What did we learned on meristems from studies on fruit tree architecture ?

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Architecture and flowering of Fruit Species
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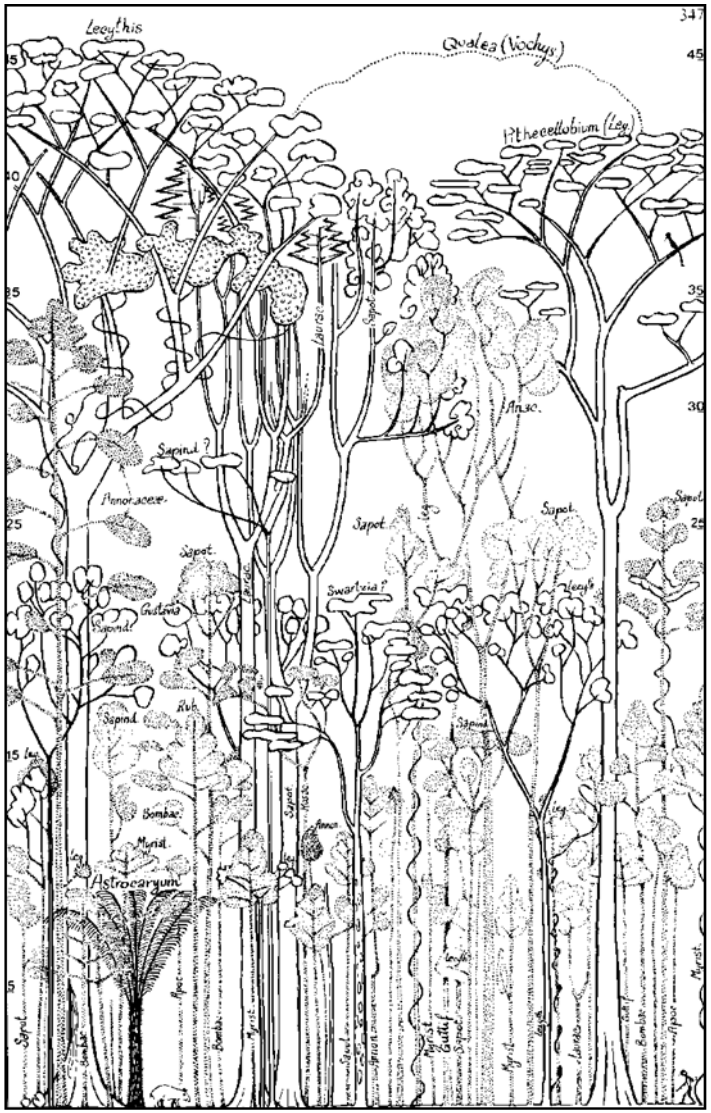
There are large variations in meristem states and behaviors



(After *Hallé, Oldeman & Tomlinson 1978*)

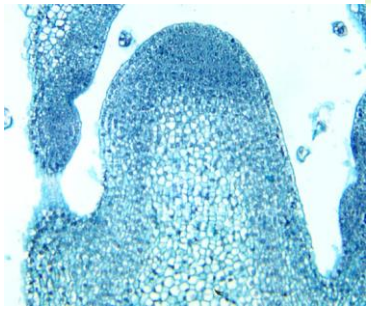
Among species

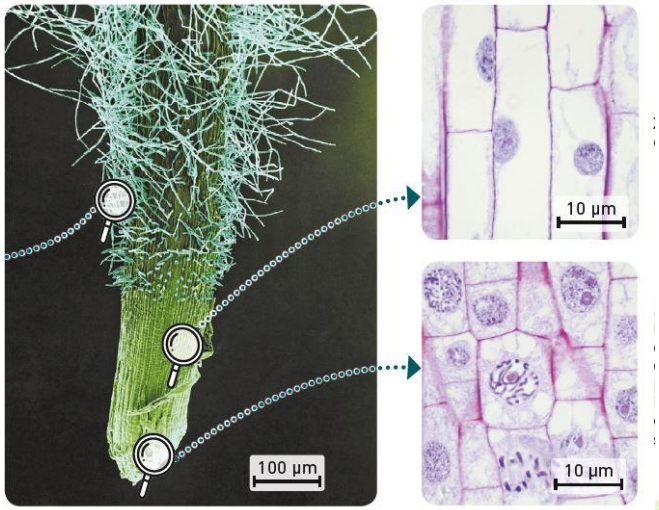
There are large variations in meristem states and behaviors

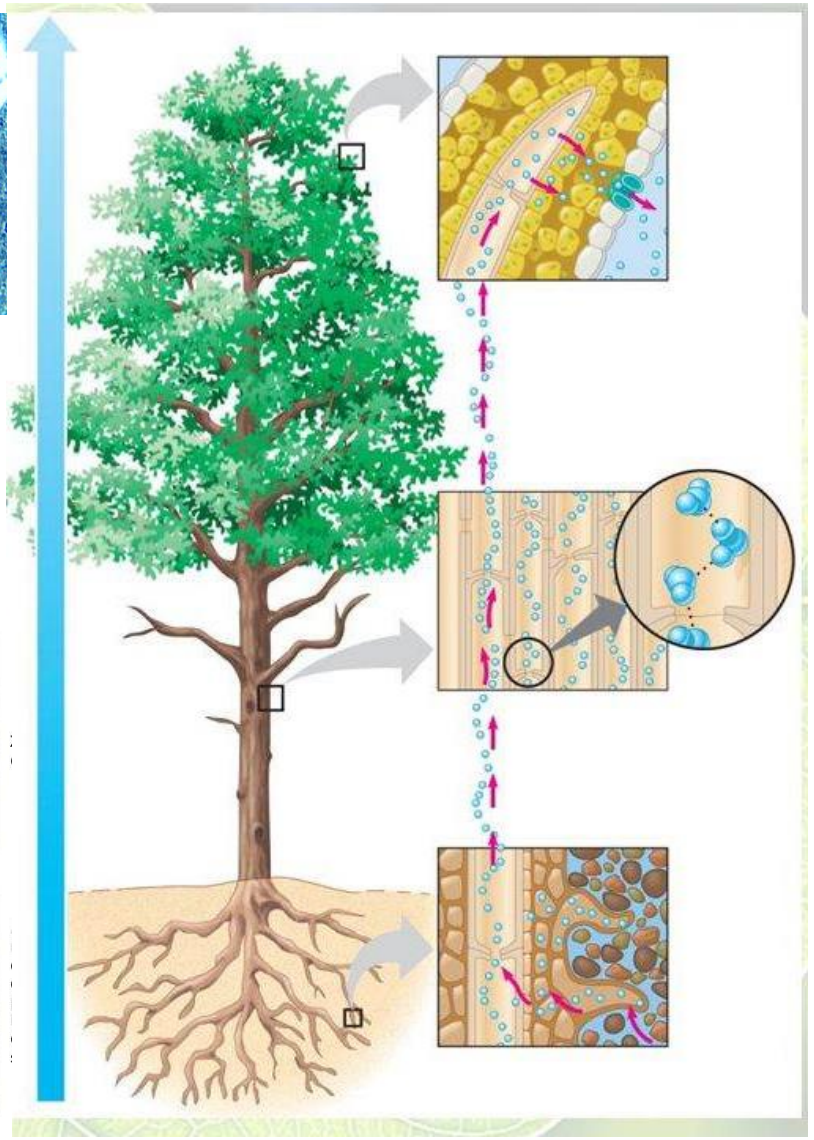
In a given species, among genotypes

In a given genotype, among years and depending on meristem position

Zooming in and zooming out a tree







Different fates and states of aerial meristems in a tree: the apple tree case

Two possible fates:
Vegetative / Floral

Different states:

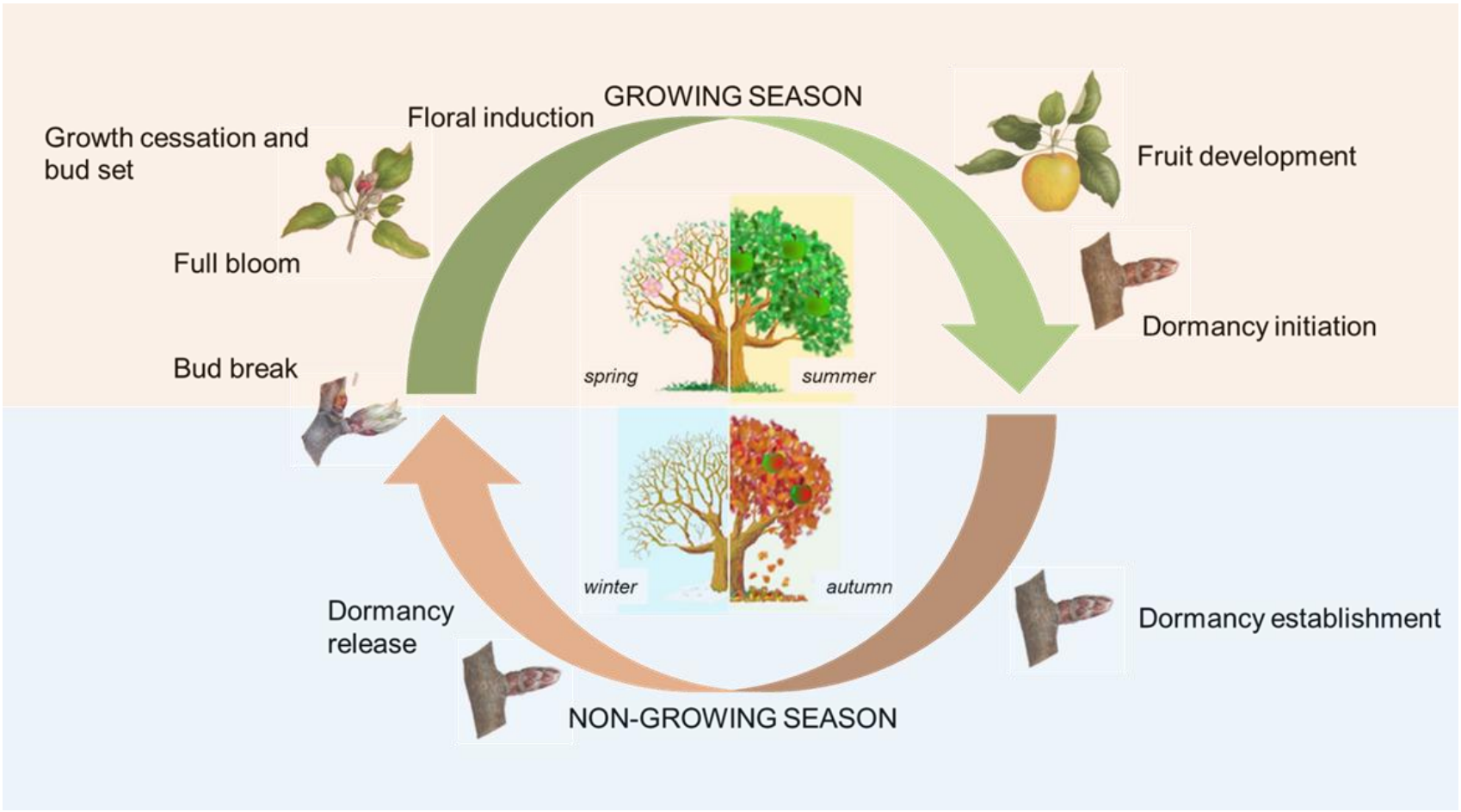
Dormant

Bursting

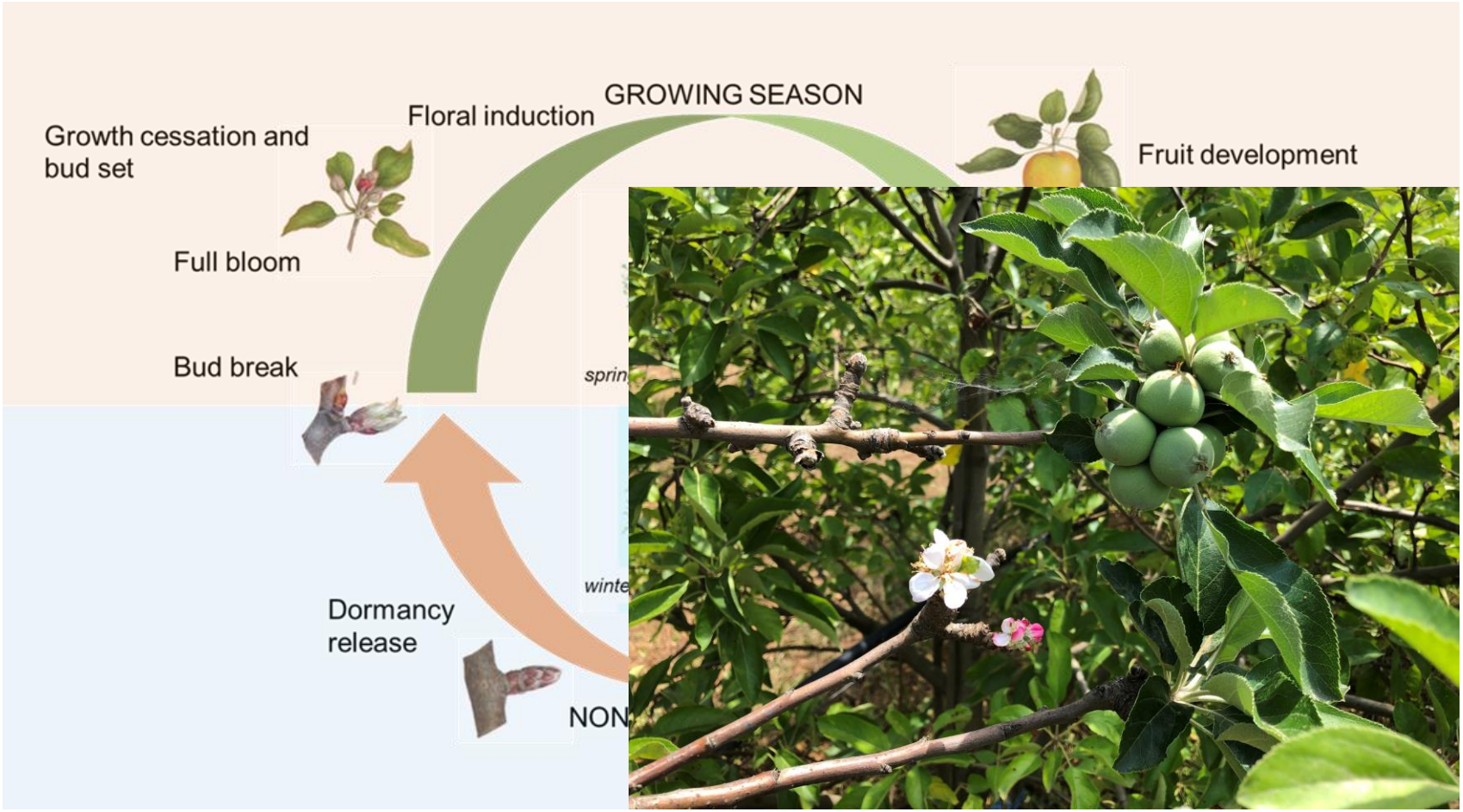
Growing

Quiescent

In temperate regions, bursting is synchronized by winter



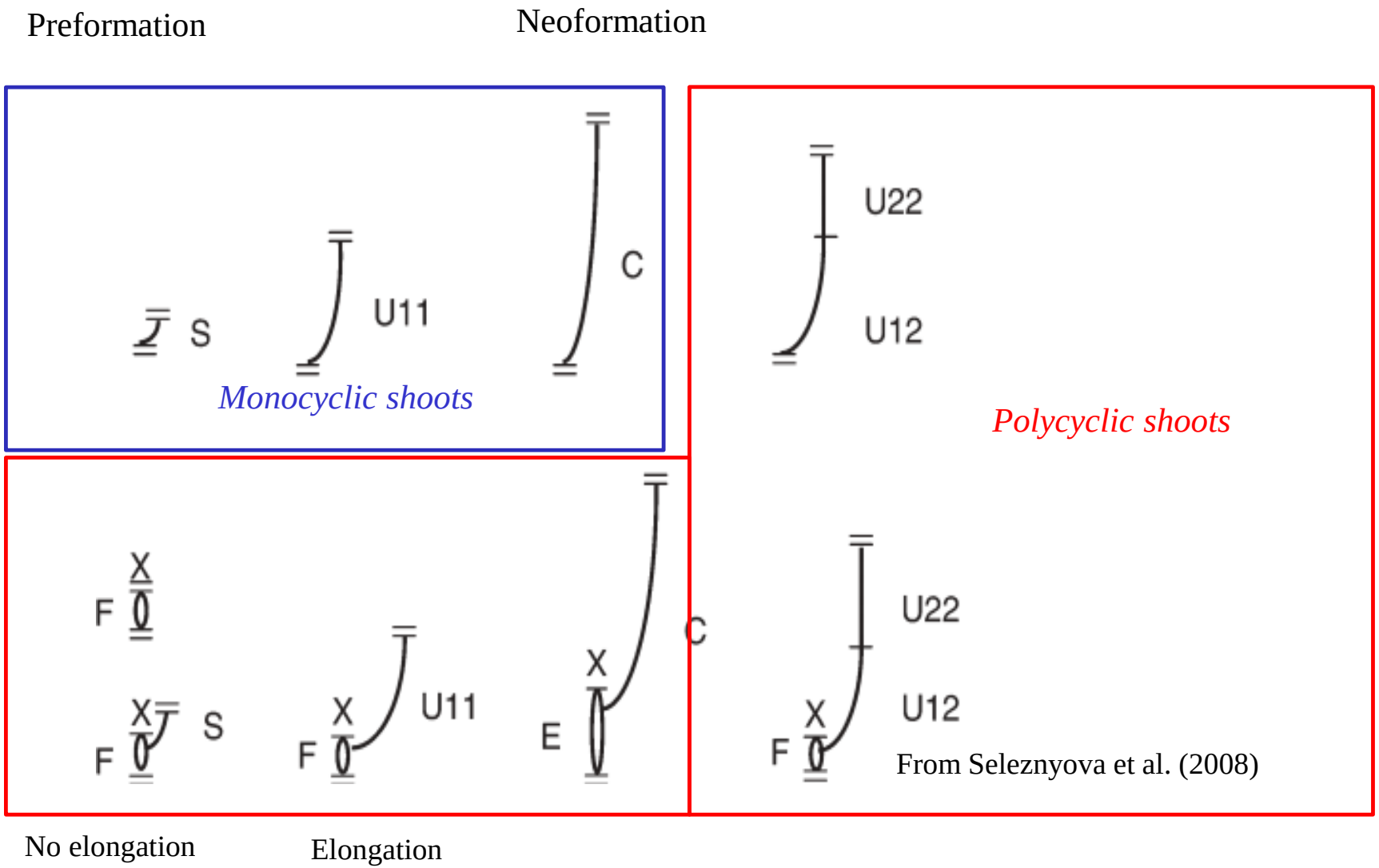
In temperate regions, bursting is synchronized by winter



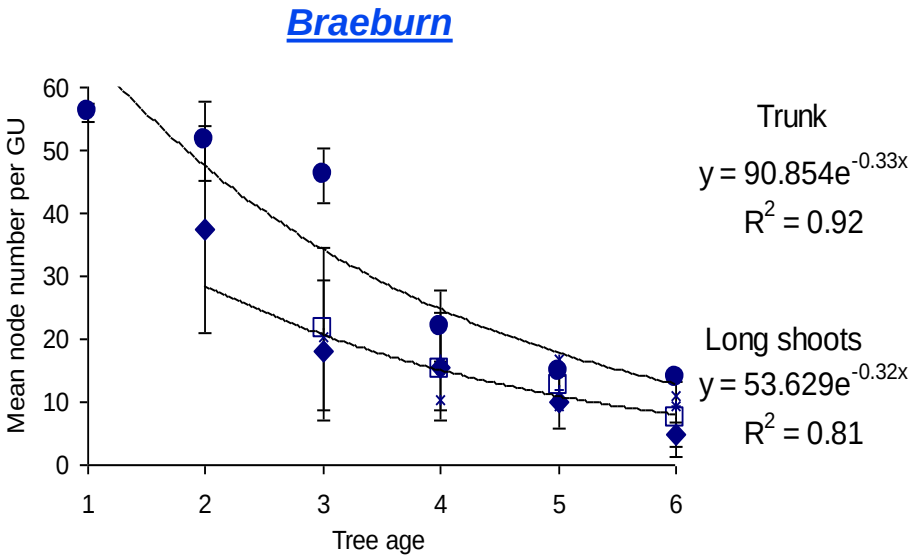
So far …

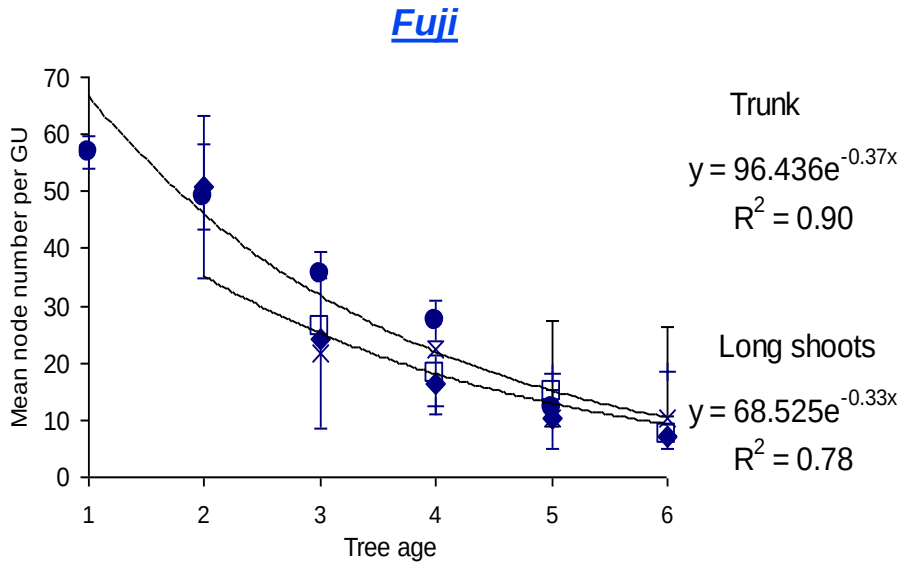
But desynchronisations start to be observed in south of France

Organogenetic activity duration give birth to different shoot types



Growth duration depends on branching orders and tree age in a coordinated manner





◇ O2 5y-old □ O2 4y-old △ O2 3y-old ✳ O3 - 4y-old + O3 - 3y-old

From Costes et al. (2003)

Shoot types are organized along the parent shoot by zones

The example of 'Reinette Blanche du Canada' apple cv

Most probable bud fate within a zone

Latent buds

Dormant buds that develop into long shoot (late growth cessation)

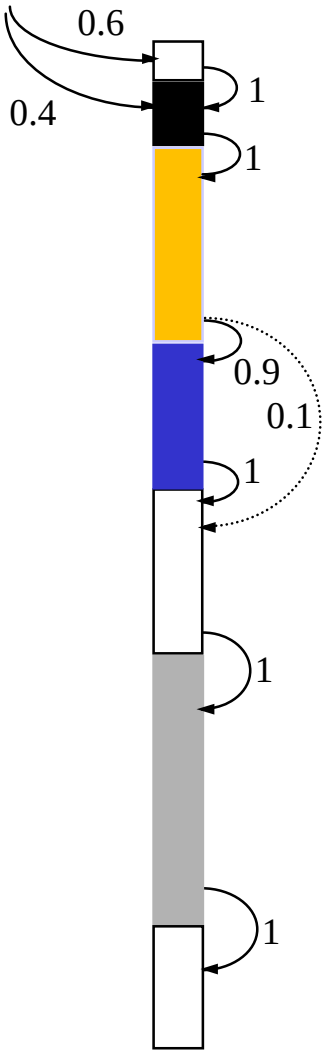
Floral buds

Dormant that develop into short shoot (early growth cessation)

Latent buds

Buds with immediate development (no quiescent or dormant phase)

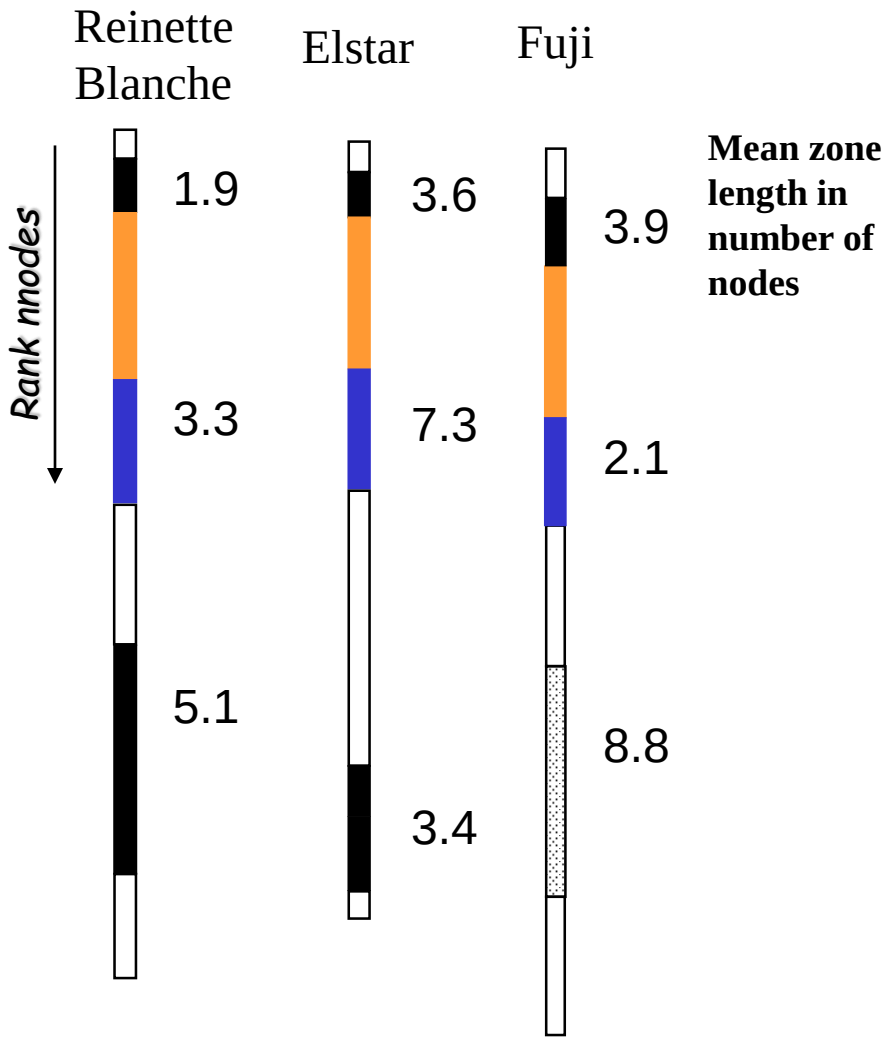
Latent buds



branching patterns

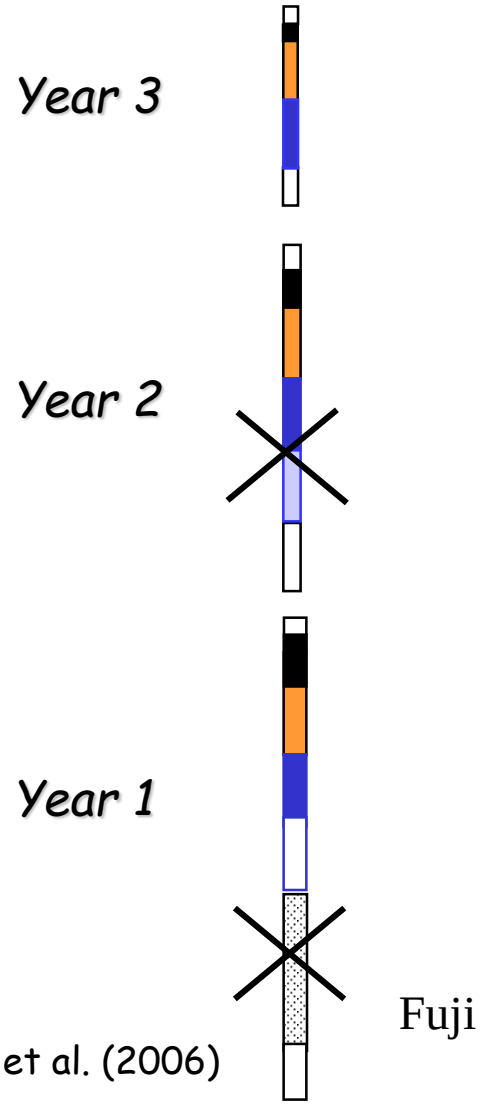
In a given species: similarities and differences among cvs

Similar patterns but different zone lengths and densities



From Costes and Guédon (2002)

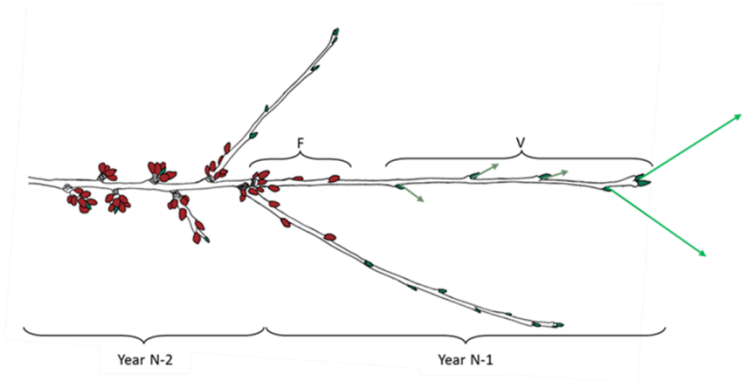
Progressive simplification of pattern over years



From Renton et al. (2006)

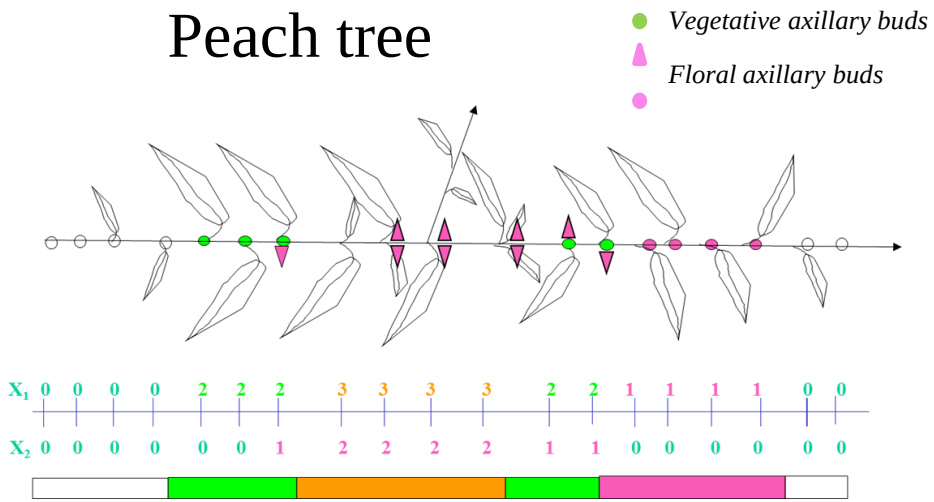
Among Rosaceae fruit tree species : similarities and differences in meristem fates organisation

Cherry tree



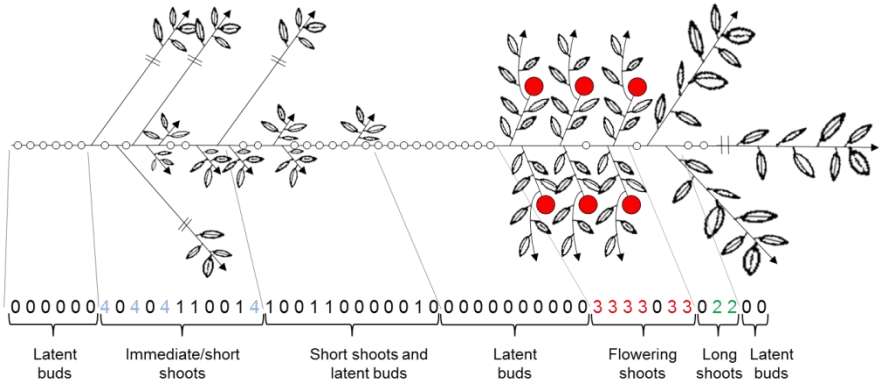
Drawing from B. Wenden, INRAE Bordeaux

Peach tree



From Fournier et al.

Apple tree



From Costes et al., 2014

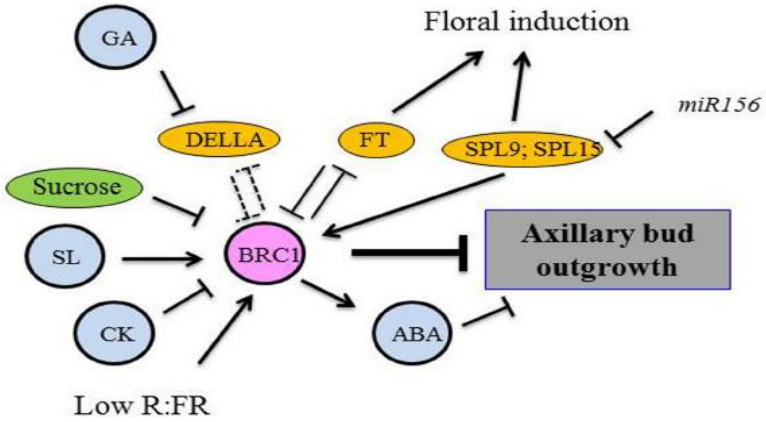
Confrontation to physiological and genetic studies on model plants (and others)

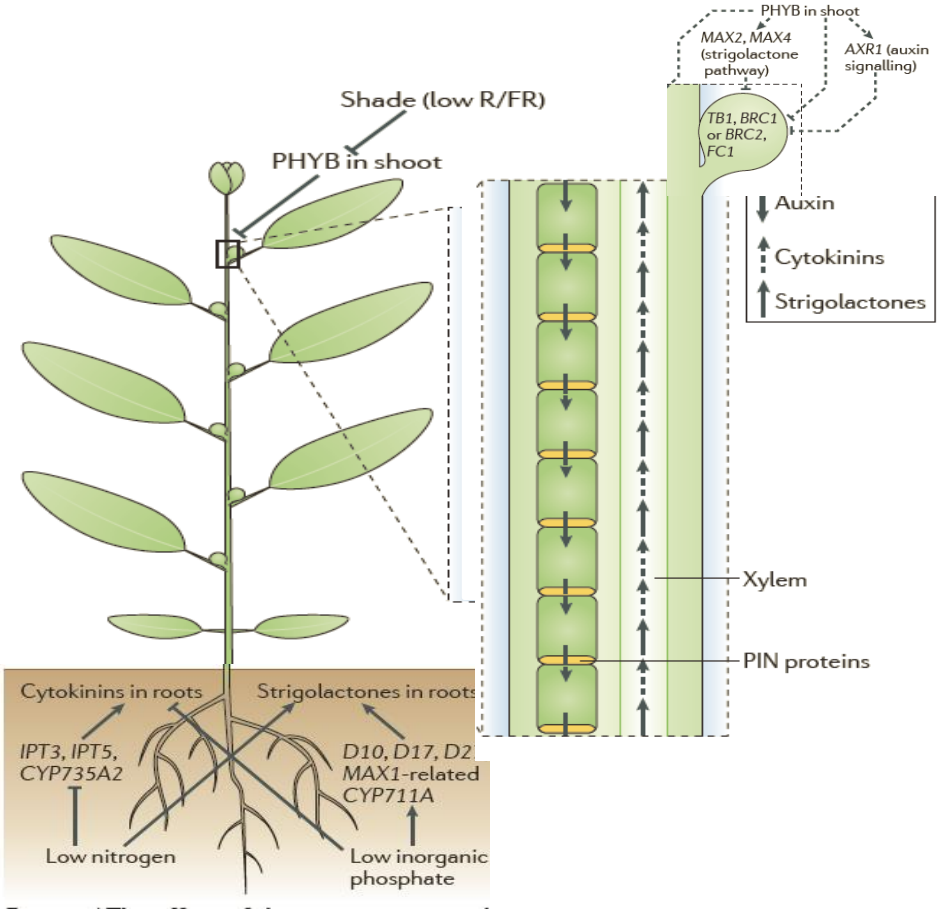
Focus on floral induction (FI) in meristems

The axillary meristems integrate numerous signals for outgrowing

Branching mutants in pea, petunia and At and physiological studies

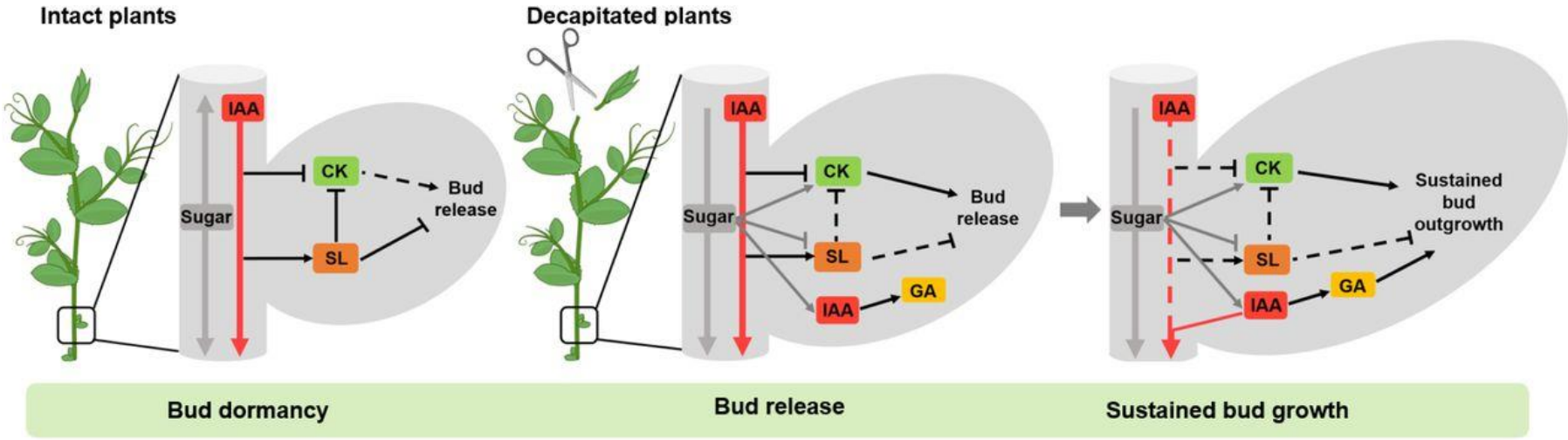
Integration of different pathways by BRC1
Rameau et al. (2017) ; Barbier et al. (2019)





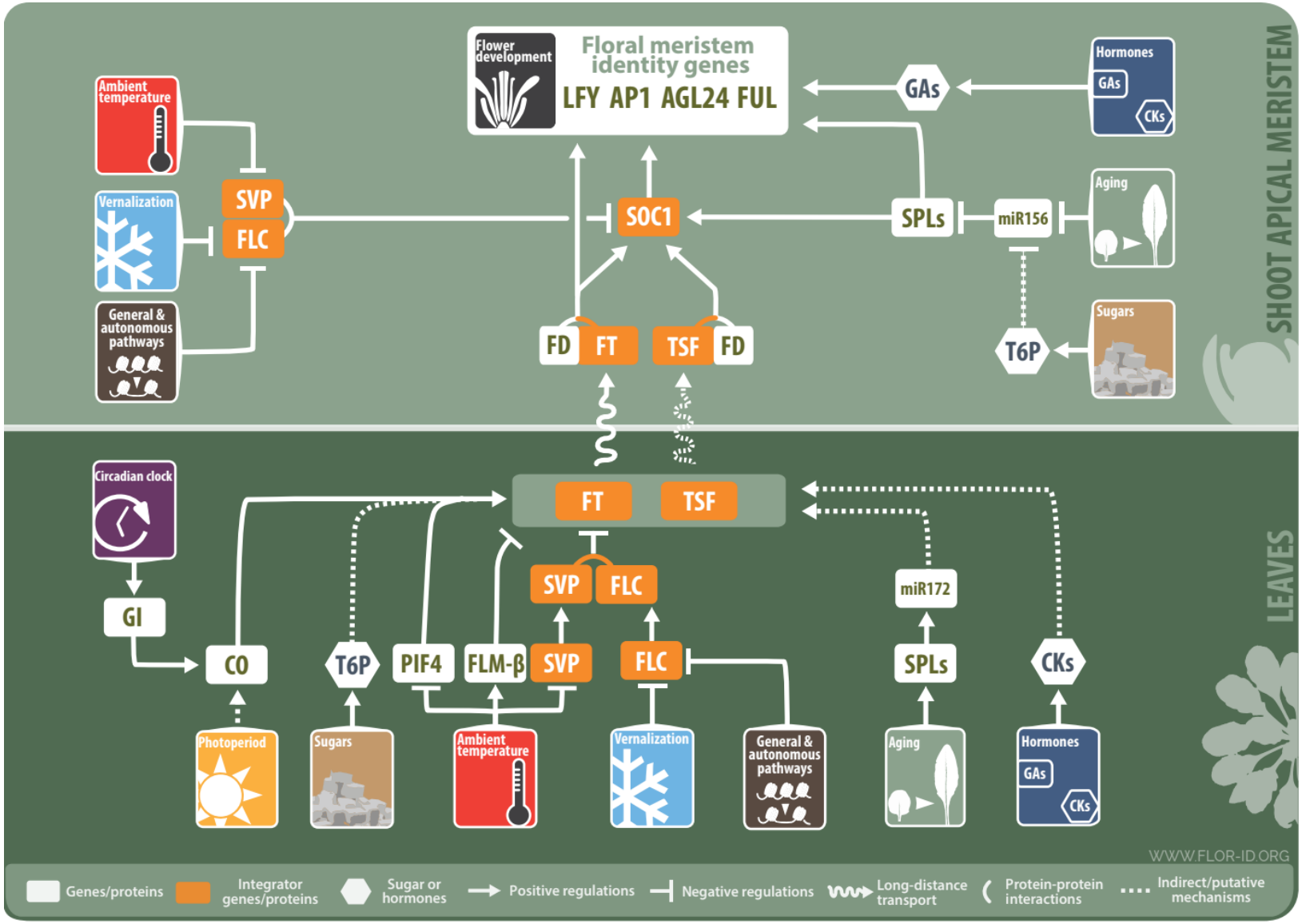
Domagalska and Leyser, 2011

… sustain growth



Cao et al. (2022)

… and for flowering



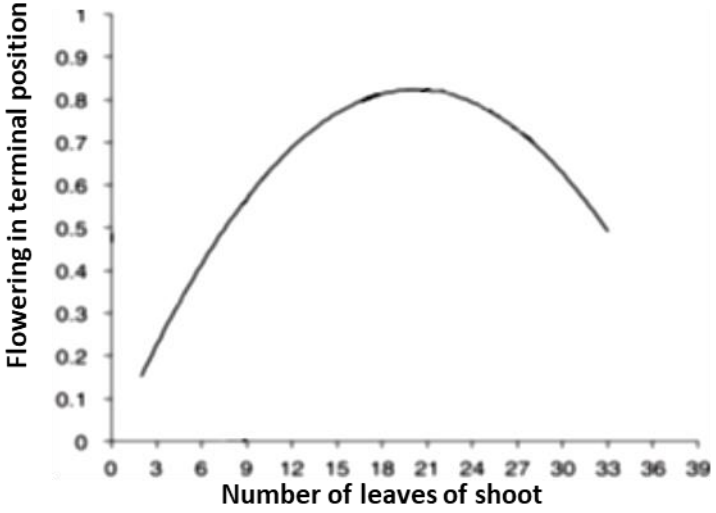
From Bouché et al. (2016)

Conditions of FI in apple tree meristems

- FI occurs in summer (~between 39 to 55 days after full bloom; Foster et al., 2003)

- FI appears not under photoperiod control (Heide et al., 2005)
- FI is favored by leaves but inhibited by fruits this leading to alternative bearing
- GA are considered as inhibitory and the role of carbohydrates remains under debate

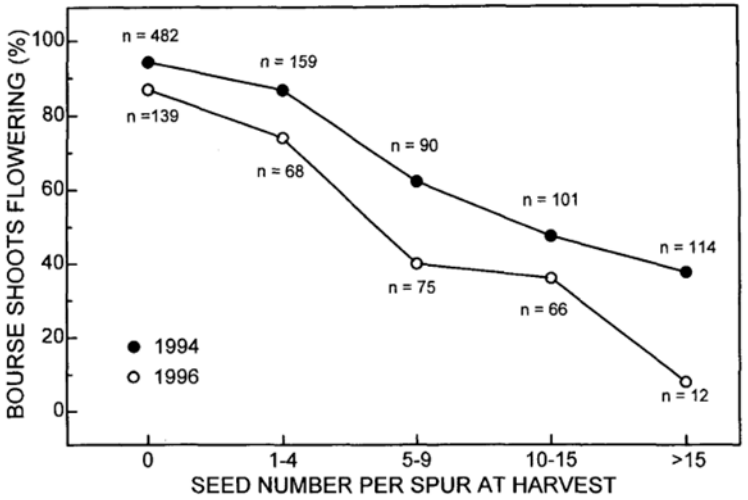
Activation by leaf



(adapted from Lauri and Trottier, 2004)

The leaves are sources of carbohydrates and sources of FT (Corbesier et al. 2007)

Inhibition by fruit



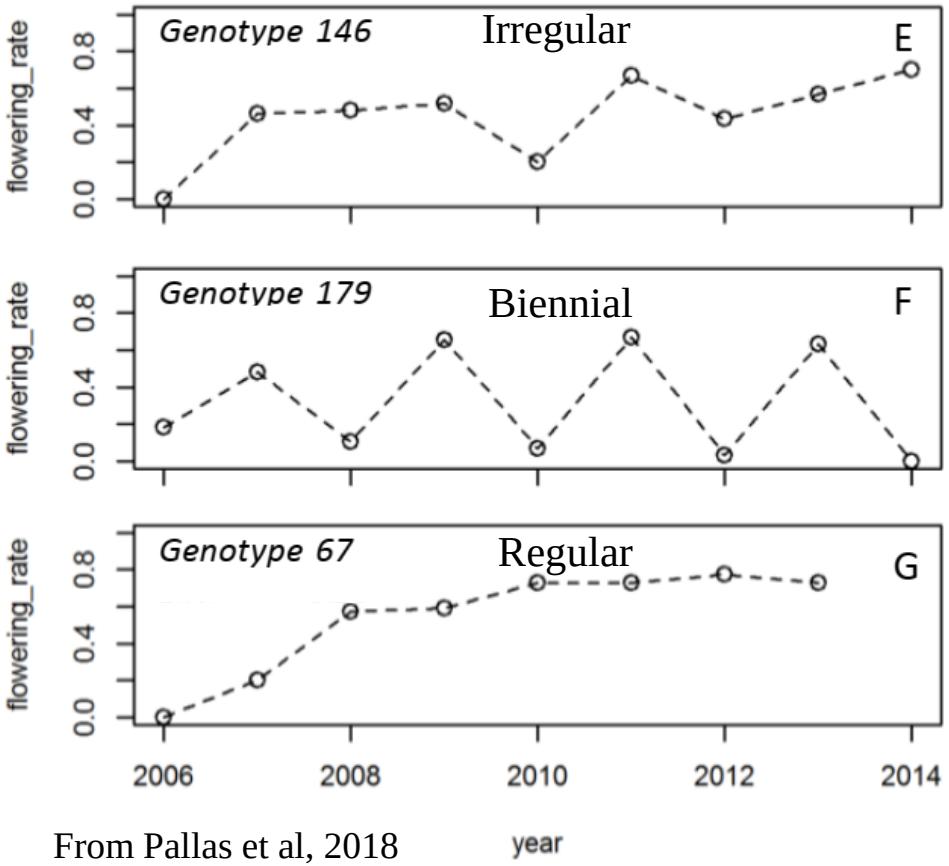
(Neilsen and Dennis, 2000)

Floral induction may be inhibited by substances produced by fruit, suspected to be gibberellins from the seeds.

Genotypic variability in FI over years

A proportion of meristems only is induced each year and this proportion varies over years

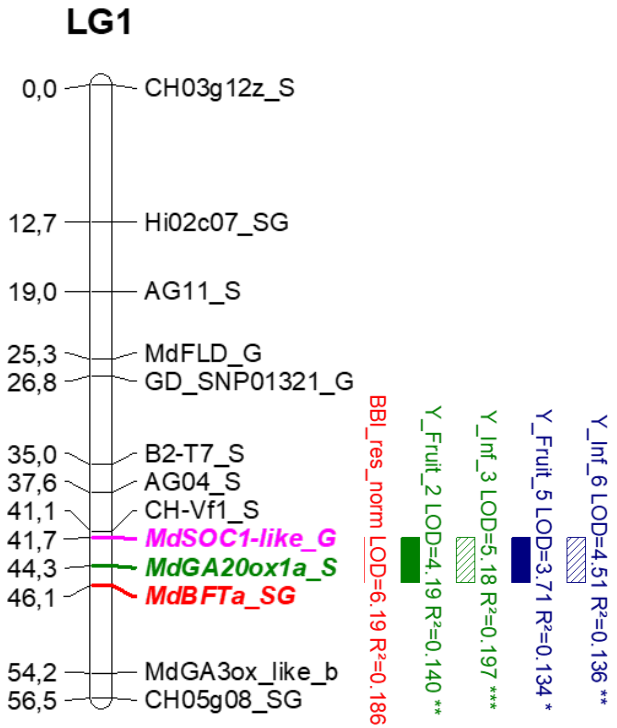
Different flowering patterns observed in segregated populations from regular to non-regular apple genotypes.
(Guitton et al., 2012; Durand et al., 2014; Pallas et al, 2018)



From Pallas et al, 2018

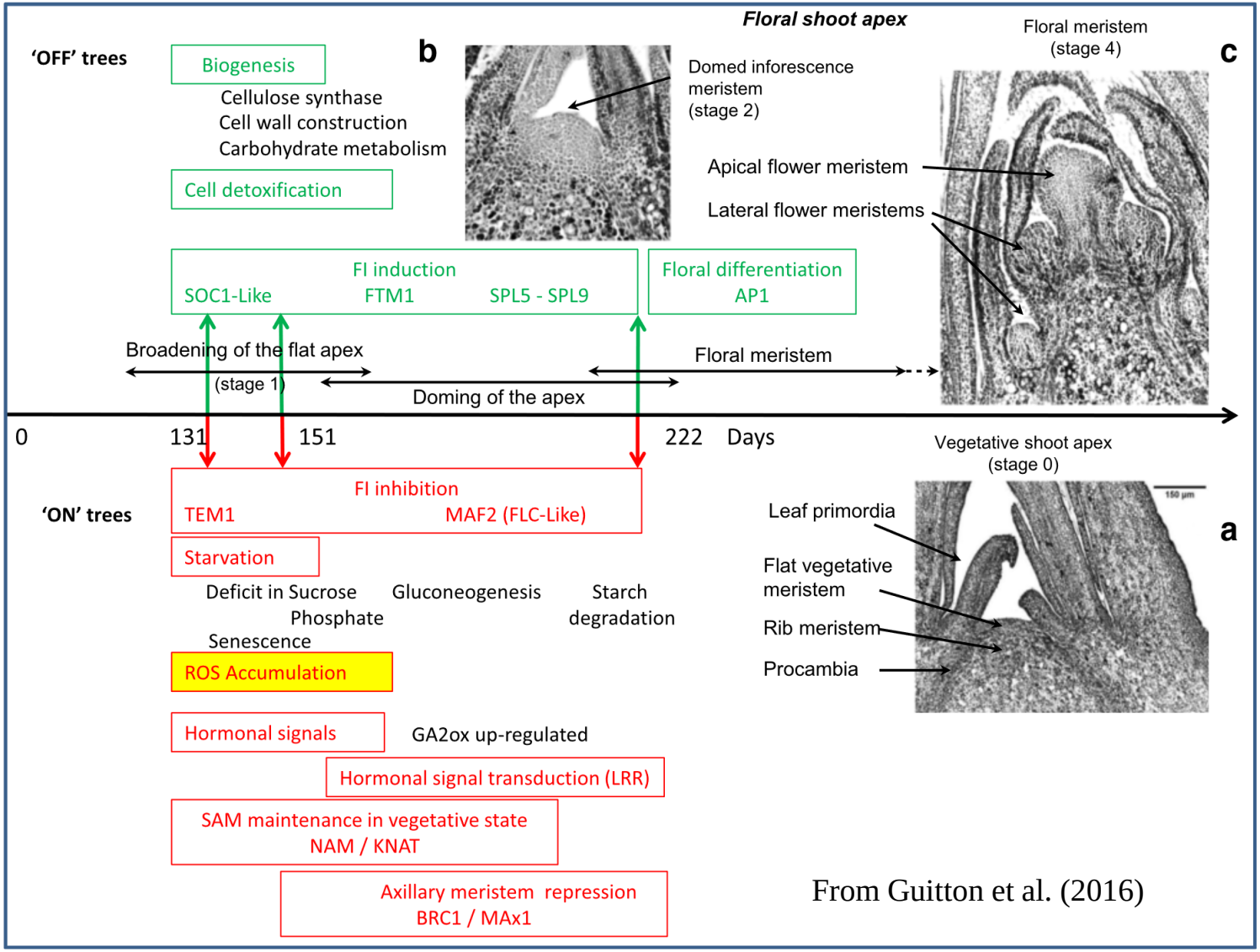
➔ *BBI: Biennial Bearing Index*

Y: Yield



From Guitton et al. (2012)

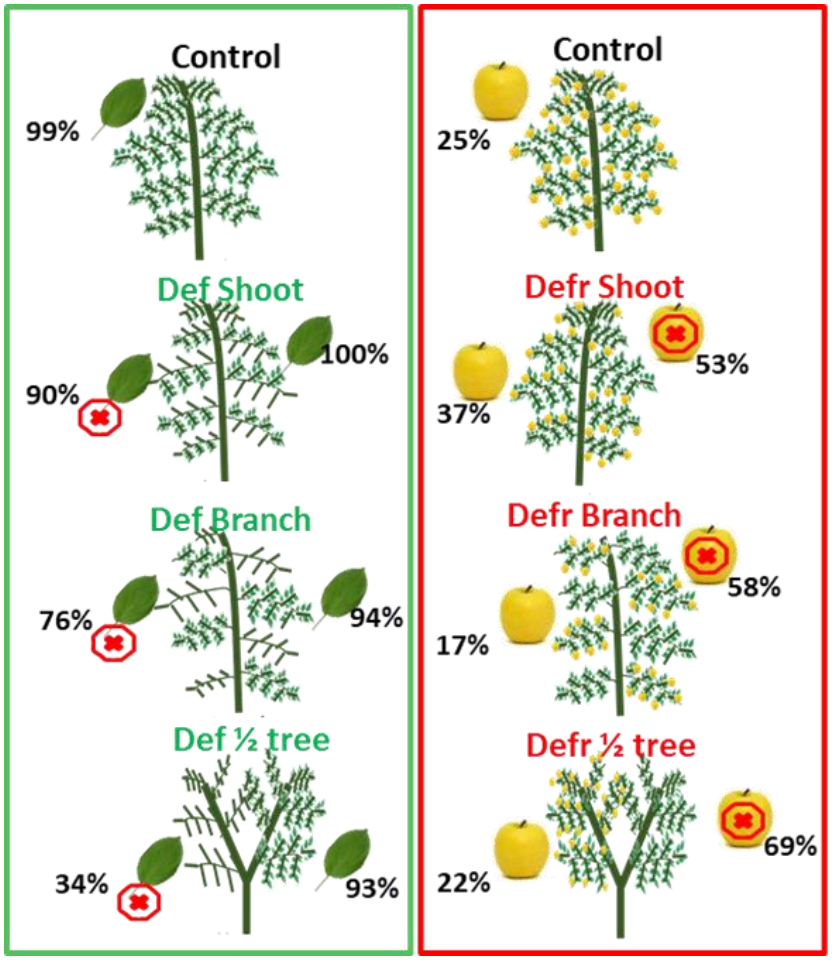
Transcriptomic analysis



From Guitton et al. (2016)

Both sugar metabolism and hormonal signaling could be involved

Deciphering the role of leaves and fruits and distances to meristems in FI



OFF trees ON trees

➔ **Effect of both leaves and fruits**
Signal from leaves appear always in sufficient quantity

➔ **Effect of within-tree distances between leaves, fruits and meristems on FI in the next spring**

Signals from fruit and leave operate at different distances

From Belhassine et al. (2019)

Genotypic variability of floral induction

What is the relationship between the **genotypic variability** of tree **architectural** and **physiological** variables with the variability in **floral induction**?

How these factors **correlate** to **different flowering patterns** according to **genotypes** ?

Architectural variability

Physiological variables

- Photosynthesis
- Carbohydrates
- Hormones

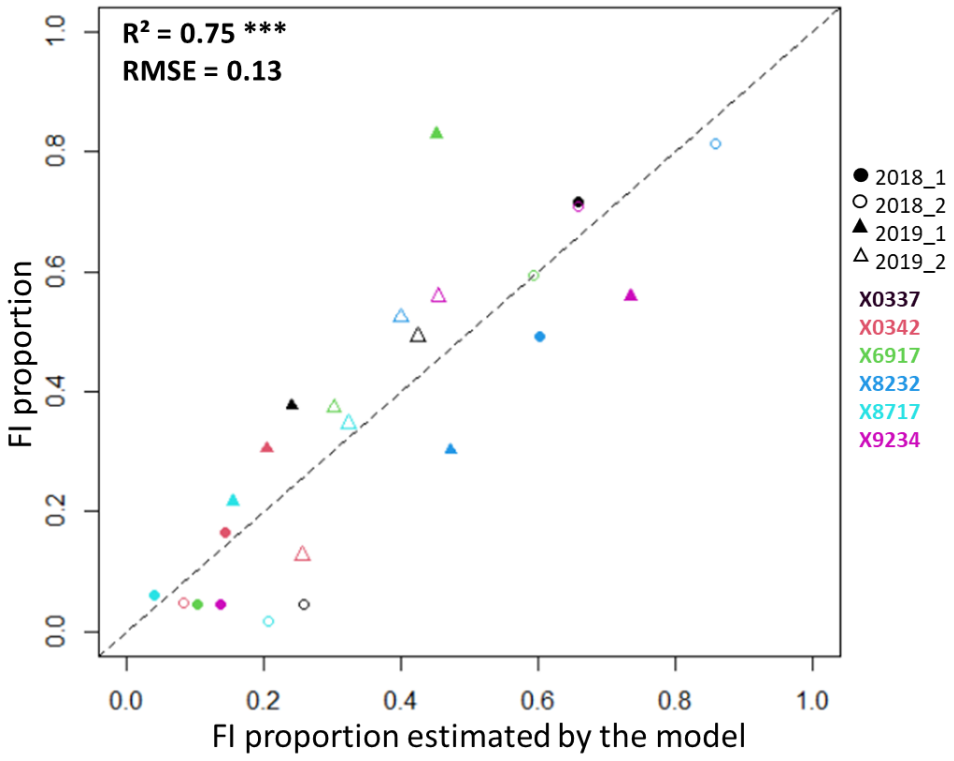
} content in leaves, stem and meristems

FI in the two successive springs

Physiological profiles of six genotypes with contrasted FI

Model predicting within tree FI proportions

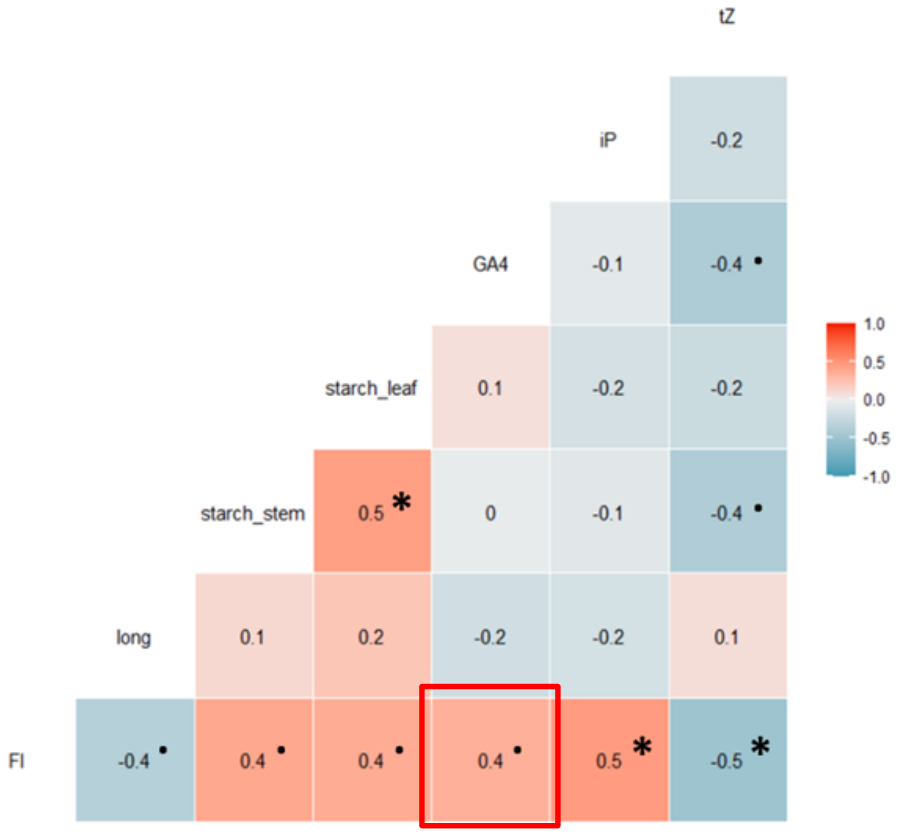
FI ~ iP + starch_stem+ starch_leaf + nb_long + GA4



Belhassine et al., 2021 Tree Physiology

Physiological profiles of six genotypes with contrasted FI

Correlations between floral induction and architecture/physiology variables



Evidence of a genotypic specific profile linked to flowering behavior

Table 3. Part of the variance of floral induction proportion explained by each explaining variables and associated level of significance in the multivariate linear model (FI ~ starch_leaf + starch_stem + Ip + Long + GA4), either including all the genotypes or excluding a given genotype. -Name of genotype corresponds to the results of the multi-variate model after having removed this genotype from the dataset. R^2 values were computed considering all the explanatory variables in each condition (all genotypes or one given genotype excluded)

	Part of explained variance (%)					*R^2*
	iP	*GA4*	*starch_stem*	*starch_leaf*	*Long*	
All Genotypes	*22.29***	*15.15***	*21.08***	*6.29**	*9.85**	*0.75*
-X0337	*15.20***	*18.79***	*24.18***	*6.86.*	*10.99**	*0.76*
-X0342	*19.32***	*11.76**	*28.61***	*10.98**	*2.14 ns*	*0.73*
-X6917	*29.33****	*21.31****	*13.54***	*12.46***	*6.77**	*0.83*
-X8232	*28.13***	*16.85***	*16.81***	*1.89 ns*	*11.77**	*0.75*
-X8717	*17.07***	*21.15***	*18.09***	*5.01 ns*	*11.76**	*0.73*
-X9234	*26.11***	*3.71 ns*	*23.61***	*6.34#*	*13.35**	*0.73*

Genotype effect was estimated by a one-way-ANOVA. *significant at $0.01 < P < 0.05$, **significant at $0.001 < P < 0.01$, ***significant at $P < 0.001$, #significant at $0.05 < P < 0.1$ and ns non-significant.

➔ Even though a common model explains the proportion of FI in trees, the different variables (architectural or physiological) do not have the same weight depending on the genotype

Belhassine et al., 2021 Tree Physiology

How to link this physiological model to flowering genes and FI in fruit trees

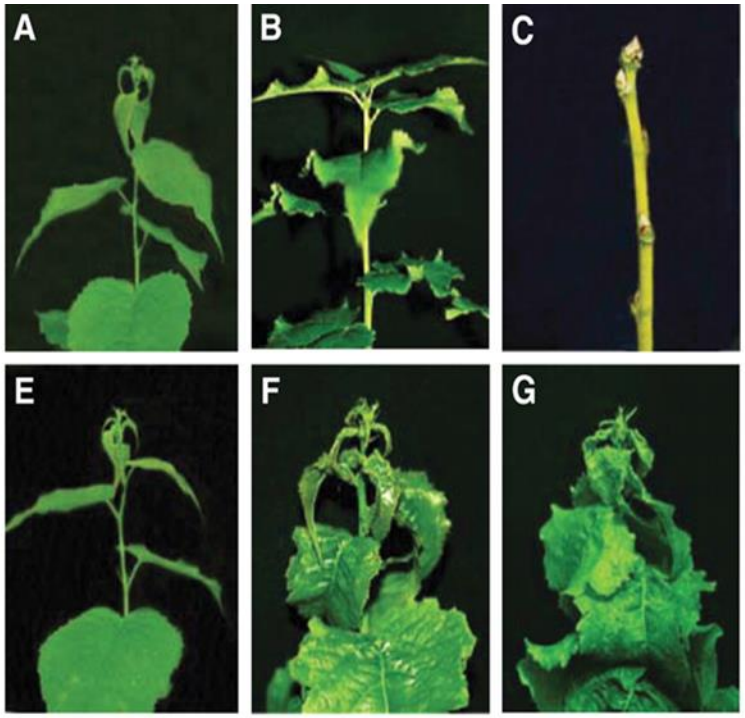
- Cytokinin promotes flowering of Arabidopsis via transcriptional activation of the FT paralogue TSF (D'Aloia et al., 2011)
- GA_4 biosynthesis genes are needed for flowering under short days in Arabidopsis (Osnato et al 2012)
- The over-expression of FT or FT-like genes was successful to drastically reduce the juvenile phase in Citrus (*Endo et al. 2005)* and apple *(Kotoda et al. 2010); (Iwata et al. (2006) for a review)*
- Silencing of MdTFL1 in transgenic apple resulted in precocious flowering (*Kotoda et al., 2006; Flachowski et al., 2012*)
- The relative expression of TFL1 correlates with the number of spurs induced in apple *(Haberman et al., 2016)* and in olive tree (*Haberman et al., 2017);*
- Similar role of the balance FT/TFL1 found in Fragaria sps (*Nakano et al., 2015; Lembinen et al., 2022*), Cotton *(Chen et al., 2019)*, ...

Main role of the balance between FT and TFL1 partially conserved mechanisms across species (Jin et al., 2021)

The other roles of FT/TFL1 family genes

- Mutants with loss of functions, ft and tsf, have altered lateral shoot growth *(Hiraoka et al., 2013);* FT can be expressed in the AxM where BRC1 interacts with FT and TSF (*Niwa et al., 2013)*

- Growth cessation in the terminal bud is mediated by environmental conditions and access to resources. In poplar, it could be mediated by CO/FT (*Böhlenius et al. 2006)*



Böhlenius et al. 2006

(**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

Some conclusions and take home messages

- Within a tree meristems are having different fates and states depending on their position

➔ a strong organization, particular for each species

- Relative positions and distances between organs (leaves, fruits, meristems) matter for bud fate (floral/vegetative) and state (growth vs growth cessation)

involving environmental signals, source-sink relationships, within-tree signaling and key gene regulation

➔ Multi-factorial control of meristems

- FI involves carbohydrates, hormones (Ctk and GA) and flowering genes control

➔ The relative weight of physiological factors triggering FI depends on the genotype

➔ The role of Ctk and GA – and their interaction with FT/TFL1 - needs clarification in fruit trees (*projects under progress*)

Acknowledgements

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