

HIGHLIGHTS

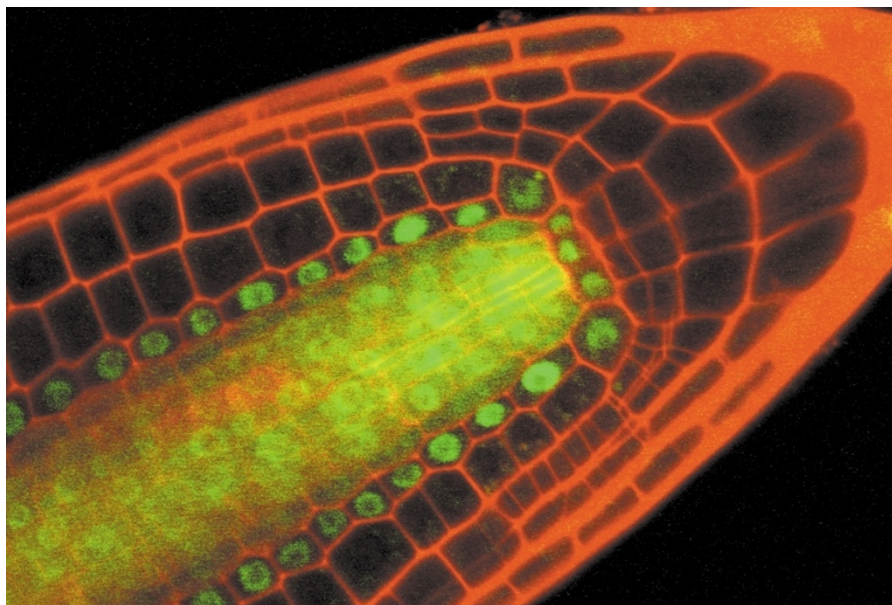
PLANT DEVELOPMENT

A short route to cell fate

In plant cell development, who you are is often determined by where you are and what your neighbours are. For example, the differentiation of photosynthetic cells in maize is controlled by their proximity to the veins of a leaf. One mechanism by which this could be achieved is the production of a signal molecule by one cell, which is detected by surrounding cells. Such systems do exist, as in the maintenance of the shoot apical meristem by a feedback loop between *wuschel*- and *clavata*-expressing cells. However, working with *Arabidopsis* roots, Philip Benfey and colleagues at New York University have uncovered a more direct mechanism.

The root of a plant is made up from a number of concentric layers of cells. The innermost of these is the stele, around which is wrapped the endodermis and cortex, both just one cell thick. Pairs of adjacent endodermis and cortex cells are formed from the division of a single cell within the root meristem. This is controlled by a gene called *SCARECROW* (*SCR*) — with *scr* mutant plants having a single combined endodermis–cortex layer.

Benfey and colleagues investigated a gene called *SHORT-ROOT* (*SHR*), mutants of which show a similar phenotype to *scr* plants. They found that *SHR* is not transcribed in the cortex or endodermis — its messenger RNA is confined to the stele. However, tagging the *SHR* gene product with green fluorescent protein lit up not only stele cells, but also the nuclei of endodermal



cells and the initial cells that divide to produce the endodermis and cortex (green in figure, cell walls are red). In fact, SHR was in the nuclei of all cells directly in contact with the stele.

From its sequence, SHR is predicted to be a transcription factor. So, perhaps SHR that is synthesized in the stele might be exported to adjacent cells, where it is rapidly transported to the nucleus to promote transcription of endodermis-specific genes, including *SCR*. To test this, Benfey and colleagues made transgenic plants containing an additional copy of *SHR* under the control of the *SCR* promoter. The roots of such plants showed a massive expansion of the endodermis, as SHR made in the stele was being exported to — and inducing endodermal character in — adjacent cells. At the same time, SHR was inducing ectopic production of more SHR in the endodermis. This SHR was then exported to cells adjacent to the endodermis, promoting transcription of yet more SHR and an avalanche of endodermis induction.

Some plant proteins are known to move between cells through plasmodesmata — pores

that punctuate plant cell walls, actively controlling the flow of material across this barrier. It seems likely that SHR moves by the same route. Equally, other transcription factors, such as *LEAFY* and *DEFICIENS* in the floral meristem, are known to move out of the cells in which they are produced, although the functional significance of their emigration is unclear.

The radiation of *SHORT-ROOT* out from the stele provides, in a single protein, both positional information and a mechanism to determine cell fate. This simple strategy will doubtless be used at the heart of many developing structures, but it is another example of an elegant innovation that is unique to the plant kingdom.

Christopher Surridge, Senior Editor, Nature

References and links

ORIGINAL RESEARCH PAPER Nakajima, K., Sena, G., Nawy, T. & Benfey, P. N. Intercellular movement of the putative transcription factor SHR in root patterning. *Nature* **413**, 307–311 (2001)

FURTHER READING Costa, S. & Dolan, L. Development of the root pole and cell patterning in *Arabidopsis* roots. *Curr. Opin. Genet. Dev.* **10**, 405–409 (2000)

WEB SITE Philip Benfey's web site: <http://www.nyu.edu/gsas/dept/bio/faculty/benfey/>

RNA EXPORT

Going separate ways

We know of two pathways for nuclear export of RNAs. Incompletely spliced Mason–Pfizer monkey virus transcripts bind the nuclear-export factor TAP through a consensus transport element (CTE), and are targeted to the nuclear pore by direct interaction between TAP and the FG-repeats of a set of nucleoporins. A similar pathway is probably used for global nuclear export of cellular mRNAs, although it is a mystery

how these bind to TAP. Incompletely spliced human immunodeficiency virus-1 transcripts, on the other hand, bind to the viral protein Rev. Rev, in turn, interacts with the exportin Crm1, which targets the transcripts to a different set of nucleoporins.

NXF3 is a close homologue of TAP, but it has deletions in the carboxy-terminal nucleoporin-binding domain as well as in the central CTE-binding domain, raising doubts as to whether it can act as an export factor. Yang *et al.* now report in *Molecular Cell* that NXF3 can be UV-crosslinked *in vivo* with endogenous poly(A⁺) RNA, that it shuttles between the nucleus and the cytoplasm, and that it can act as an export factor when bound artificially to RNAs. But surprisingly, when the authors used a

binding assay they found that instead of interacting directly with nucleoporins like TAP, NXF3 interacts with NUP214 and RAB/hRIP — a binding profile characteristic of Rev in this assay. Like Rev, NXF3 binds to Crm1 through a leucine-rich nuclear-export signal.

So, despite having 52% identity with TAP and a similar cellular function, NXF3 uses an entirely different molecular mechanism. But whereas TAP is ubiquitous and probably involved in the export of most cellular RNAs, NXF3 is mostly expressed in testis, suggestive of a tissue- and possibly RNA-specific function.

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References and links

ORIGINAL RESEARCH PAPER Yang, J. *et al.* Two closely related human nuclear export factors utilize entirely distinct export pathways. *Mol. Cell* **8**, 397–406 (2001)