Article:

Bennett, T orcid.org/0000-0003-1612-4019 (2020) Root Development: A Go-Faster Stripe and Spoilers. Developmental Cell, 53 (4). pp. 372-374. ISSN 1534-5807

https://doi.org/10.1016/j.devcel.2020.04.017

Root development: a go-faster stripe and spoilers

Tom Bennett[1*]

[1]School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT, UK

Abstract

Root growth depends on spatially-distinct cell division and elongation activities in the root meristem. The correct positioning of a 'transition zone' boundary between the division and elongation zones is critical for efficient root growth; new work from Salvi et al sheds light on how this boundary is established and maintained.

50 words

Main text

Hidden beneath the ground, billions of roots are constantly growing, striving to supply water and nutrients to shoot systems, which in turn provide roots with sugars from photosynthesis. Balance is a key property of this system; root growth must meet the demands of the shoot system, but without exceeding the supply of energy. Complicating matters, not all roots are equally useful; growth priority must be given to those roots best placed to supply water and nutrients (Oldroyd & Leyser, 2020). An individual root must thus integrate both global cues (shoot demand and energy supply) and local stimuli (resource availability) to determine how much it should grow, and somehow the growth decisions of individual roots must add up to a coherent system. While we are still some way from understanding how all these 'root trips' are coordinated, recent work from Salvi et al (Salvi et al., 2020) takes us one step closer to understanding the high-performance engineering that allows each root to both accelerate and reach a steady speed.

Almost all longitudinal root growth happens at the tip of each root, in a specialized zone called a 'meristem'. The root meristem can be divided into 3 key parts; an organizing zone, the division zone (DZ) and the elongation zone (EZ) (Motte et al., 2019). In the DZ, cells are small and cytoplasmically dense, and undergo quasi-coordinated rounds of mitosis. The resulting intercalation of new cells into the DZ constantly 'pushes' the cells at its shootward boundary into the EZ, where the cells undergo a radical change in appearance; they become highly elongated and no longer divide. Thus, while the DZ provides the 'fuel', the real 'engine' of root growth is the EZ. The sustained growth of the root requires these division and elongation activities to be carefully balanced. If cells divide but fail to move into the EZ, the root will not grow effectively, but if cells move into the EZ faster than they divide, the meristem will rapidly shrink, preventing further growth. Thus, to accelerate, a root must not only 'throttle up' the rate of cell division, but also the rate at which cells transit from the DZ into the EZ.

While we do not yet fully understand either aspect of this system, understanding how cell division can ramp up is at least conceptually straightforward. Conversely, understanding how the cellular balance between the DZ and EZ can be stably maintained, but also dynamically altered, is far from simple. As such, this carefully calibrated 'fuel-injection system' represents a highly intriguing developmental biology problem, which has been the focus of Sabrina Sabatini's research group at the University of Rome *La Sapienza*, for the last decade or so. Together with her collaborators, Sabatini has sought to understand the thin 'transition zone'

(TZ) that regulates passage of cells between the DZ and EZ, and how this ‘go-faster stripe’ of functions to regulate the rate of root growth. In an opening salvo, Sabatini’s group showed that two plant hormones – auxin and cytokinin – interact to regulate the position of the TZ within the root meristem (Dello Ioio R et al., 2007; Dello Ioio R et al., 2008). But knowing that an engine has sparkplugs and pistons, is not to understand how an engine works. Sabatini’s group have therefore worked tirelessly to determine how these two key components are able to stably yet dynamically maintain the TZ, resulting in an impressive string of publications (Moubayidin et al., 2010; Moubayidin et al., 2013; Di Mambro et al., 2017; Pacifici et al., 2018; Di Mambro et al., 2019). Along the way, more components have been identified, but crucially, the group has also started to produce an ‘engine map’ for the TZ, using mathematical modelling to better understand how the components operate together to produce a consistent output (Di Mambro et al., 2017; Pacifici et al., 2018; Di Mambro et al., 2019).

In the latest addition to the emerging TZ instruction manual, Salvi et al now shed light on two key unresolved questions: how does the ‘engine’ start, and how does it reach a steady speed? Through detailed observations of immediate post-embryonic root development, the authors show that mitotic activity in the DZ only starts 24 hours post germination. Even when mitotic activity starts, cells originating in the DZ do not start to enter the EZ until 36 hours post germination, suggesting that the TZ is only formed at this point. Over the next 84 hours, the size of the DZ continues to increase, until by 5 days post germination mitosis in the DZ is balanced by the passage of cells to the EZ, allowing the DZ to reach a steady size. Using a combination of mathematical modelling and experimentation, the authors show that key to the establishment of the TZ is a drop in cellular protein levels of PLETHORA (PLT) transcription factors; while they are initially uniform through the DZ, they become diluted at the shootward boundary once mitoses start to occur. This drop allows expression of the ARR12 transcription factor in the presumptive TZ, which in turn represses PLT2 expression, sharpening the boundary between the two activities. ARR12 then acts to negatively regulate the level of cellular auxin in the proto-TZ, creating the auxin ‘minimum’ needed for TZ function. But while ARR12 activity is sufficient to specify the TZ, the authors elegantly show that it is not sufficient to stabilize the position of the TZ at 5 days post germination. Rather, the authors show that a close relative, ARR1, which is also expressed in the TZ, stabilizes the position of the TZ by directly repressing cell division itself, stopping the further expansion of the DZ. Thus, the authors demonstrate that two related but separate, self-organizing feedback loops regulate the initiation and maintenance of the TZ.

Whilst Salvi et al emphasise the stability of the TZ position after 5 days, this is only really true under constant experimental conditions. In the real world, meristem size is constantly changing in response to external and internal conditions, signalled by the changing levels of molecules such as auxin and cytokinin. Thus the next challenge is to understand how roots continually integrate all this information into the positioning of the TZ, to dynamically alter the ‘speed’ of root growth, and how this can be coordinated across the root system as a whole. Like a discerning driver, roots know when to push the pedal to the floor, but also keep their eyes firmly on the road ahead.

1013 words

Declaration of Interest

The author declares no competing interests.

References

Dello Ioio R, Linhares FS, Scacchi E, Casamitjana-Martinez E, Heidstra R, Costantino P, Sabatini S. Cytokinins determine Arabidopsis root-meristem size by controlling cell differentiation. Curr Biol. 2007 Apr 17;17(8):678-82.

Dello Ioio R, Nakamura K, Moubayidin L, Perilli S, Taniguchi M, Morita MT, Aoyama T, Costantino P, Sabatini S. A genetic framework for the control of cell division and differentiation in the root meristem. Science. 2008 Nov 28;322(5906):1380-4.

Di Mambro R, De Ruvo M, Pacifici E, Salvi E, Sozzani R, Benfey PN, Busch W, Novak O, Ljung K, Di Paola L, Marée AFM, Costantino P, Grieneisen VA, Sabatini S. Auxin minimum triggers the developmental switch from cell division to cell differentiation in the *Arabidopsis* root. Proc Natl Acad Sci U S A. 2017 Sep 5;114(36):E7641-E7649.

Di Mambro R, Svolacchia N, Dello Ioio R, Pierdonati E, Salvi E, Pedrazzini E, Vitale A, Perilli S, Sozzani R, Benfey PN, Busch W, Costantino P, Sabatini S. The Lateral Root Cap Acts as an Auxin Sink that Controls Meristem Size. Curr Biol. 2019 Apr 1;29(7):1199-1205.

Motte H, Vanneste S, Beeckman T. Molecular and Environmental Regulation of Root Development. Annu Rev Plant Biol. 2019 Apr 29;70:465-488.

Moubayidin L, Perilli S, Dello Ioio R, Di Mambro R, Costantino P, Sabatini S. The rate of cell differentiation controls the Arabidopsis root meristem growth phase. Curr Biol. 2010 Jun 22;20(12):1138-43.

Moubayidin L, Di Mambro R, Sozzani R, Pacifici E, Salvi E, Terpstra I, Bao D, van Dijken A, Dello Ioio R, Perilli S, Ljung K, Benfey PN, Heidstra R, Costantino P, Sabatini S. Spatial coordination between stem cell activity and cell differentiation in the root meristem. Dev Cell. 2013 Aug 26;26(4):405-15.

Oldroyd G, Leyser O. A plant's diet, surviving in a variable nutrient environment. Science 2020 Apr 3;368(6486). doi: 10.1126/science.aba0196

Pacifici E, Di Mambro R, Dello Ioio R, Costantino P, Sabatini S. Acidic cell elongation drives cell differentiation in the *Arabidopsis* root. EMBO J. 2018 Aug 15;37

Salvi E, Rutten J, Dello Ioio R, Di Mambro R, Negri R, Licursi V, Polverari L, Ten Tusscher K, and Sabatini S. A Self-organized PLT/Auxin/ARR-B network controls the dynamics of root zonation development in Arabidopsis Thaliana. Dev Cell, this issue.

Figure Legends

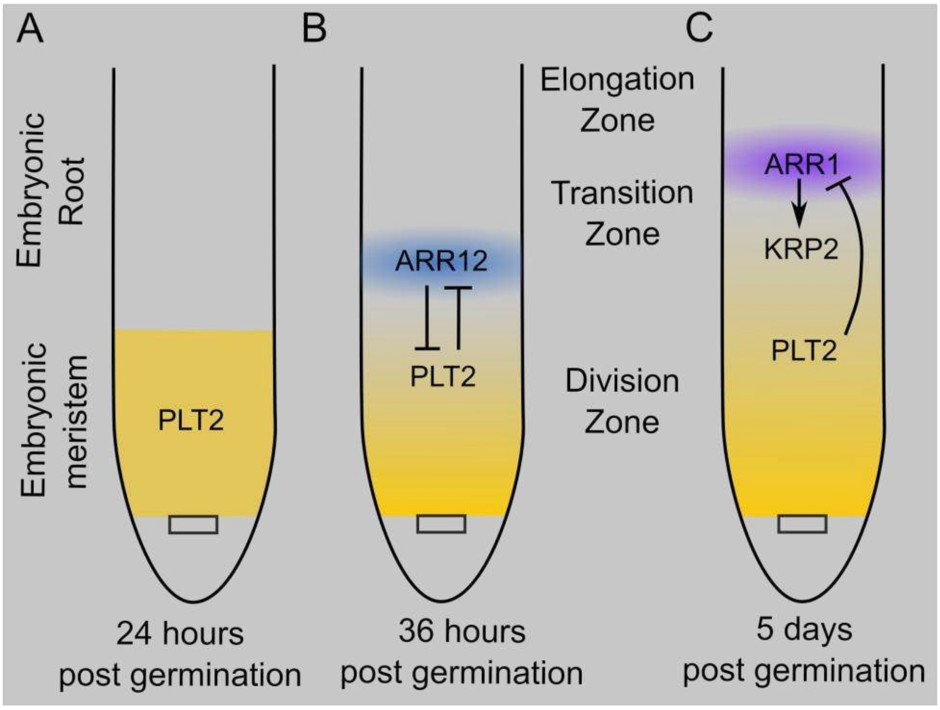

Figure 1: Model for establishment and stabilization of transition zone positioning

a) Immediately after germination, PLT2 levels (yellow) are high throughout the embryonic meristem of the root. Mitosis starts 24 hours after germination, creating the division zone. Elongation occurs in the embryonic root cells.

b) By 36 hours post germination, PLT2 levels at the shootward boundary of the division zone have been diluted by mitosis. This allows expression of ARR12 (blue), which specifies the formation of the transition zone by its action on PLT2 and auxin. Cells now pass from the division to elongation activity by passing through the transition zone.

c) By 5 days post germination, expression of ARR1 (purple) in the transition zone is established. ARR1 directly represses cell division by inducing expression of KRP2, an inhibitor of cyclin-dependent kinases, thereby stabilizing the position of the transition zone.