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Modeling auxin fluxes and *Arabidopsis* root ramification at different scales

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Introduction

Plant primary growth occurs in two opposite directions, stems and roots both generating branched patterns during their development. However, where stem development appears extremely regular, based on phyllotactic patterns, root architecture appears somewhat random, controlled essentially by external clues such as nutrients concentration (Malamy et al. 2005).

The regularity of stem development has been ground to a large panel of pure mathematical and physical modeling (Adler et al. 1997). By contrast, the apparent chaos of root development has essentially directed the modeling effort toward ecophysiological and environmentally constrained models (Doussan et al. 2003).

Yet, as the biological knowledge of development and the available microscopy tools evolves, mathematicians and computer scientists are now able to glimpse at the cellular level of development. They can create new models taking into account previously ignored mechanisms and giving rise to new perception on ancient problems, as described by Barbier de Reuille et al. (2006), Jönsson et al. (2006), and Smith et al. (2006) on the topic of phyllotaxis.

Until recently, root systems development was considered too chaotic to be modelled on the same basis as shoot development. However, recent biological results suggest that lateral root initiation (LRI), main determinant of root architecture, may itself be more regular than first supposed (Dubrovsky et al. 2000; Dubrovsky et al. 2006; De Smet et al. 2007; Lucas et al. 2007). Global root architecture now appears as the superposition of regular LRI and irregular emergence, the latter phenomenon being more strongly subjected to environmental conditions.

As LRI and root development both depend on complex auxin fluxes and genetic interactions, we used a modeling approach to integrate the large biological knowledge available on root development and the complexity of flux dynamics. The models we choose to develop address the control of LRI by auxin fluxes. Our aim was to test various hypotheses concerning LRI regularity and the positioning of root primordia.

Modeling root development and auxin fluxes

Auxin fluxes occurring during root development can be considered at the macroscopic (tissue level) or microscopic (cellular level) scales. We will here distinguish between two kinds of models we developed, each aiming to reproduce the fluxes at one of those two levels.

The first kind of model is centered on the whole root. It is geared toward a representation of the whole developmental sequence, and well adapted to treat the problem of the regularity and distribution of LRI. The spatial representation of the root in this model can be considered as almost linear. The main computational topic of this model is one of competition and transport within a dynamic system based upon a dynamic structure, also known as (DS)². The principal advantage of this model is the ultimate possibility to generate LRI distribution to be compared with LRI distribution observed *in vivo*. We addressed the inherent lack of precision on the positioning of LRI at the microscopic scale by developing our second model.

Based on the cellular structure of a single root slice, the second model is geared towards the simulation of cellular auxin fluxes dynamics. This approach is similar to the one currently applied to stem apical meristem modeling (Barbier de Reuille et al. 2006). The cellular structure of the root slice is here represented as a static graph taking into account each cell and its cell wall. The main

computational topic associated with this kind of model is the complex flux dynamics and the study of its stability. This model has the advantage to allow us to test various hypotheses concerning the precise positioning of root primordia, and to experiment *in silico* on the consequences of auxin fluxes perturbation on initiation. It is however static, and as such can only be used to simulate a snapshot of the auxin accumulation points during root development.

Results

The large scale model was developed based on L-System. Biological studies indicates that LRI is caused by basipetal auxin fluxes, flowing back from the apical root meristem along the lateral root cap, and that primordia development and lateral root emergence are caused by acropetal auxin fluxes coming from the aerial parts (Casimiro et al. 2001; Bhalerao et al. 2002). We introduced those two fluxes in our model as well as auxin production in the aerial parts and at the apex. We were able to generate auxin accumulation at the root apex under certain conditions, and to test which parameters influence this accumulation, as well as other characteristics of the fluxes (fig. 1).

Introducing LRI in the model proved to be problematic, as little was known of the precise dynamic of auxin fluxes which take place above the root apical meristem and are responsible for initiation. We proceeded to a thorough structural analysis of LRI. We showed that LRI appears tightly co-regulated with gravitropism in *Arabidopsis*, as the mechanisms controlling those two phenomena involve a common auxin transport route (Lucas et al. 2007). We suggested that observed LRI regularities may in fact be linked to the periodical nature of gravitropic and thigmotropic responses.

We integrated those results in the fine scale model, as well as known dynamics of auxin fluxes in root tissue whenever such data was available (Friml et al. 2002; Blilou et al. 2005; Swarup et al. 2005; Sauer et al. 2006; Fukaki et al. 2007) (see fig. 2 for an example of flux dynamics). To palliate for the lack or imprecision of data concerning some tissues, we implemented in our model rules for PIN dynamics such as those described in Feugier et al. (2005, 2006), Jönsson et al. (2006) and Smith et al. (2006).

We will insist in our talk on the cellular modeling approach and on the associated problems. One of the main topics we will address is how to account for the observed inconsistency between the positions of the gravitropic responsive tissues and the lateral root primodium. Indeed, the auxin maximum causing the gravitropic response in the epidermis appears on the inside of root turns, whereas LRI always takes place on the outside of root turns, where one would expect the lowest auxin level. We will present one hypothesis to explain this paradox and the results of its implementation in our model. We will also discuss of the potential evolution of the cellular model toward a (DS)² model.

References

Adler I, Barabe D, Jean RV. 1997. A History of the Study of Phyllotaxis. *Annals of Botany* **80**, 231-244

Bhalerao RP, Eklöf J, Ljung K, Marchant A, Bennett MJ, Sandberg G. 2002. Shoot-derived auxin is essential for early lateral root emergence in Arabidopsis seedlings. *The Plant Journal* **29**, 325-332

Blilou I, Xu J, Wildwater M, Willemsen V, Paponov I, Friml J, Heidstra R, Aida M, Palme K, Scheres B. 2005. The PIN auxin efflux facilitator network controls growth and patterning in Arabidopsis roots. *Nature* **433**, 39-44

Casimiro I, Marchant A, Bhalerao RP, Beeckman T, Dhooge S, Swarup R, Graham N, Inzé D, Sandberg G, et al.. 2001. Auxin transport promotes Arabidopsis lateral root initiation. *The Plant Cell* **13**, 843-852

Barbier de Reuille P, Bohn-Courseau I, Ljung K, Morin H, Carraro N, Godin C, Traas J. 2006. Computer simulations reveal novel properties of the cell-cell signaling network at the shoot apex in *Arabidopsis*. *PNAS* **103**, 1627-1632.

De Smet I, Tetsumura T, De Rybel B, Frei Dit Frey N, Laplaze L, Casimiro I, Swarup R, Naudts M, Vanneste S, et al.. 2007. Auxin-dependent regulation of lateral root positioning in the basal meristem of Arabidopsis. *Development* **134**, 681-690

Dubrovsky JG, Doerner PW, Colón-Carmona A, Rost TL. 2000. Pericycle cell proliferation and lateral root initiation in Arabidopsis. *Plant Physiology* **124**, 1648-1657

Dubrovsky JG, Gambetta GA, Hernández-Barrera A, Shishkova S, González I. 2006. Lateral Root Initiation in Arabidopsis: Developmental Window, Spatial Patterning, Density and Predictability. *Annals of Botany (Lond)* **97**, 903-915

Feugier FG, Mochizuki A, Iwasa Y. 2005. Self-organization of the vascular system in plant leaves: inter-dependent dynamics of auxin flux and carrier proteins. *J Theor Biol.* **236**, 366-75

Feugier FG, Iwasa Y. 2006. How canalization can make loops: A new model of reticulated leaf vascular pattern formation. *J Theor Biol.* **243**, 235-244

Friml J, Wiśniewska J, Benková E, Mendgen K, Palme K. 2002. Lateral relocation of auxin efflux regulator PIN3 mediates tropism in Arabidopsis. *Nature* **415**, 806-809

Fukaki H, Okushima Y, and Tasaka M. 2007. Auxin-Mediated Lateral Root Formation in Higher Plants. *International Review of Cytology* **256,** 113-137

Jönsson H, Heisler MG, Shapiro BE, Meyerowitz EM, Mjolsness E. 2006. An auxin-driven polarized transport model for phyllotaxis. *PNAS* **103**, 1633-1638

Lucas M, Godin C, Jay-Allemand C, Laplaze L. 2007. Auxin fluxes in the root apex co-regulate gravitropism and lateral root initiation. Submitted to Journal of Experimental botany.

Malamy JE. 2005. Intrinsic and environmental response pathways that regulate root system architecture. *Plant Cell Environment* **28,** 67-77

Doussan C, Pages L, Pierret A. 2003. Soil exploration and resource acquisition by plant roots: an architectural and modelling point of view. *Agronomie* **23,** 419-431

Sauer M, Balla J, Luschnig C, Wisniewska J, Reinöhl V, Friml J, Benková E. 2006. Canalization of auxin flow by Aux/IAA-ARF-dependent feedback regulation of PIN polarity. *Genes & Develpment* **20,** 2902-2911

Smith RS, Guyomarc'h S, Mandel T, Reinhardt D, Kuhlemeier C, Prusinkiewicz P. 2006. A plausible model of phyllotaxis. *PNAS* **103,** 1301-1306

Swarup R, Kramer EM, Perry P, Knox K, Leyser HM, Haseloff J, Beemster GT, Bhalerao R, Bennett MJ. 2005. Root gravitropism requires lateral root cap and epidermal cells for transport and response to a mobile auxin signal. *Nature Cell Biology* **7,** 1057-1065
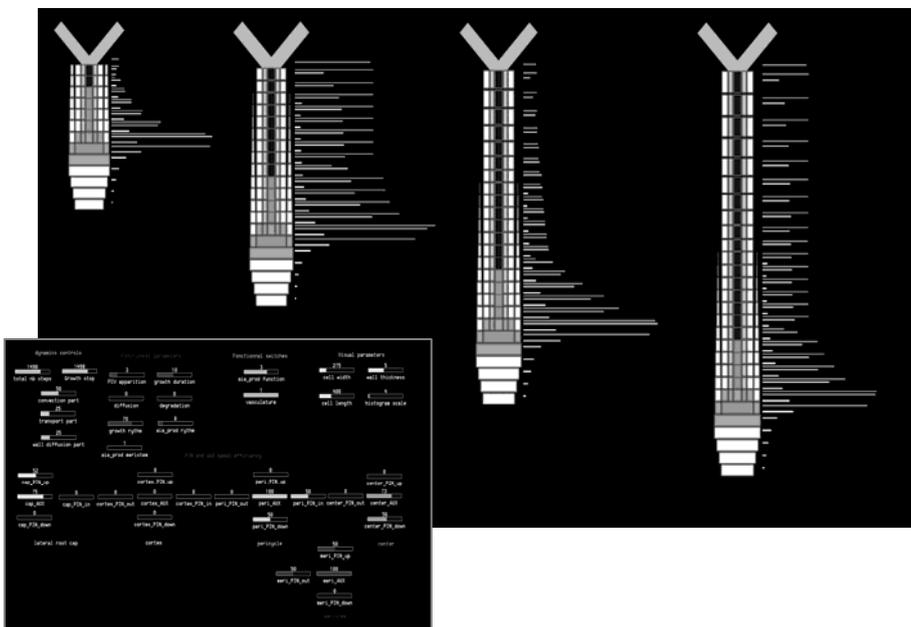
Figure 1.
L-System based model of auxin fluxes in a growing root

Global auxin fluxes are the synthesis between cell wall diffusion, cell/cell diffusion, active transport and convection of auxin.

Auxin production takes place in the aerial part and at the root apex.

The control panel on the bottom left show the various parameters that can be changed to challenge the stability of the model.
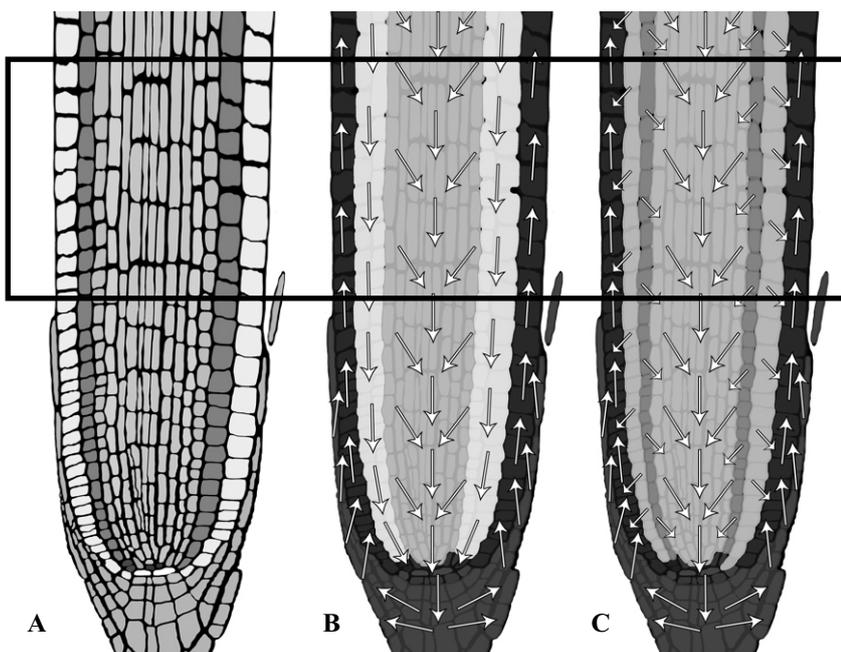

Figure 2.
Dynamic of auxin fluxes in root tissues

A. Root superstructure. Each colour identifies a specific tissue.

B. Global auxin fluxes. Tissues are grouped under a new common colour when they direct the flux along a common path.

C. Changes in auxin fluxes patterns during an exogenous auxin application. Tissues react according different rules, creating divergent auxin paths and isolating inner tissues from auxin present in outer tissues.

The black border define the size and position of the root slice considered in the fine scale model.