Cell division, endoreduplication and expansion processes: setting the cell and organ control into an integrated model of tomato fruit development

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Fruit size: the first trait of visual quality and one main yield component

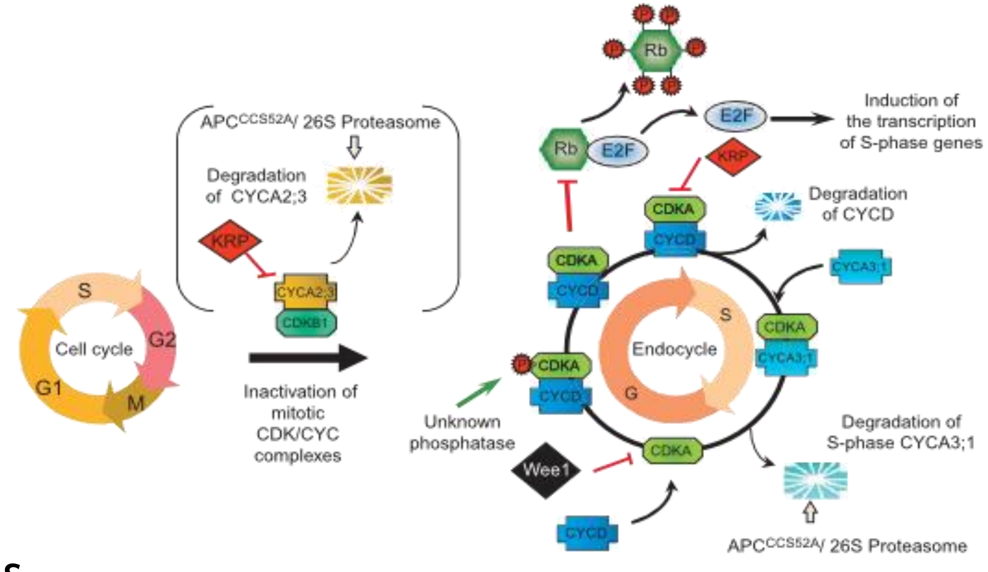
A large genetic diversity

Strong variations within the plant and along the season

Final fruit size emerges from interactions among several processes during fruit development

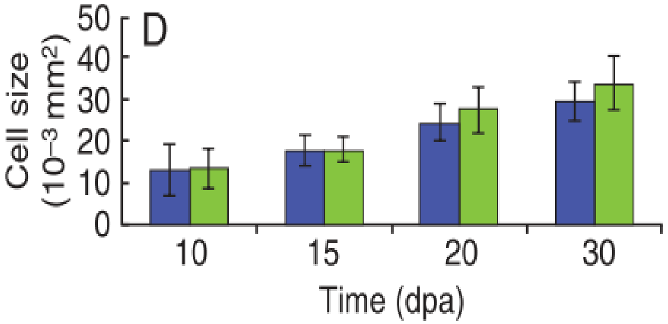
Endoreduplication

Cell division Cell expansion Ripening

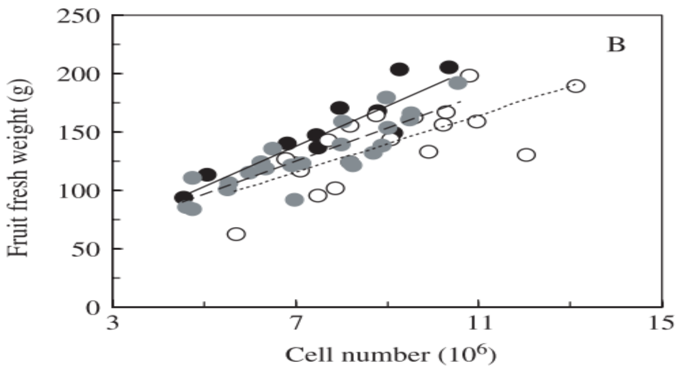


Cell expansion is responsible for the fruit volume increase, but final fruit size is highly correlated to the number of cells and endoreduplication level

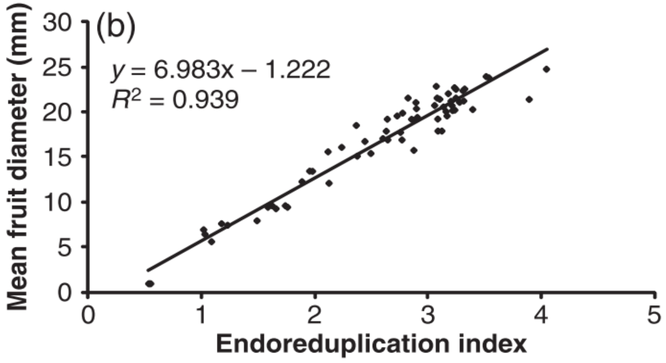
Chevalier et al. (2011)



Chevalier et al. (2011)



Bertin (2005)

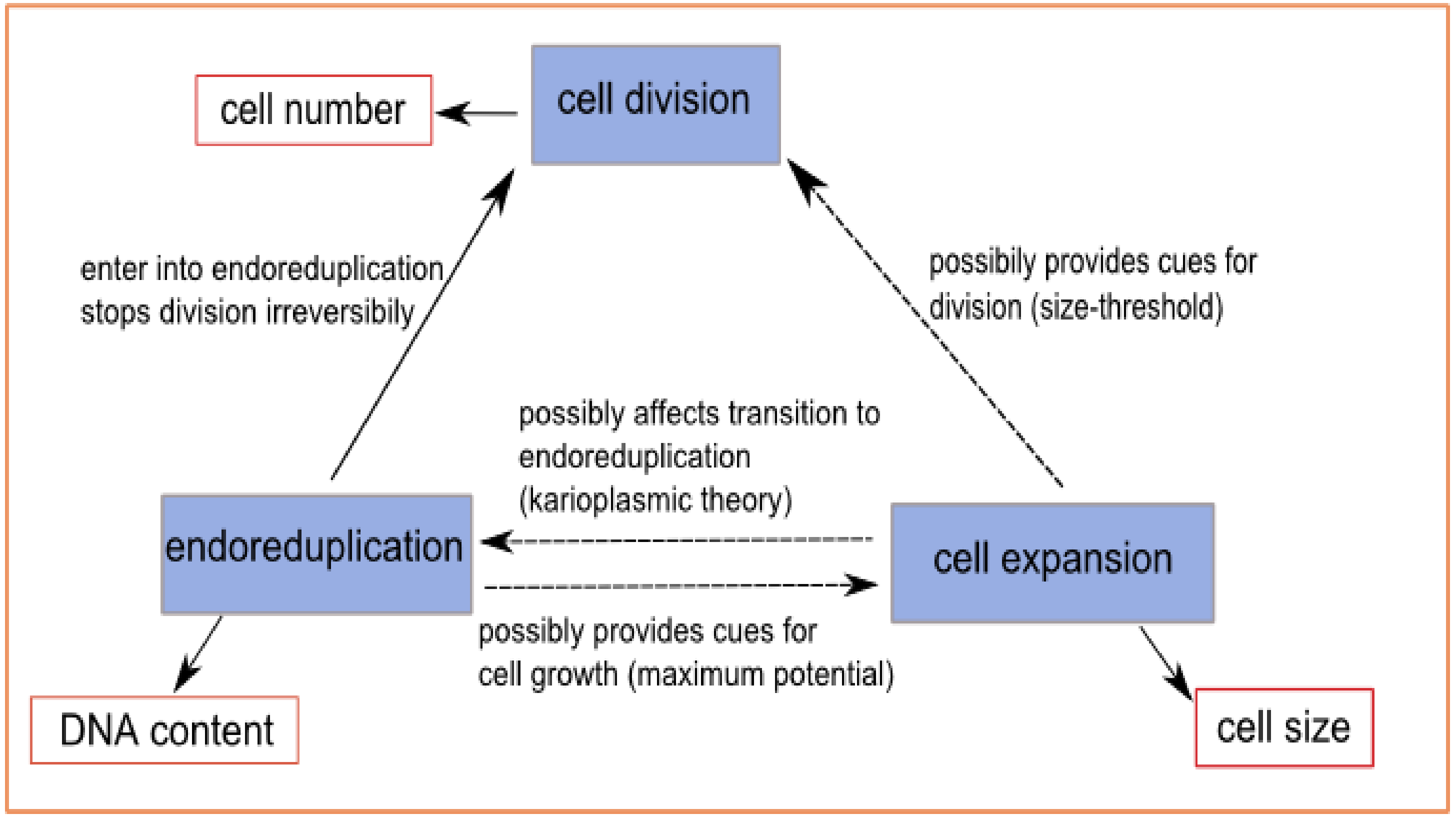


Nafati et al. (2011)

Individual effects on fruit growth are known..

… But interdependency among processes is unclear

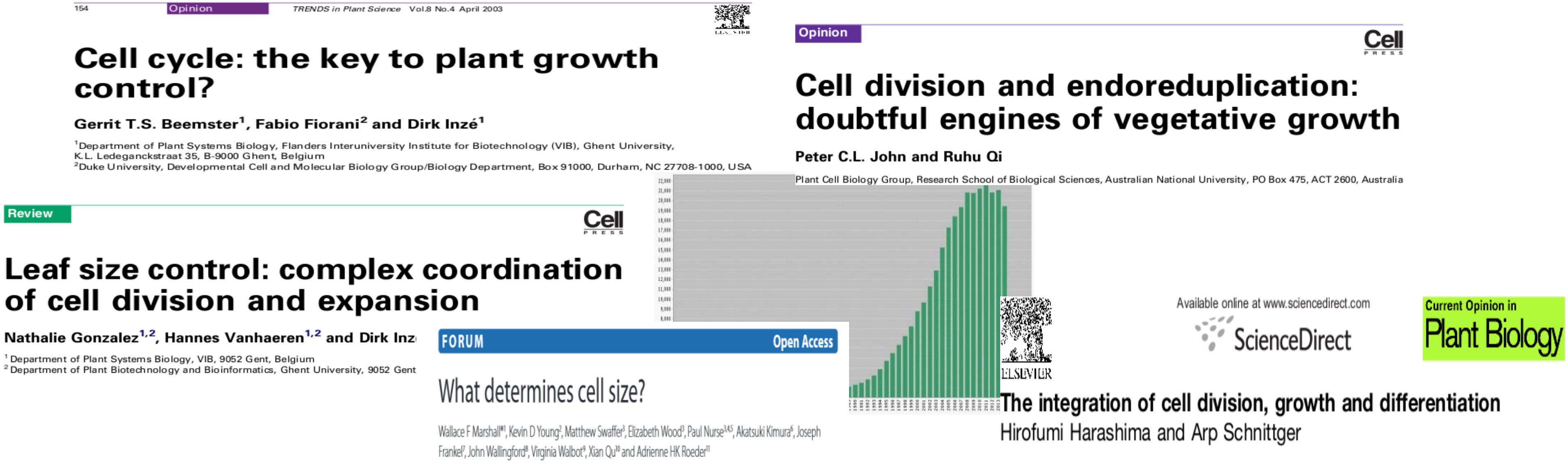
Organ growth and size



Compensatory effects between division and expansion

- Depending on the genotype
- In response to environmental factors

Control of organ growth: A challenging question..and a big debate!



154 Opinion TRENDS in Plant Science Vol.8 No.4 April 2003

Cell cycle: the key to plant growth control?

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Opinion Cell Press

Cell division and endoreduplication: doubtful engines of vegetative growth

Peter C.L. John and Ruhu Qi

Plant Cell Biology Group, Research School of Biological Sciences, Australian National University, PO Box 475, ACT 2600, Australia

Review Cell Press

Leaf size control: complex coordination of cell division and expansion

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FORUM Open Access

What determines cell size?

Wallace F Marshall, Kevin D Young, Matthew Swaffer, Elizabeth Wood, Paul Nurse, Akatsuki Kimura, Joseph Frankel, John Wallingford, Virginia Walbot, Xian Qu and Adrienne HK Roeder

Available online at www.sciencedirect.com ScienceDirect

Current Opinion in Plant Biology

ELSEVIER

The integration of cell division, growth and differentiation

Hirofumi Harashima and Arp Schnittger

Cellular perspective:

•Cells are tissue elementary building blocks with an autonomous developmental program
•Cell division and cell expansion drive tissue growth

vs

Organismal perspective:

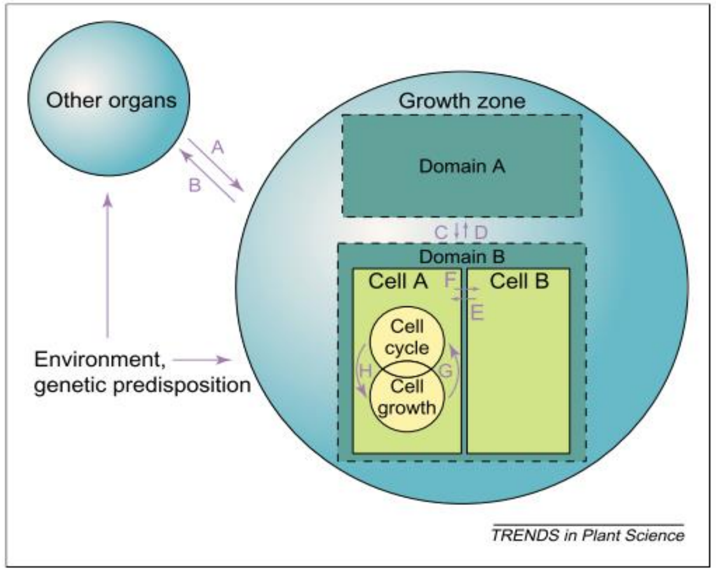
•Tissue expansion and synthesis of cytoplasm is the primary process
•Expansion drives cell division and endoreduplication, as mechanisms to maintain a correct DNA-cytoplasm ratio
•Organ control over development

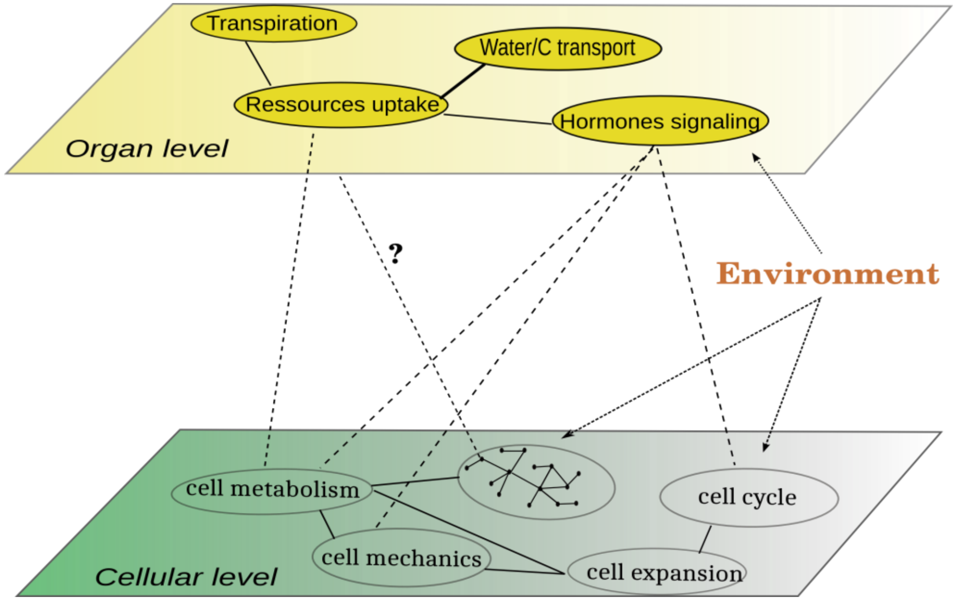
Truth might be in the middle..

An emerging consensus view:

"an integrated model whereby individual cells are the units of plant morphogenesis through their cell cycle and expansion activity. However, growth processes are coordinated within the organ(ism) as a whole by growth-substance signaling thus creating an interaction between cellular and whole-organ behaviour .. "

Beemster. Et al. (2003); Inzé et al. (2006)





But still many open questions :

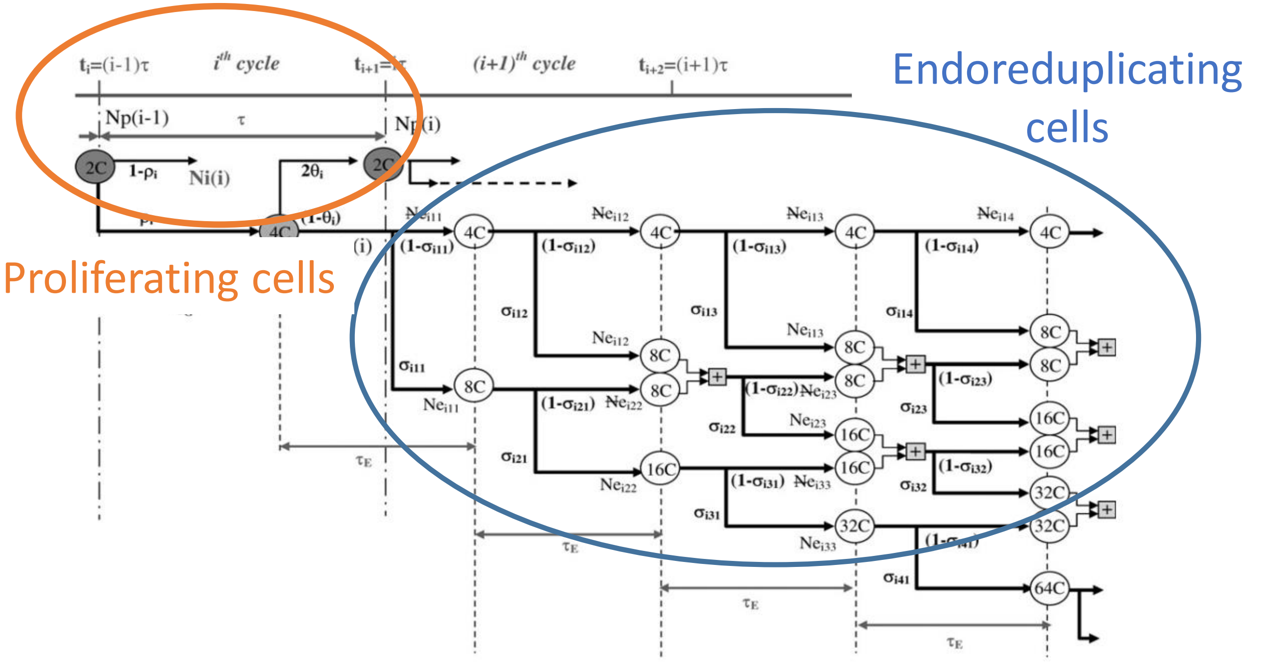
- Which interactions among cellular processes?
- Communication among different organizational levels
  - Which mechanisms?
  - Which are the coupling processes/variables?
- Effect of environment ?
  - How coordination among different processes is achieved?

An integrated division-endoreduplication-expansion model

Coupling of two existing models

A model of cell division-endoreduplication

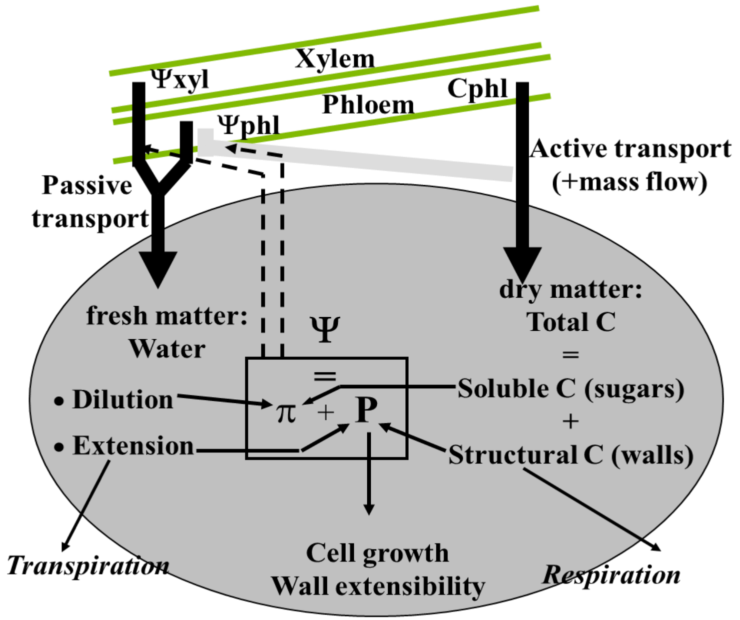
(Bertin et al. 2007)



•Cell division dynamics
•Decrease of the proliferative activity during development and onset of endoreduplication
•Asynchronous endoreduplication progression

A model of cell expansion

(Fishman Génard 1998; Liu et al. 2007)



•Turgor-driven expansion (Lockhart equation) depending on environmental conditions
•Carbon and water fluxes
•Changes in wall extensibility during fruit development

Modeling hypothesis for coupling cell division, endoreduplication and expansion processes

- Fruit is seen as a collection of cells population, each one having a specific age, volume (mass), DNA ploidy

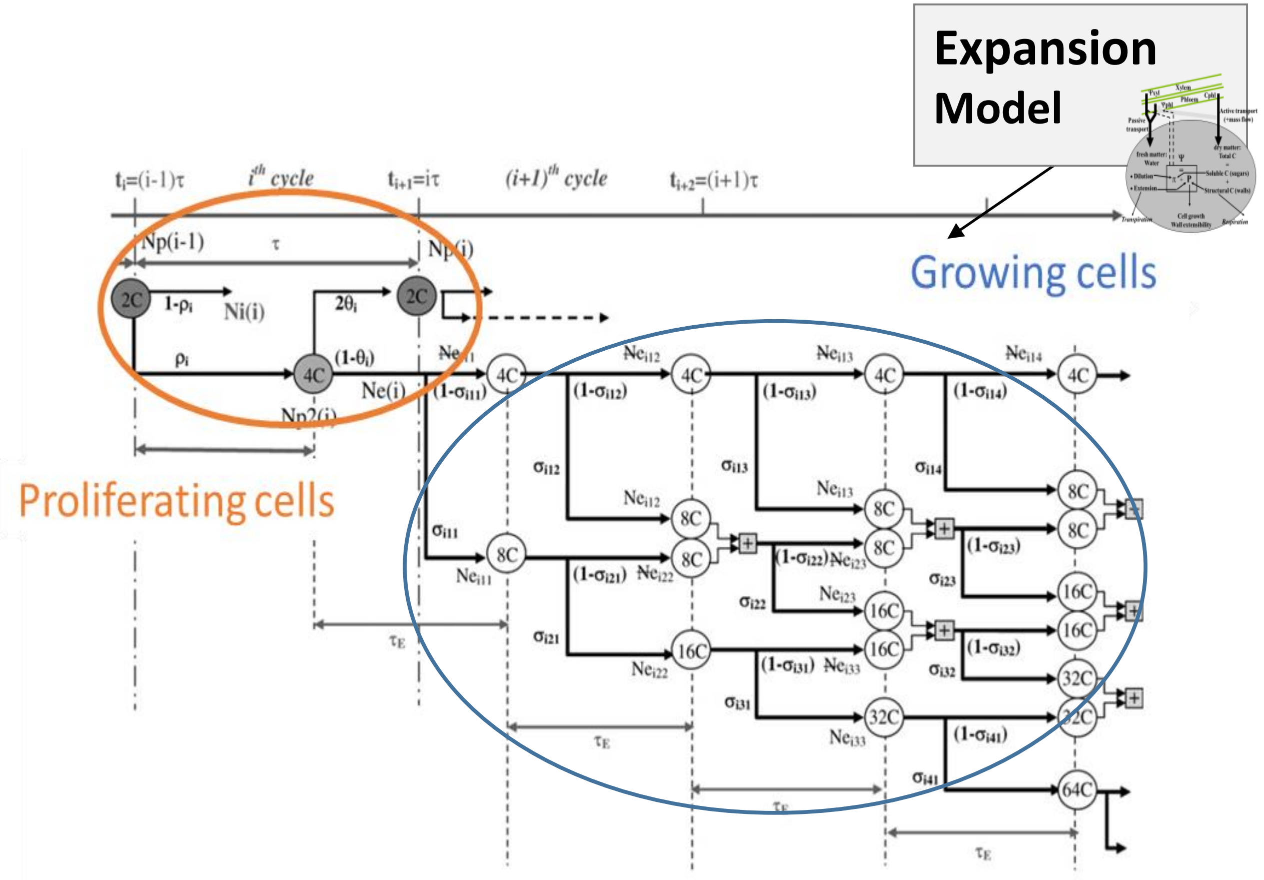
- The integrated model starts at the end of the pure division phase, once expansion phase begins

- Division-Endoreduplication model defines the number, age (birth date) and physiological state (proliferating or growing cells) of each population

- Endoreduplicating cells are assumed to be expanding

- At any time, cells leaving the proliferating phase start to grow, according to the expansion model

- Cell expansion depends on plant status and environmental factors



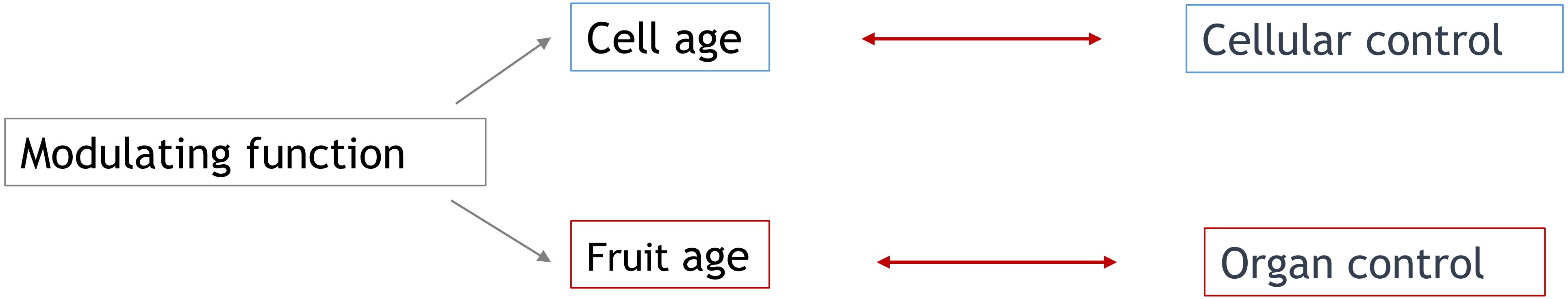
Baldazzi et al. (2013)

What about organismal/cell-based control?

In the model, developmental control is represented through the presence of specific *age-dependent* functions, that modulate cell processes (C import, metabolism, cell mechanics..)

Two distinct time scales are recognizable:

1. Cell age i.e. time spent since an *individual* cell has left the proliferating phase
2. Fruit age i.e. the time spent since the first expanding cells have appeared



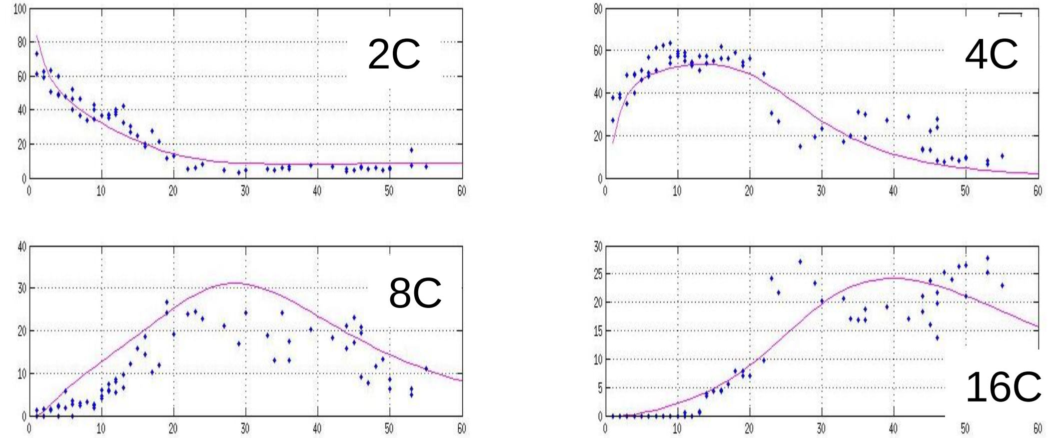
In silico test of different control schemes

Previous integrated model by *Fanwoua et al. (2011)*

Experimental data on cervil genotype

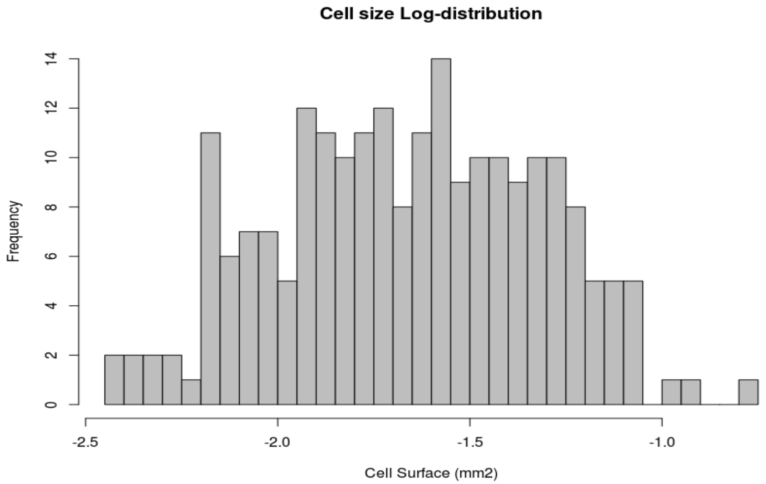
Cells Number

Cells endoreduplication dynamics



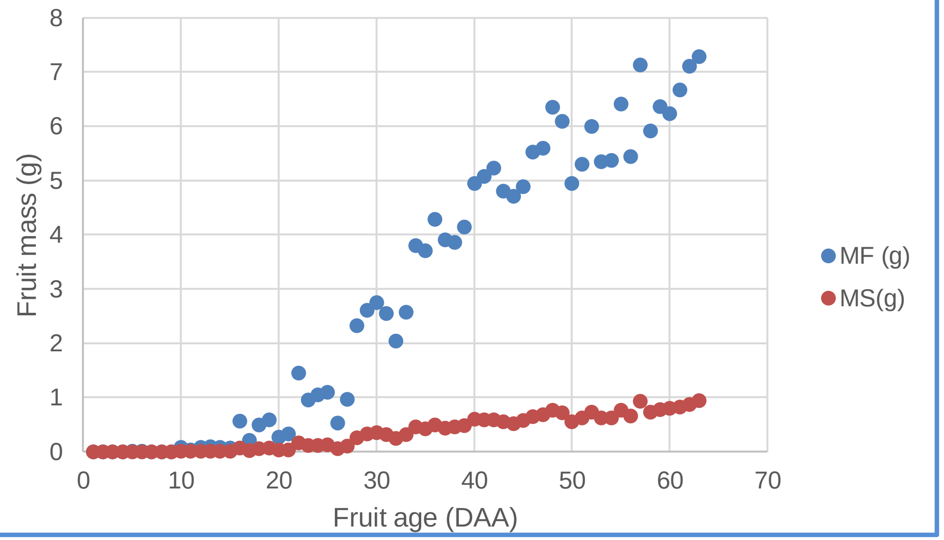
Model calibration

Cell size distribution



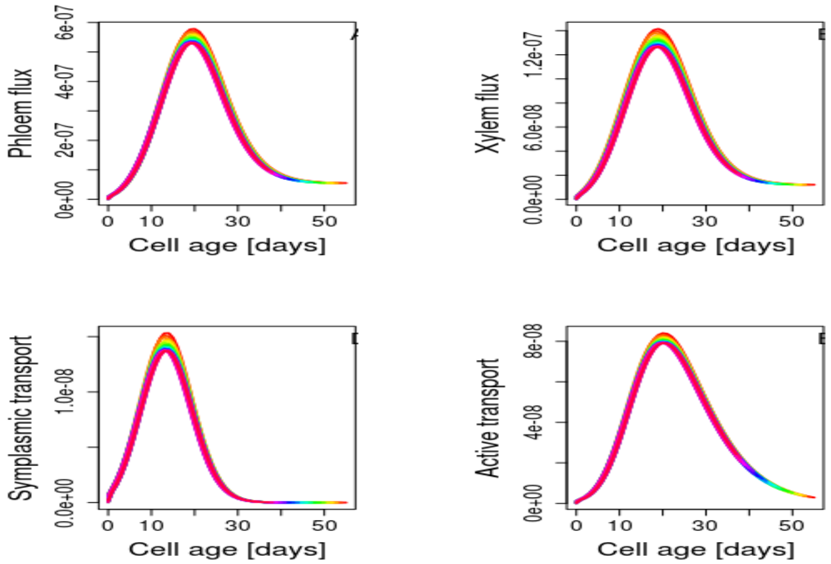
Validation

Fruit Mass



A simple cell-based control scheme

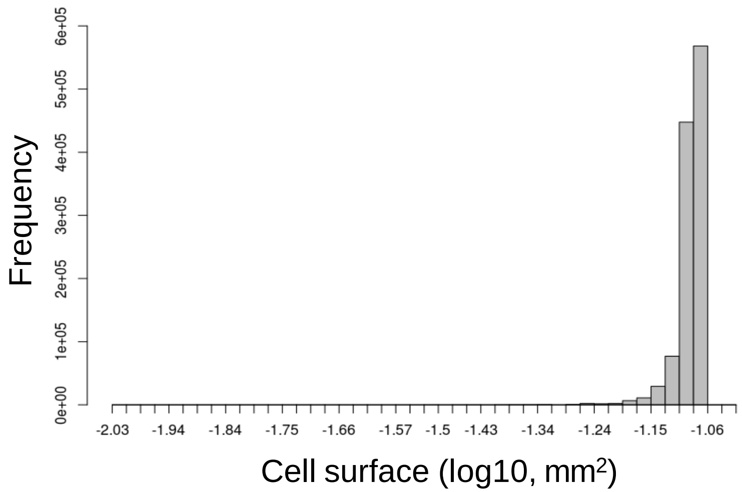
Two cells with the same age even if born at different fruit stages will behave *identically*



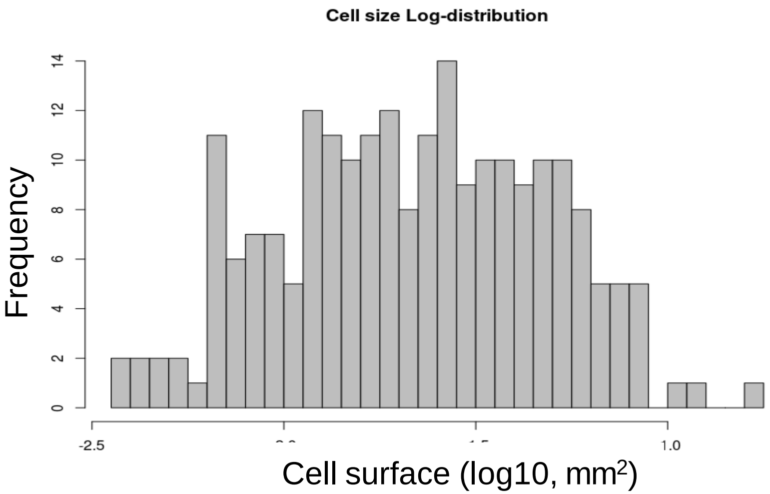
Cells size distribution:

- Very narrow compared to real data
- Only large cells are present
- Asymmetric on the left side

Model prediction:



Experimental data:



Add an organ-control mechanism

On cell wall plasticity

Bargel and Neinhuis, 2005; Catala et al., 2000

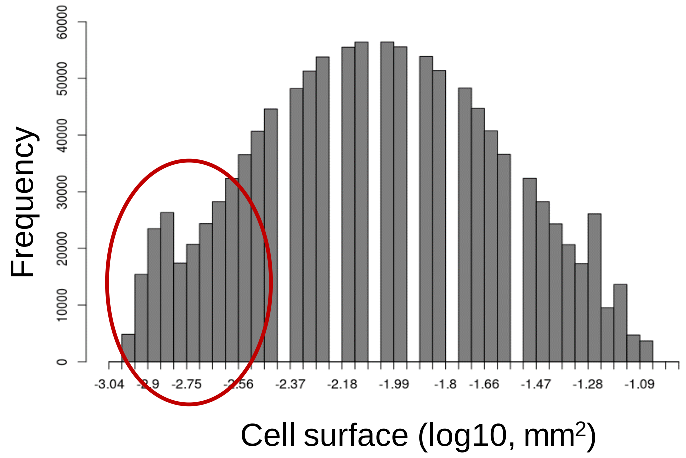
Cell size distribution:

•Extremely large with respect to data
•Unnatural small cells appear
•Pretty symmetric

↔

Unnatural flux dynamics:

•high internal pressure
•water and sugar backflow from fruit cells to plant



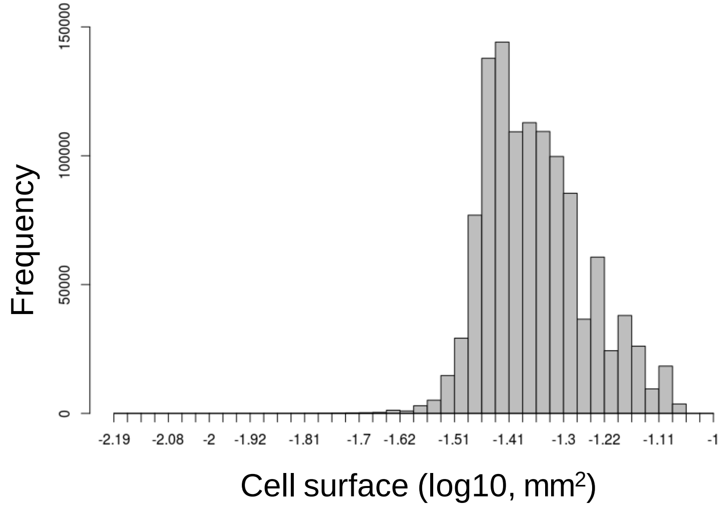
On C symplasmic transport

Crawford and Zambryski, 2001; Zambryski, 2004

Cell size distribution:

•Larger but less than data
  •Min et max cell size are over(under)-estimated
•A little asymmetric on the right side

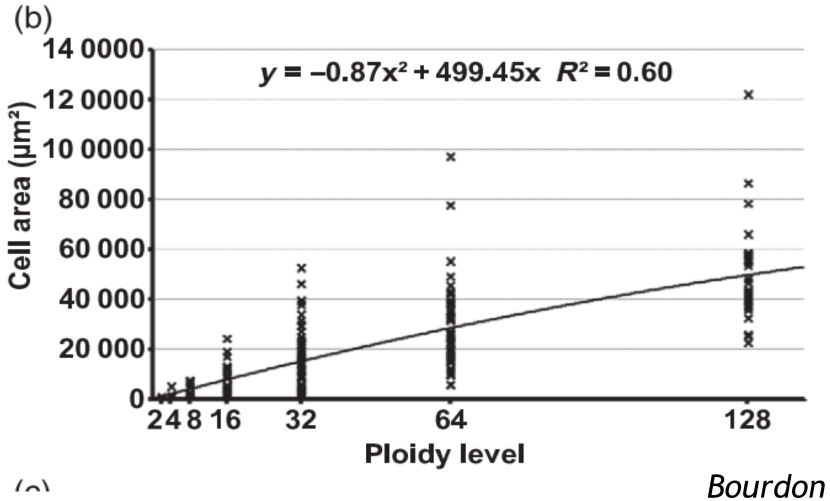
Additional mechanism needed in order to spread cells variability



Endoreduplication effect on cell expansion capabilities ?

*"The data thus argue for a physiological role of **endoreduplication** as a **facilitator of cell growth** (Nafati et al., 2011), but more importantly as an accelerator for organ growth, such as in fruit (Gonzalez et al., 2007; Bourdon et al., 2010; Mathieu-Rivet et al., 2010b).* » *Chevalier et al. 2011*

*« it is reasonable to assume that an increase in ploidy by endocycling **sets the maximum capacity for cell growth** instead of strictly determining the exact level of cell growth."* Breuer et al. (2010)



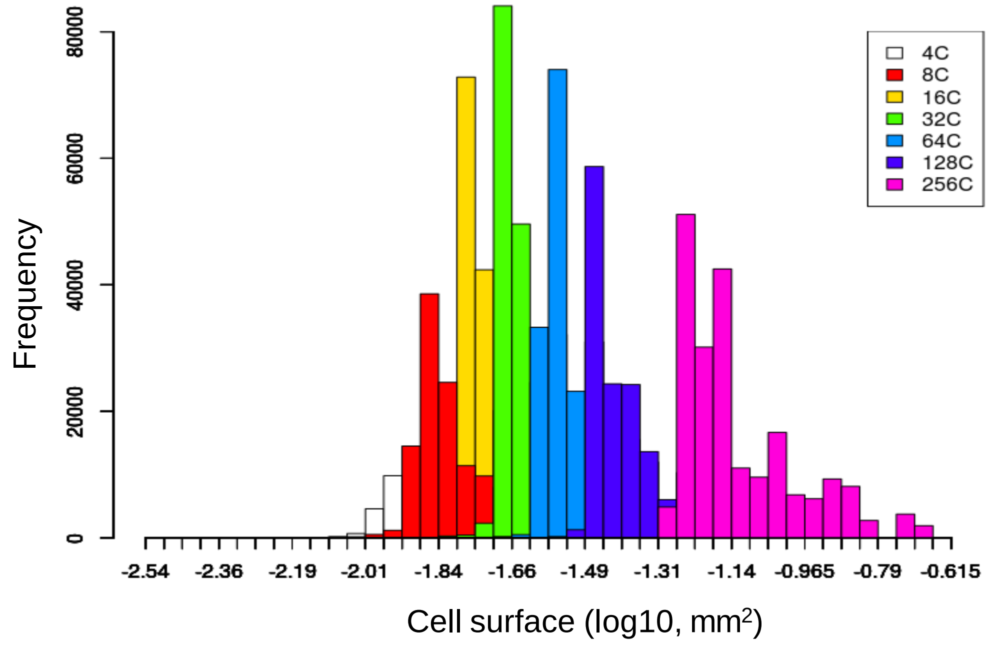
Bourdon et al. 2011

➡ *In silico* test:

Set maximum C import rate as a function of ploidy level

Cell size distribution:

- Large, closer too data
- Asymmetric on the right
- Large cells correspond to high ploidy levels



Conclusions and Perspectives

- Integrated model used for investigating the interactions among cellular processes and their control by cell/organ scale

The model supports:

- Need for an organ-based control
  - A pure cell-based control is unable to reproduce observed cells distribution
  - Symplasmic transport as a good candidate mechanism
- Endoreduplication as a modulator of cell’s expansion capabilities

Other mechanisms can contribute to observed cells variability

- Cell-cycle stochasticity
- Environmental variability

In perspective, the model could be used to quantify the importance of different mechanisms and evaluate their role in the control of organ growth, under different environments

Thank you for your attention!