

ROOT DEVELOPMENT

Pulse control

The length of root hairs, a critical determinant of a plant's absorption capacity, is dictated by a translational pulse of the transcription factor RSL4. The intensity and duration of this pulse depends on the integration of endogenous and environmental information that tunes the phenotypic readout to the environment.

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Cell size is important for the execution of developmental programmes and essential for correct cell function, causing diseases and decreased fitness when not properly regulated. In plants, shape, size and arrangement of cells are highly responsive to external cues, conferring phenotypic plasticity that adjusts development to environmental conditions. How the duration of growth and thus the final size of plant cells are controlled remains enigmatic. In this issue of *Nature Plants*, Sourav Datta *et al.* propose a solution to this problem, by demonstrating that the abundance of the basic helix-loop-helix transcription factor ROOT HAIR DEFECTIVE 6-LIKE 4 (RSL4) is directly correlated with the size of root-hair cells¹.

Root hairs, tubular extensions of specialized cells on the epidermis of roots referred to as trichoblasts, are important in plant–soil interactions and assist in water and nutrient uptake from the soil. Their growth ceases when the hair reaches a genetically predetermined length. RSL4 acts downstream of genes that assign the hair fate to epidermal cells, and initiates polar growth in trichoblasts by orchestrating the expression of genes required for root-hair growth², thus occupying a central node between cell fate commitment and cell differentiation. RSL4 mRNA is present in the nuclei of root cells predestined to produce hairs in the elongation zone immediately prior to initiation of root-hair outgrowth. RSL4 transcripts are, however, lacking in cells in which root-hair elongation has been initiated. This finding indicates that transcriptional control of RSL4 is insufficient to define the final size of the cell, and a regulatory intervention at the protein level is required. RSL4 appears to be rapidly degraded after root-hair formation is initiated. In support of this post-translational modulation, Datta *et al.* showed that both RSL4 abundance and root-hair length are increased when protein degradation via the 26S proteasome is compromised. Thus, a strictly controlled spatiotemporal pulse of RSL4 synthesis

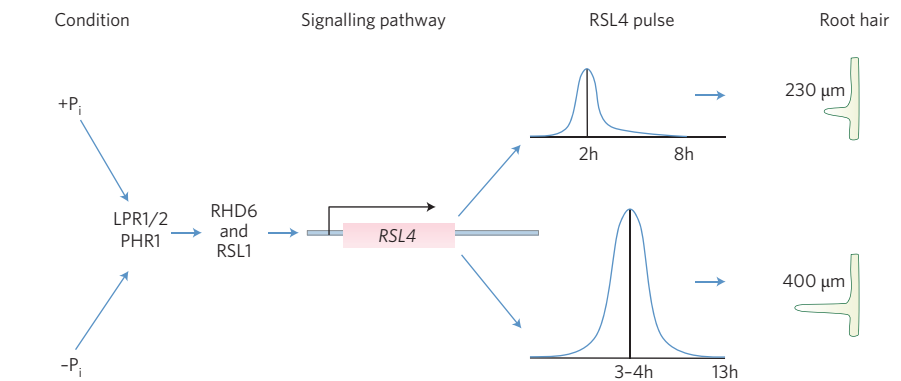


Figure 1 | Integration of environmental and developmental signals defines the length of root hairs. The inorganic phosphate (P_i) status is sensed by the multicopper oxidases LPR1 and LPR2, and conveyed via the transcription factor PHR1 to regulate the expression of the basic helix loop helix transcription factors RHD6 and RSL1, which in turn are controlling the expression of RSL4. The duration of RSL4 transcription and the half-life of the RSL4 protein define the amplitude of a translational pulse that dictates the length of the root hairs. Under P_i-replete conditions (top), the peak reaches its maximum 2 h after the first appearance of RSL4 and is detectable for a period of 8 h. Under P_i-deficient conditions (bottom), the peak of RSL4 protein abundance is approximately two-fold higher, occurs later and is more sustained than under P_i-replete conditions.

is crucial for controlling the growth of trichoblasts.

Compensating for the lack of behavioural routes, plants respond with high plasticity to environmental signals. These responses require tuning of gene activity both at the transcriptional and post-transcriptional levels. As an example of such environmental acclimation, the length of root hairs is increased upon restricted availability of soil resources with low phyto-availability such as phosphate, an essential but often growth-limiting mineral nutrient. Longer hairs increase the root radial uptake capacity and thereby decrease the phosphate depletion zone resulting from the restricted diffusion of phosphate in the soil. As a consequence, exploitation of fertile soil microsites by the plant via interception is greatly increased. The results reported by Datta *et al.* show that phosphate deficiency increases the pool size of RSL4 due to prolonged synthesis and increased half-life of RSL4, which in combination translate into a significant increase in root-hair length (Fig. 1). Thus,

the size of the trichoblasts is defined by the intensity of the RSL4 pulse, which is an integration of developmental and environmental signals.

Several examples underpin a close linkage between the function of transcriptional regulators, their synthesis and proteasome-mediated degradation³. Liam Dolan and colleagues now show that such dynamics can be directly correlated with phenotype¹, and underline the mandatory requirement for assessing the dynamic behaviour of biological process components if a holistic understanding of the underlying mechanisms is to be obtained. One question still remains: how are internal and external cues integrated to tune the amplitude of the RSL4 pulse? Although in the case of RSL4 the exact molecular mechanisms for the integration of developmental and nutritional signals remains elusive, recent advances pinpoint the importance of gene expression dynamics for nodes that determine the root phenotype and in particular the traits that are

important for nutrient foraging. Oscillatory synthesis of a negative regulator of root-hair growth, the kinase PINOID (PID), is controlled by a chromatin loop that encompasses the *PID* promoter⁴. Chromatin topology is dynamically regulated in response to the plant hormone auxin that also affects expression of *RSL4* (ref. 2). Such oscillatory expression patterns have also been described for genes that determine the formation of lateral roots⁵, the number of which increases upon phosphate starvation. Thus it appears that transient gene expression and protein turnover are critical for environmentally mediated tuning of developmental programmes, particularly those that are highly sensitive to environmental cues.

How is the proteolytic turnover of *RSL4* linked to the transcriptional pulse? Ubiquitination of transcription activators

is often preceded by phosphorylation to recruit E3 ubiquitin ligase enzymes that attach ubiquitin to the target protein⁶. Recruitment of proteasome components can also be facilitated by binding of transcription factors to their target promoters⁷, a scenario that could also relate to the findings reported by Datta *et al.* Manipulation of the proteolytic turnover of *RSL4* has direct consequences on the absorptive capacity of roots. This is an important trait to achieve optimal yield in most cropping systems, which among other things require the application of costly and environmentally problematic phosphate fertilizer. Moreover, the reserves of rock phosphate are limited, placing high priority on the development of phosphate-acquisition-efficient crops. Thus, the significance of elucidating the mechanisms that control cell growth and its alteration upon perception of environmental

signals goes well beyond the academic importance of describing developmental model organisms, and may have important implications for the development of germplasm with efficient foraging for soil resources. □

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