



Figure 1 | Passage cells in the plant root. A protective layer of endodermal cells, rendered impermeable by deposition of the polymer suberin (red), surrounds the water- and nutrient-transport tissues at the core of the plant root. But certain endodermal cells, known as passage cells, do not contain suberin, and these cells have been proposed as cellular gatekeepers that control how water and nutrients reach the inner root tissues^{1–4}. Andersen *et al.*⁵ report studies in the model plant *Arabidopsis thaliana* that shed light on how passage cells develop. The authors find that the cells form adjacent to the region of developing xylem (blue), which is part of the plant's transport tissues. The protein AHP6 (not shown) moves from the developing xylem into endodermal cells. It inhibits the signalling pathway mediated by the hormone cytokinin, and prevents suberin from being deposited in the cell walls in response to the hormone abscisic acid (not shown). The lack of suberin enables the formation of passage cells.

endodermis, the number of passage cells was reduced compared with controls, and ABA addition had no effect on this, either.

Andersen and colleagues propose that most endodermal cells usually have a high level of cytokinin signalling activity, enabling them to undergo ABA-mediated suberization, and that these cells eventually reach a level of suberization that makes them impermeable. However, endodermal cells adjacent to the developing xylem receive AHP6, resulting in low levels of cytokinin signalling, and these cells also have high auxin signalling. These characteristics render some of the cells unresponsive to ABA, so they remain unsuberized and form passage cells. The authors suggest that stochastic differences in cytokinin-mediated ABA sensitivity may determine which of the cells become passage cells, but it will be fascinating to discover whether this process is fine-tuned by other factors, such as nutrient sensing.

Additional work will be required to elucidate the genetic and hormonal interactions that mediate this patterning network. Does cytokinin regulate sensitivity to ABA in the endodermis, and do auxin transporter proteins concentrate auxin to aid passage-cell formation? Alternatively, is auxin distribution in the endodermis determined by the auxin dynamics in the underlying transport tissues¹⁰?

Andersen and colleagues also investigated passage-cell function. Although it has been proposed that these cells are involved in nutrient intake, only a few studies have investigated their role^{4,5}. A previous study¹¹ in *A. thaliana* roots found that the expression of a gene encoding a phosphate transporter protein is correlated with the location of passage cells. Andersen and colleagues confirmed this finding, and showed that the transporter gene and several related genes are expressed in adjacent cortical and epidermal cells in the outer layers of the root. This pattern of phosphate transporters suggests that phosphate, and perhaps other nutrients, might be funnelled through passage cells towards the water- and nutrient-transport system.

The authors found that nutrient deficiency leads to more-widespread expression of the phosphate transporter in xylem-associated endodermis and a reduction in suberization of these cells. This shows that plants can dynamically adjust the number of passage cells according to a plant's nutrient status. Finally, Andersen *et al.* discovered that monitoring the expression of phosphate transporters allowed passage cells to be identified at an early stage of development. Identification occurred before the initial deposition of suberin in neighbouring endodermal cells that do not form passage

cells, providing a tool for future studies of the early events in passage-cell formation.

This latest work opens the door to further investigation of the role of passage cells. Genetic manipulation of passage-cell formation using the mutants and genetic tools developed in this study could be used to investigate the spectrum of nutrients that might be transported through passage cells, as well as to assess the cells' role in nutrient uptake. Another area for future research would be to investigate whether these cells are a potential entry point for microorganisms that cause disease, or those that form a mutually beneficial relationship with plants².

It is interesting that the key genes modulating the cytokinin and auxin fluxes involved in passage-cell formation also act in the patterning of the embryonic root⁸ and water-conducting tissues⁹. Plant development is a continuous process that probably requires developing structures to integrate information from hormonal signalling pathways acting at different times and in different parts of the plant. A key question is how the dynamics of the hormonal signalling interactions that drive so many aspects of plant development are integrated to link these developmental processes. ■

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CORRECTION

The News & Views 'A surprising chill before the cosmic dawn' by Lincoln Greenhill (*Nature* **555**, 38–39; 2018) incorrectly said in the seventh paragraph that a putative absorption signal looks back as far as 180 million years ago. This should have said "as far back as 180 million years after the Big Bang".