

PLANT SCIENCE

SCARECROWS at the Border

Liam Dolan

An important process during the development of multicellular organisms is the laying down of boundaries between groups of different cell types. The emergence of such borderlines usually requires cells on either side of the boundary to communicate with each other. In many organisms, these signals may be proteins that move from one cell group to another, eliciting responses that result in two distinct cell populations. In plants, a small number of proteins that control development move from the cytoplasm of one cell to that of neighboring cells. In a report on page 421 of this issue, Cui *et al.* (1) describe a mechanism that spatially restricts the movement of one such mobile protein between two adjacent groups of cells in plant roots. This may constitute a general means by which multicellular organisms control the formation of tissue boundaries.

In the plant *Arabidopsis thaliana*, SHORTROOT (SHR) is a GRAS family transcriptional regulator that only moves the distance of a single cell from its cell of origin (2). How is SHR movement restricted to this distance? It was previously shown that SHR protein is synthesized in the innermost tissue of the root, the stele, and moves to the adjacent endodermal tissue where a similar GRAS family transcription factor called SCARECROW (SCR) is expressed (3, 4) (see the figure). Together, SHR and SCR positively regulate development of the endodermis and cortical tissue from a common set of stem cells. In addition, SHR moves from the stele into the endodermis to positively control SCR expression.

The model proposed by Cui *et al.* explains why SHR protein moves no farther than one cell layer. Once transported to an endodermal cell (by a currently unknown mechanism), SHR binds to SCR, forming a transcriptionally active complex that can no longer move from cell to cell. This complex, located in the

nucleus, then positively regulates the production of more SCR, which in turn, traps any mobile SHR protein in the endodermal cell. This forms a positive feedback mechanism for SCR production in response to SHR transport. SHR therefore activates the production of its own trap, one cell layer away, a strategy that may account for the formation of a stele surrounded by a single layer of endodermis in the developing root.

Perhaps the most elegant part of this report is the test of this model. The authors geneti-

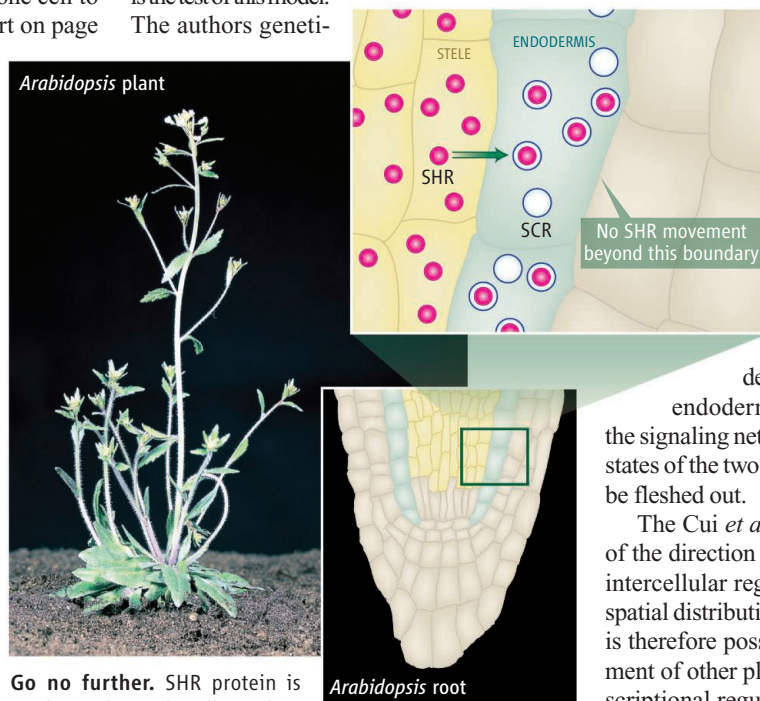
The trapping of a diffusible regulatory protein by its binding partner is a central component in the development of a structure in plants that has the thickness of a single cell.

ment of another layer of endodermal cells. It was previously shown that ectopic expression of SHR induces the development of supernumerary endodermal layers (3). Indeed, Cui *et al.* found that plants with less SCR protein develop supernumerary layers of endodermis, consistent with the model that SCR restricts the mobility of SHR to a single layer of cells.

The proposed positive feedback loop that ensures sufficient SCR to trap SHR in the endodermal cell requires an initial developmental state in which there is a low background level of SCR expression in the endodermis, although there is no direct evidence for this yet. It also requires robust expression of SHR in the stele, which has been shown (3). The model of Cui *et al.* accounts for the stabilizing of these fields of expression with defined, constant boundaries and the development of a single layer of endodermis. The characterization of the signaling network that leads to these initial states of the two cell populations now needs to be fleshed out.

The Cui *et al.* results suggest that control of the direction and distance of movement of intercellular regulators is determined by the spatial distribution of their binding partners. It is therefore possible that the observed movement of other plant proteins, such as the transcriptional regulators CAPRICE (in the root epidermis) and KNOTTED/SHOOT MERISTEMLESS (in the shoot apical meristem) (5, 6), is determined by the presence of a binding partner in the cell to which the regulator moves. In principle, the same mechanism could operate during animal development in which transcriptional regulators such as chick Engrailed2 move from cell to cell (7). Whereas chick Engrailed2 protein moves from the cell in which it is synthesized to its neighboring cell via a secretion and reuptake mechanism, it is unclear how plant proteins are moving from cell to cell.

Cui *et al.* also suggest that their proposed mechanism of endodermal boundary formation may be conserved through evolution, because the rice orthologs of SCR and SHR have similar expression patterns. The endoder-



Go no further. SHR protein is synthesized in stele cells in plant (*Arabidopsis thaliana*) roots, and moves the distance of one cell where it binds to SCR protein. The complex remains trapped in these cells, triggers production of more SCR, and directs the cells to develop into a single layer of endodermis that surrounds the stele.

cally engineered plants with decreased expression of SCR (SCR-knockdown plants). Although the SCR-knockdown plants accumulate less of the SHR-trapping protein (SCR) relative to normal plants, they produce normal amounts of SHR. If SCR does indeed sequester SHR in the endodermis, then decreased amounts of SCR in the endodermal cells should be insufficient to bind all of the incoming SHR protein. Consequently, excess, nontrapped SHR could pass through this layer of endodermal cells and proceed to outer cells of the root, potentially triggering the develop-

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mis of most land plants is uniseriate (comprising one layer), and if SHR and SCR orthologs control development in these species, this mechanism may have evolved early in the history of land plants. But there are some rare exceptions. For example, extant members of the Equisetales (horsetails), whose forebears were important species in Carboniferous forests 300 million years ago, have two layers of endodermis in some organs (8). These horsetails have apparently tinkered with their *SCR* and *SHR* genes to allow SHR to escape the clutches of SCR in the first endodermal layer, thus extending the endodermis to further layers.

Why is the structure of a single-layered endodermis so conserved across most land

plants? Autotrophic plants rely on the uptake of nutrients and water from the soil, so tight spatial regulation of endodermal development reflects its significance. The endodermis is highly specialized in that intercellular spaces between the cells are sealed, prohibiting the free diffusion of water and ions through the interstices. If water and ions are to pass through this roadblock, they must do so in a regulated manner, via the cytoplasm of endodermal cells. This affords strict control over transport and may well have provided a survival advantage—the highest level of control over a specialized tissue of very limited size. If so, this discovery may explain the evolution of a tightly regulated developmental program in

angiosperms (flowering plants) and also points to changes in developmental programs that may have occurred during the past 470 million years of land plant evolution.

References

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GEOCHEMISTRY

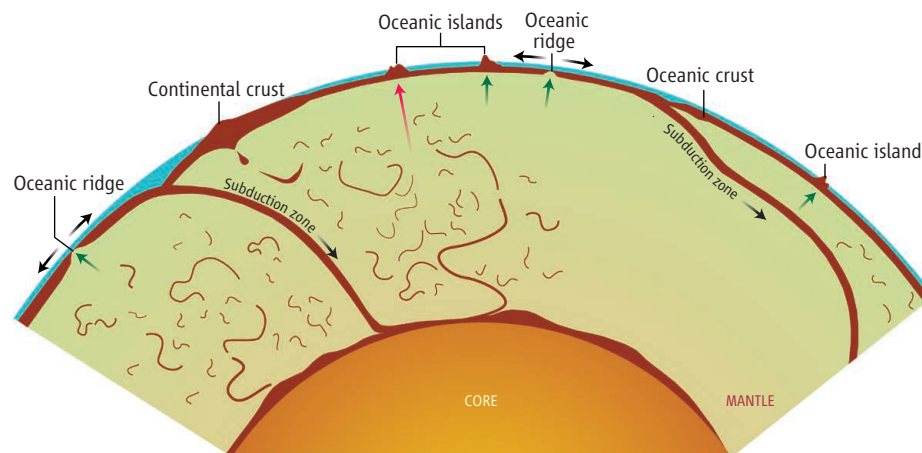
Food for a Volcanic Diet

Claude Herzberg

Volcanic eruptions have the power to reshape Earth's landscape, alter climate, and affect life. To understand how this works requires that we go deep into the Earth to learn exactly what kind of rock melts to produce magmas and the chemistry of this source rock. These are fundamental problems in geology, and they are also among the most difficult to understand. On page 412 in this issue, Sobolev *et al.* (1) describe a method for identifying some of these source rocks. We can think of them as food for volcanoes in the sense that they melt to provide the magmas that can erupt to the surface. To understand what Sobolev *et al.* have done and the ramifications that go beyond Earth science, we need to start with a refresher in geology.

Earth's mantle consists mostly of peridotite, a rock rich in the mineral olivine $(\text{Mg,Fe})_2\text{SiO}_4$. When peridotite partially melts, the liquids collect to magmas that rise to the crust, give off gases like SO_2 , CO_2 , and H_2O , and solidify to basalt, a rock rich in the minerals clinopyroxene $[\text{Ca}(\text{Mg,Fe})\text{Si}_2\text{O}_6]$ and plagioclase $[(\text{Ca,Na})(\text{Al}_{1-2}\text{Si}_{2-3})\text{O}_8]$. Portions of these outer layers can be recycled back into the mantle at subduction zones and below thickened continents (see the figure). The recycled basaltic crust is transformed to a new rock called pyroxenite, so-called because it is rich in clinopyroxene. It may pile up on Earth's core, or be mixed back into the mantle with structures that have

Chemical analyses of lava can now reveal the nature of the rocks deep in the Earth that melted and rose to generate specific volcanoes.



Models of Earth's crust and mantle. Oceanic crust (brown) is solidified liquid that forms by partial melting of mantle peridotite (green) at oceanic ridges; together with sediment, oceanic crust can be recycled back into the mantle at subduction zones (2, 3, 6). Continental crust (brown) forms at subduction zones and can be recycled when it thickens by delamination (5, 15). All crust (brown) is transformed to pyroxenite (brown) when recycled. Green arrow denotes melting peridotite. Red arrow denotes melting pyroxenite. Recycled crust may be distributed uniformly throughout the mantle, or it may be concentrated in certain hemispheres or depths. Crustal thickness is exaggerated for clarity, but ranges from ~6 to 40 km at the present time. Recycling is expected to reduce crust to dimensions ranging from micrometers to kilometers.

been described as marble cake (2), plum pudding (3), spaghetti (4), and gumbo (5) (see the figure). Volcanoes like those of Hawaii can melt from source rocks consisting of peridotite and/or pyroxenite from recycled crust. Sobolev *et al.* describe a method for identifying this rock based on the chemistry of lavas on volcanoes.

Sobolev *et al.* determined that many volcanoes melted from recycled crust, a conclusion that is not new (6). However, there has always been some ambiguity with past methods of identifying recycled crust based on the isotope

and trace-element geochemistry of lavas at the surface. New interpretations suggest that many oceanic islands melted from mantle peridotite that had been modified by melts that flowed through it (7, 8), a process called metasomatism (9). Because it makes no difference to an atom of lanthanum, for example, whether it ends up concentrated in the crust or as metasomatized peridotite, using it as a tracer can be ambiguous and nonunique (7, 8).

A breakthrough came when Sobolev *et al.* (10) showed that the nickel contents of many

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