



Chomiki et al., 2017

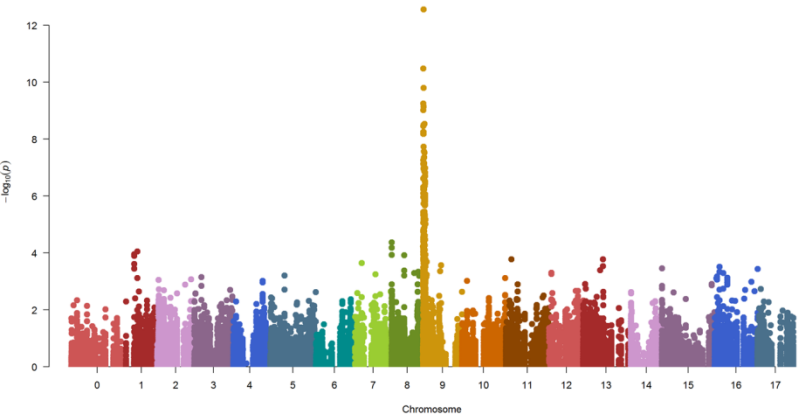
Linking genes ad genomes to organ and plant form

- **Mutants with phenotypes linked to architecture**



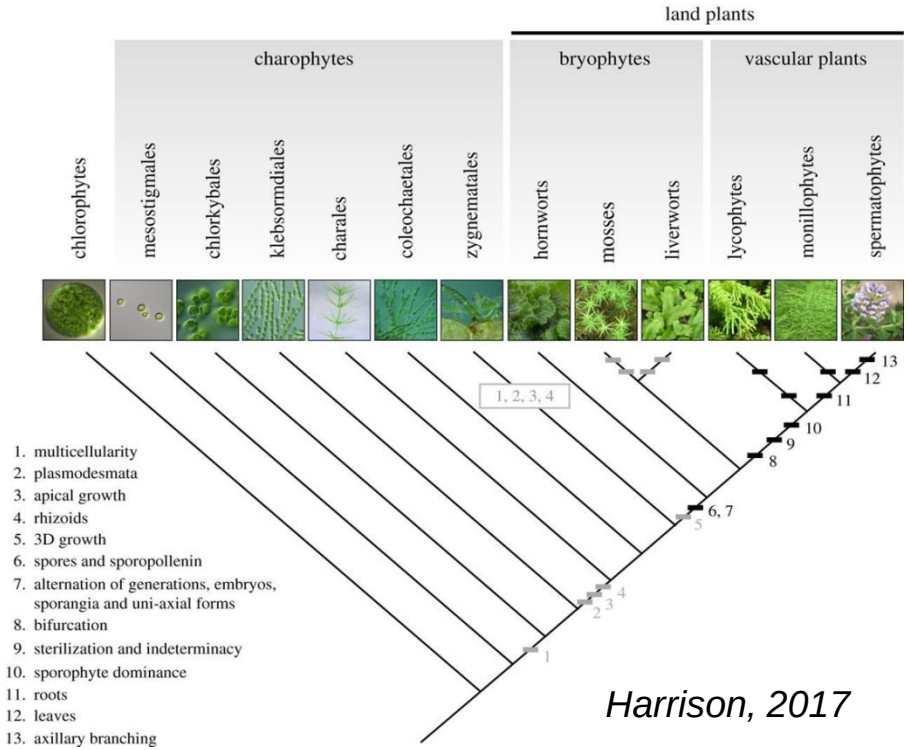
Nogushi et al., 1999

- **Associations studies**



Andres et al., unpublished

- **Eco-devo studies (Ecological Development)**



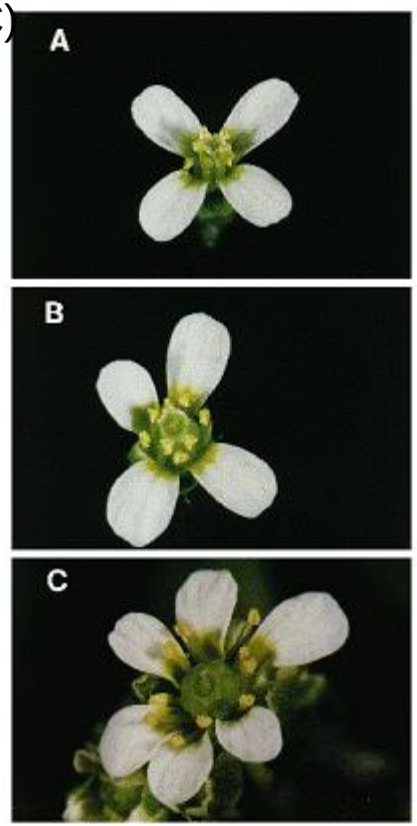
Harrison, 2017

Mutants have been created for most characters

- SAM control:
  - ✓Determinate vs indeterminate growth
  - ✓Organogenesis and phyllotaxy
  - ✓Growth cessation and rhythmic growth
- Axillary bud control
  - ✓Formation
  - ✓Outgrowth
- Either SAM or axillary bud:
  - ✓Floral induction
- Secondary growth
- Root growth and branching

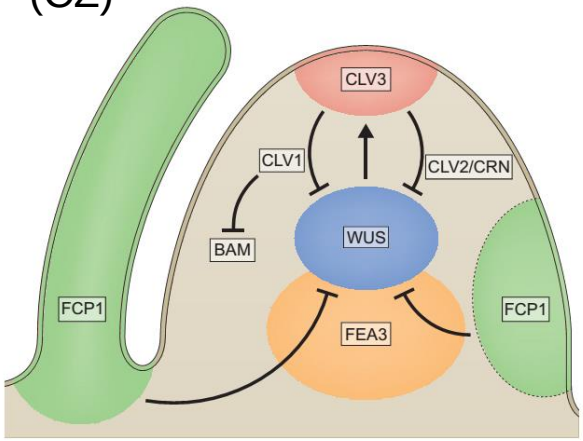
Shoot apical meristem maintenance in *Arabidopsis thaliana*

Flowers of At wild-type (A) and *clavata1* mutants (B; C)

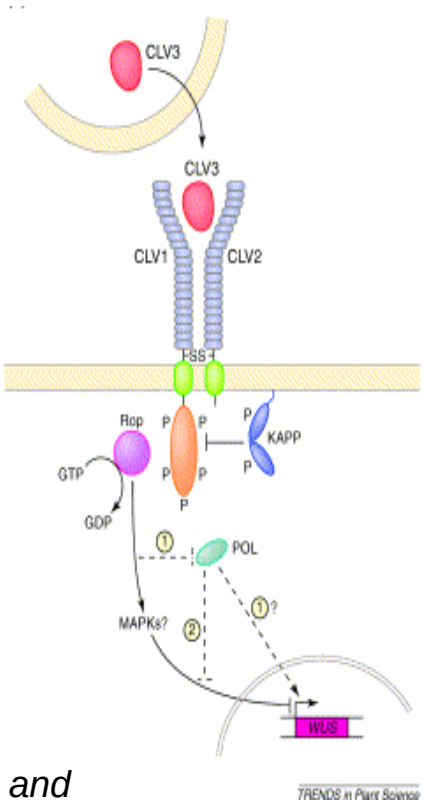


Clark et al. (1993, 1995)

Group of pluripotent stem cells is maintained in the central zone (CZ)



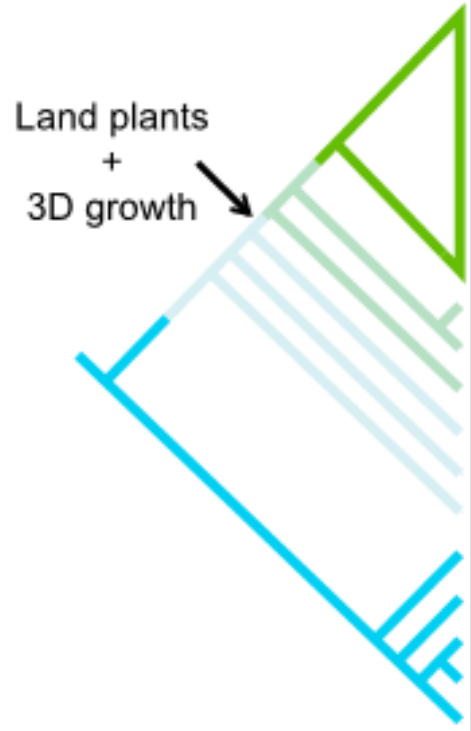
Somssish et al. (2016)



Carles and Fletcher (2003)

SAM maintenance: variation among species

A



B

Clade	Species	*CLE*	*TDIF*	*CLV1/BAM*	*RPK2*	*CLV2*	*CRN*
VP	*Arabidopsis thaliana* (G)	32	5	4	1	1	1
	Glycine max (G)	38	6	10	5	2	2
	Oryza sativa (G)	36	3	4	2	1	1
	Amborella trichopoda (G)	8	1	5	2	1	1
	Picea abies (G)	52	17	4	3	1	1
	Diplazium wichurae (T)	2	0	2	2	0	0
	Selaginella moellendorffii (G)	15	4	3	1	0	0
L	*Marchantia polymorpha* (G)	2	1	1	1	0	0
M	*Physcomitrella patens* (G)	7	0	2	1	0	0
H	*Anthoceros agrestis* (G)	1	1	1	0	0	0
Cha	*Coleochaete nitellarum* (T)	0	0	0	0	0	0
	Spirogyra sp. (G)	0	0	0	0	0	0
	Chara braunii (G)	0	0	0	0	0	0
Chl	*Ostreococcus tauri* (G)	0	0	0	0	0	0
	Chlorella vulgaris (G)	0	0	0	0	0	0
	Volvox carteri (G)	0	0	0	0	0	0
	Chlamydomonas reinhardtii (G)	0	0	0	0	0	0
	Ulva spp. (T)	0	0	0	0	0	0

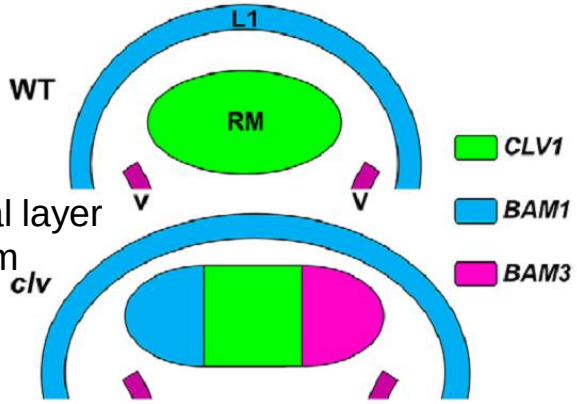
Whitewoods et al. (2018)

In Arabidopsis, **24 expressed CLE family members** have been implicated in stem cell maintenance in the SAM, the root apical meristem and the vascular cambium (Casamitjana-Martínezetal.,2003;Cock and McCormick, 2001; Fletcher et al., 1999; Ito et al., 2006; Stahl et al., 2009)

Redundancies and compensations for a conserved mechanism

Compensation among ligand and receptor paralogs is critical for stem cell homeostasis

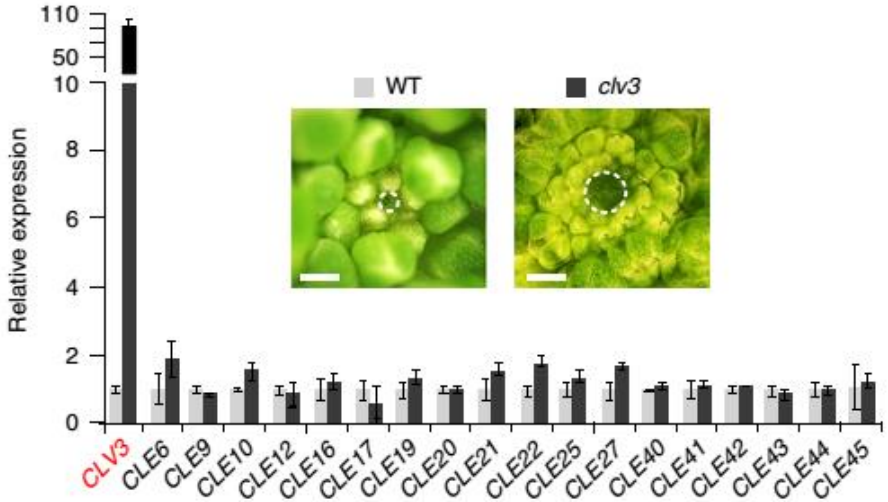
Arabidopsis t.



L1, L1 epidermal layer
RM, rib meristem
V, vasculature

Nimchuk et al., 2015

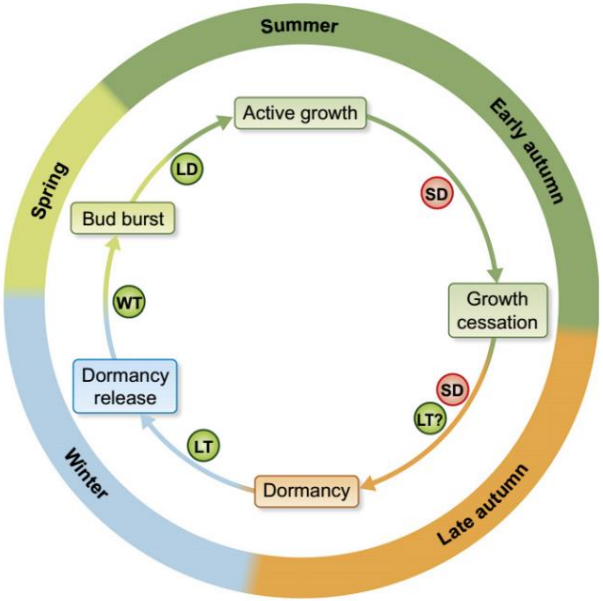
Tomato

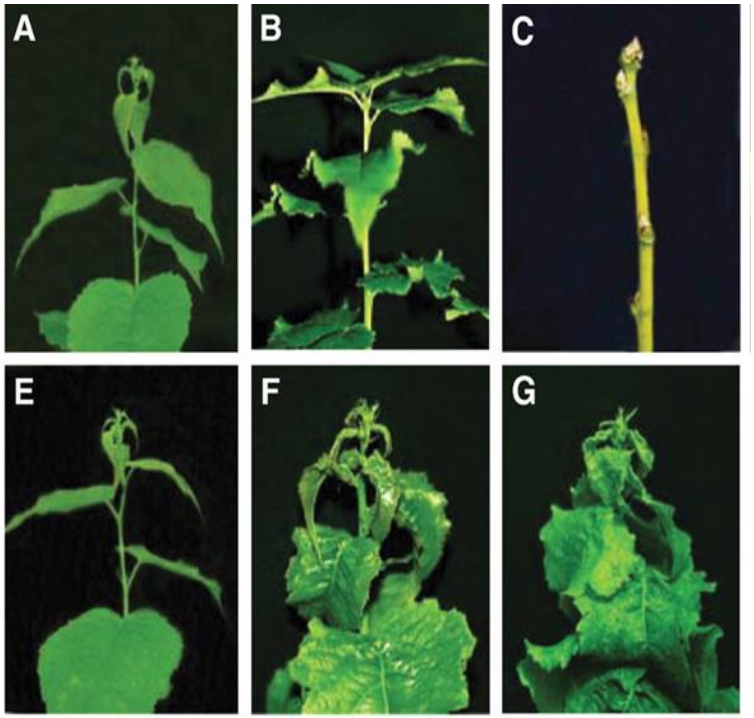


Rodriguez-Leal et al., 2019

Growth cessation

Growth cessation in the terminal bud is mediated by environmental conditions and access to resources.
In poplar, it could be mediated by CO/FT



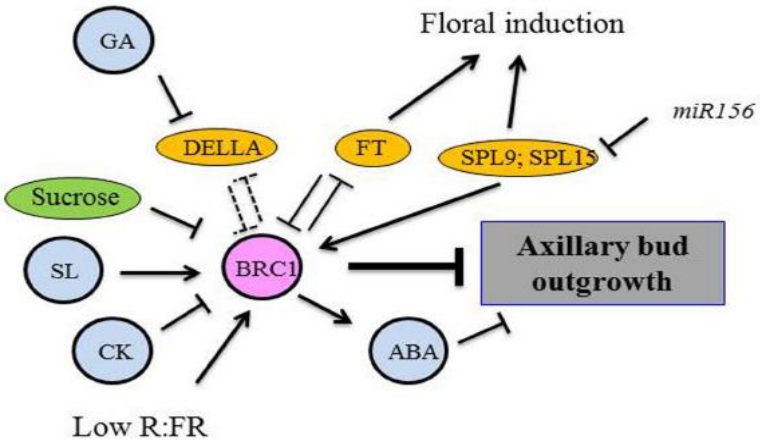


(**A** to **C**) Wild-type plants and
(**E** to **G**) *35S::PtFT1 Populus tremula x tremuloides* in long days [(A) and (E)], 32 short days [(B) and (F): no growth cessation)] 63 short days and 5 days in darkness at 5°C
[(G)): no growth cessation

Böhlenius et al. 2006

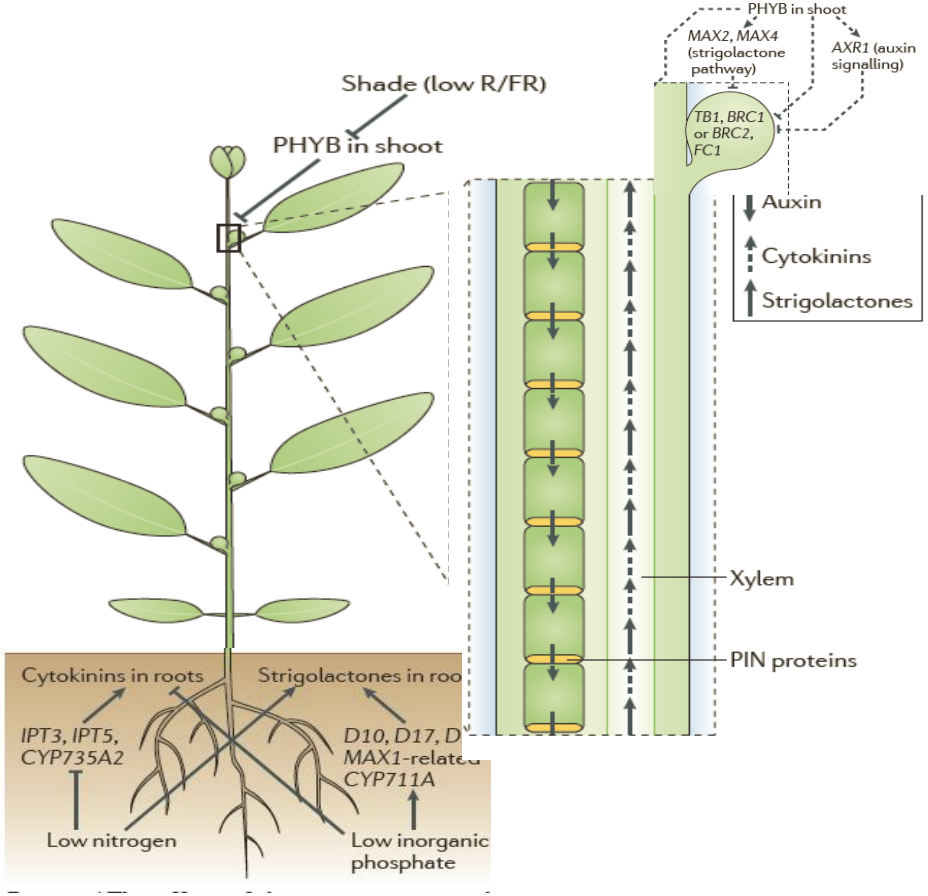
Common actors across processes?

Branching mutants in pea, petunia and At and physiological studies



Integration of different pathways by BRC1

Rameau et al. (2017) ; Barbier et al. (2019)



Domagalska and Leyser, 2011

Common actors between processes?

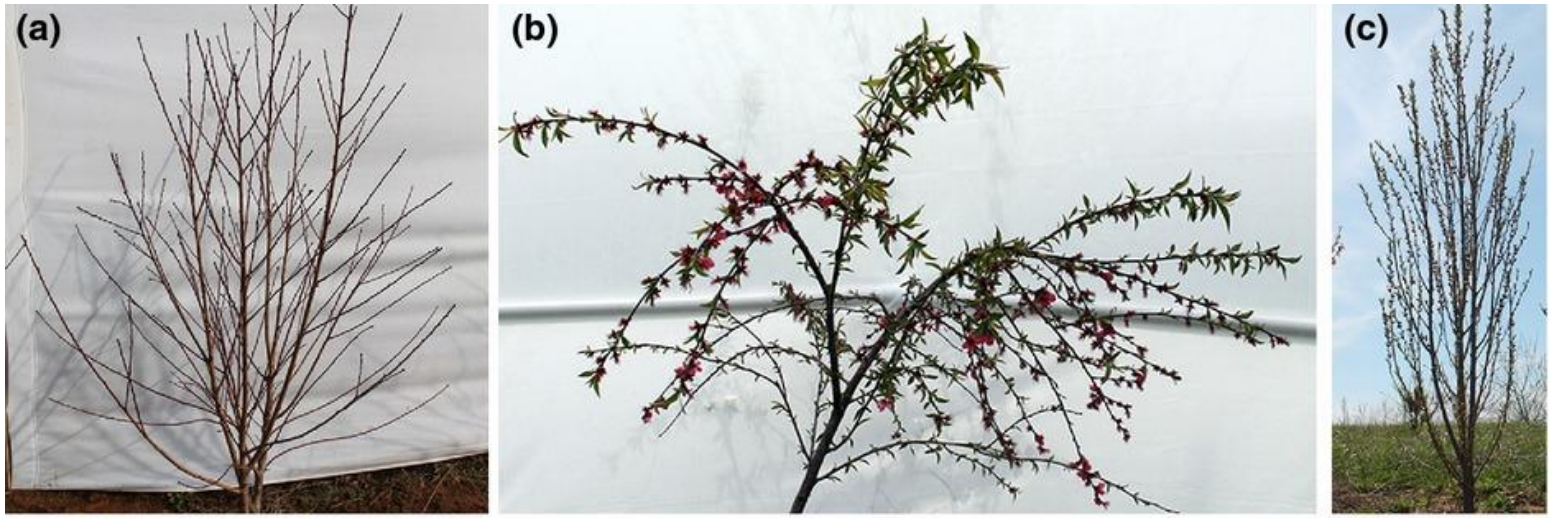
- ✓ The overexpression of LEAFY in apple tree, initially assumed to lead to early flowering, has led to a columnar phenotype, with short internodes and many axillary shoots (*Flachowsky et al., 2010)*

- ✓ More axillary branching (max) orpin-formed mutants, that are expected to generate phenotypes in branching, have been shown to display phenotypes with reduced secondary growth (*Ragni and Greb, 2018)*

- ✓ Necessary coordination between growth cessation and flowering *(Lifschitz et al., 2014)*;
- ✓ Evolutionary advantage of synchronized events for adaptation and success of reproduction (Borchert et al., 2015, Chomiki et al., 2017)

Large genetic variability of architecture within a species

Peach tree

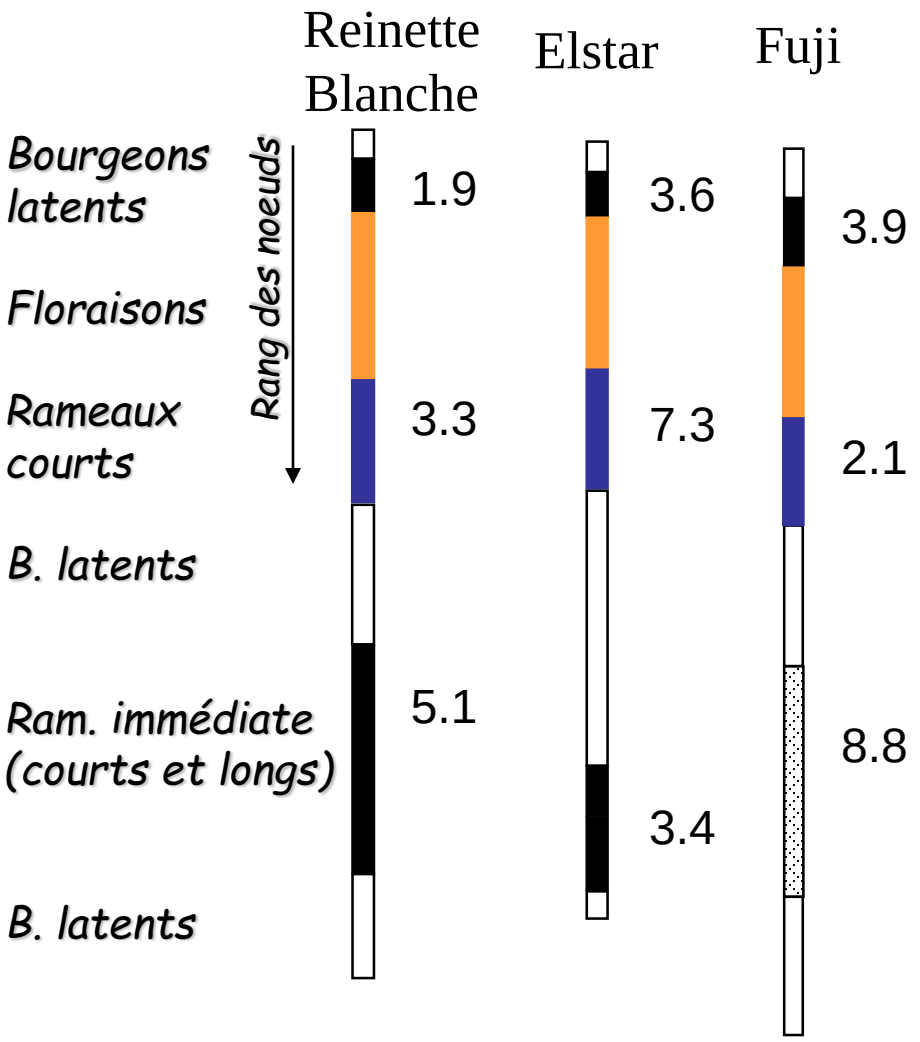


Bassi et al., 1994; photos from Hollender and Dardick, 2014)

Apple tree

Lespinasse, 1992

La ramification comparée chez différentes variétés de pommier

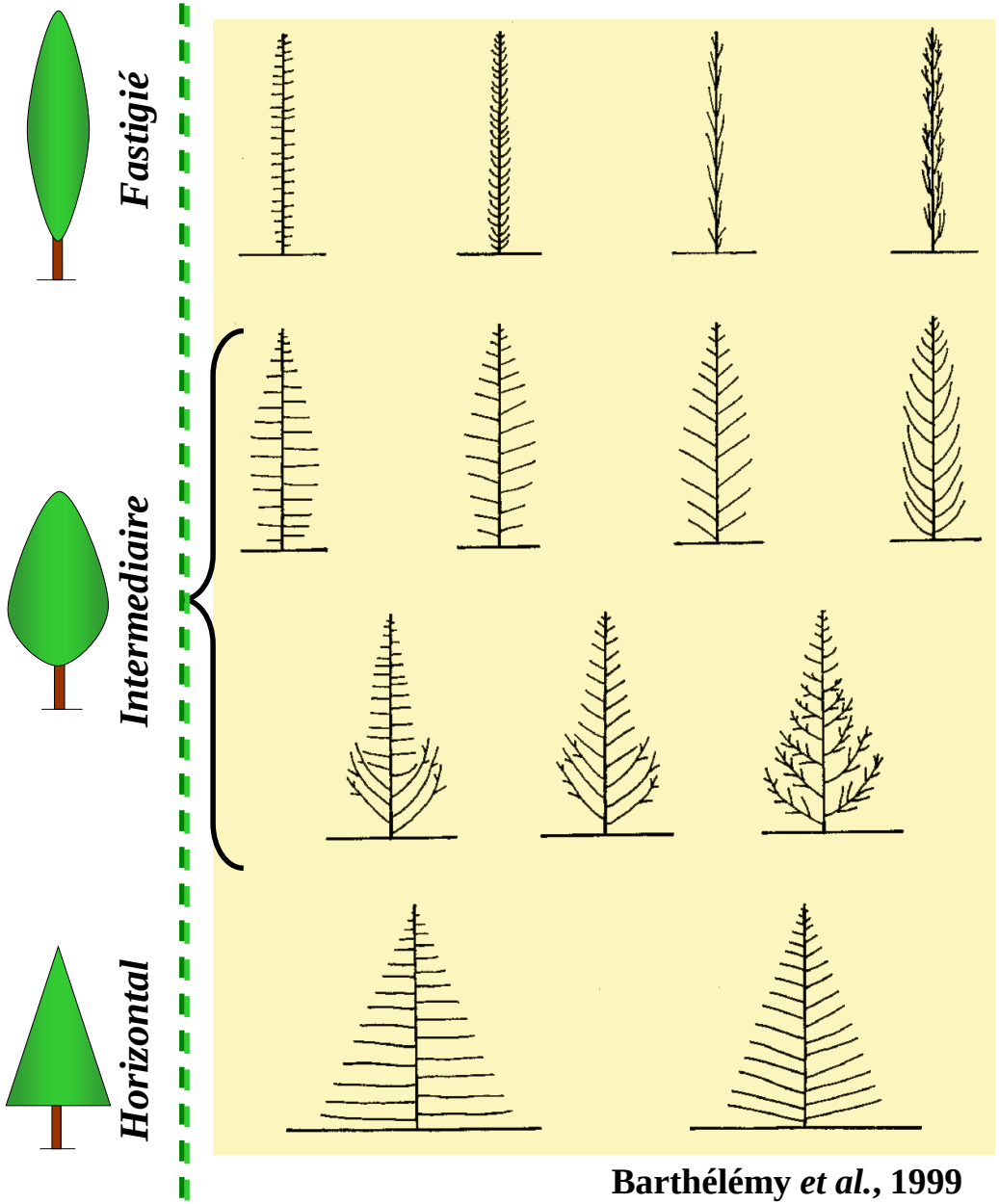


Chez différentes variétés:

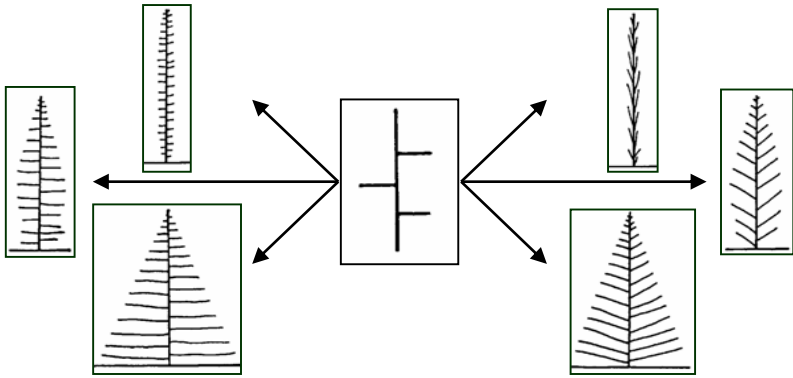
-Le devenir des méristèmes axillaires s'organise selon une même succession de zones

- Différences d'intensité de ramification dans les zones et de longueur des zones

Cupressus sempervirens



Barthélémy *et al.*, 1999



Take home messages

- Plant architecture results from a defined set of rules that can be enumerated (limited number) and combined
- Each species is build according to a specific combination

➔genetic control, likely due to master regulators of morphogenesis and growth

➔ Within species variability does not change the specific rules: phyllotaxy/axes direction, position and type of branching or flowering, etc.

➔But among genotypes, organ form and geometry in space and the number of organs (topology) can vary

Some bibliographic ressources

- Cours UVED: http://greenlab.cirad.fr/GLUVED/html/P1_Prelim/Bota/Bota_intro.html
- Website archi: http://amap.cirad.fr/architecture/accueil.html
- Papers

Barthélémy, D., Caraglio, Y., 2007. Plant Architecture: A Dynamic, Multilevel and Comprehensive Approach to Plant Form, Structure and Ontogeny. Annals of Botany, 99 : 375-407.

Costes E., Lauri P.E., Régnard, J.L. 2006 Tree Architecture and Production. In Horticultural Reviews 32: 1-60.

Costes E., L. Crespel, B. Denoyes, P. Morel, MN Démené, P.E. Lauri, B. Wenden. Bud relative organization and branching patterns along shoots in Rosaceae species: a review. Frontiers in Plant Science. 2014. Section Plant Biophysics and Modeling. doi: 10.3389/fpls.2014.00666

- Books…

Hallé, F., Oldeman, R. A. A., 1970. Essai sur l'architecture et la dynamique de croissance des arbres tropicaux. Paris : Masson, 176 p. (Monographie de Botanique et de Biologie Végétale, vol.).

Hallé, F., Oldeman, R. A. A., Tomlinson, P. B., 1978. Tropical trees and forests: an architectural analysis . Berlin : Springer, 441 p.

Millet, J., 2012. L'architecture des arbres des régions tempérées. Québec : Multimondes, 397 p. (Hors collection, vol.).

Bell, A., 1991. Plant form. Oxford Univ. Press. 341p.

Acknowledgements

- Slides and drawing from S. Sabatier, P. Heuret and Y. Caraglio (UMR AMAP)
- Photos from D. Barthélémy, P. Heuret, P.E. Lauri

Thank you for your attention