

in the past. Much of this system is hidden under a thick layer of inland ice, which means that there is limited direct evidence for the relative motion of these two tectonic blocks (with the exception of movement that occurred after 43 million years ago<sup>8</sup>). Reconstructions of Antarctic plate tectonics before 43 million years ago therefore rely on circumstantial geological evidence<sup>9</sup>. This matters in attempts to reconstruct the tectonic history of the Andes: to model the past relative motion between South America and plates in the Pacific Ocean Basin, we need to understand the relative movements of the nearby South America, Africa, East Antarctica, West Antarctica and Farallon–Nazca plates, whose collective behaviour affects Andean tectonics (the Farallon plate is subducting under the Americas, and has fragmented into several smaller plates, including the Nazca plate).

Chen *et al.* now ingeniously show that the proposed periods<sup>7</sup> of divergence between South America and the subducting Farallon–Nazca plate are consistent with the extent of subducted slabs in the lower mantle under South America, as measured using seismic imaging, and with the geological history of the Andes. To prove their point, they used a computational method to simulate how subducted ocean floor can be pulled back out of the mantle. This ‘unsubduction’ method reverses the path taken by the deeply buried material and ultimately restores the slabs to the surface.

The results reveal that subduction was initiated around 80 million years ago, and slowly propagated from north to south. Subduction along the entire length of western South America, as observed today, did not occur until 55 million years ago. The subducting slabs first interacted with the lower mantle 10 million to 30 million years after subduction initiation. This new model is consistent with the idea that the Andes started to form during the Cenozoic, and might explain the presence of the slab gap — the authors propose that the gap arose as a result of reorganization of the subduction sometime before 80 million years ago. Chen and colleagues’ reconstruction also suggests that subduction initiation along central and southern South America explains the lull and the subsequent increase in Andean magmatism that occurred around 80 million years ago.

An open question concerns the history of Andean subduction before 90 million years ago; this will be crucial for understanding what caused the slab gap. Information about the subducted plates buried deep in the mantle (far below 1,500 km) in this region might help to improve the constraints on local and global tectonic and geodynamic models. It might also shed light on the origin of the enigmatic reorganization of tectonic plates that occurred around 100 million to 105 million years ago, which led to the termination of subduction along the eastern margins of Australia and Antarctica<sup>7</sup>.

Chen and co-authors’ method could potentially be applied to many subduction systems, particularly given that seismic images of the mantle are becoming sharper, and are increasingly being used to unravel the evolution of regions of complex tectonic activity<sup>10,11</sup>. Recent advances<sup>12</sup> in seismic methods and Earth-model development will aid the imaging of the deep mantle, especially in regions where seismic imaging doesn’t work well and where surface instruments for recording seismic images are sparse. These advances, combined with improvements in geodynamic models that assimilate seismic images of the mantle<sup>13,14</sup>, will transform our understanding of the evolution of the solid Earth. ■

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#### DEVELOPMENTAL BIOLOGY

# Plant-thickening mechanisms revealed

**In roots, stem cells in the cambium region form vascular tissues needed for the long-distance transport of water and nutrients. How these stem cells are specified and regulated has now been illuminated. SEE LETTERS P.485 & P.490**

SEBASTIAN WOLF & JAN U. LOHMANN

When plants evolved a vascular system containing cells that facilitate the transport of water and nutrients, this not only allowed them to conquer land, but also provided the structural stability that enabled them to increase dramatically in stature, bulk and complexity<sup>1</sup>. The cells that give rise to vascular tissue are specified in the embryo, but in many flowering plants they undergo substantial rounds of proliferation only during post-embryonic development, in a process that drives radial growth and expands the circumference of roots and shoots. This radial growth depends on the division of stem cells located in an inner cylindrical layer of cells called the cambium, which gives rise to wood and the woody fibre used for textiles, called bast.

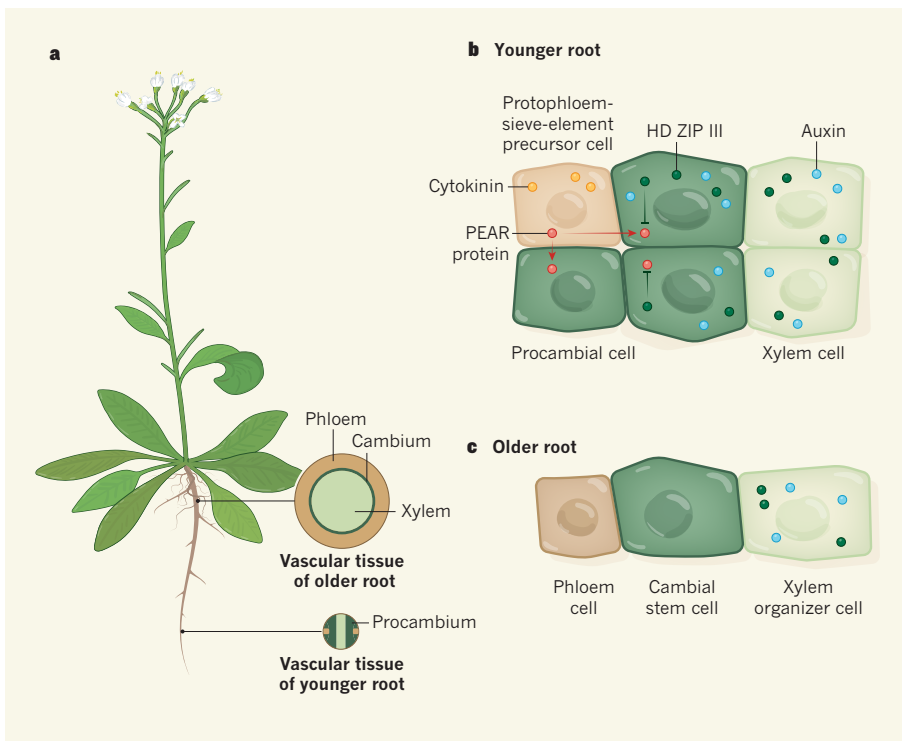
It has been estimated that woody plant material (arising from cambial cells) accounts for more than half of Earth’s biomass<sup>2</sup>. Yet despite the importance of the cambium, our level of understanding about cambial stem cells and their regulation lags behind our knowledge of stem cells in the plant root or shoot tips, probably because the cambium is more difficult to access, given its location in the interior of fully differentiated organs.

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Miyashima *et al.*<sup>3</sup> (page 490) and Smetana *et al.*<sup>4</sup> (page 485) now offer insights into cambium development on the basis of studies of roots of the model plant *Arabidopsis thaliana*.

Plant vascular tissue is comprised of water-transporting xylem cells and nutrient-transporting phloem cells, both of which are typically located in a central region of the mature root and stem. These specialized cell types can be separated by the cambium, which is home to dividing cells that drive the expansion of the xylem (which forms wood) and the phloem (which forms bast)<sup>5</sup>. Through an analysis of plants containing mutations in certain genes, and the use of imaging techniques to track fluorescently tagged proteins, Miyashima and colleagues reveal the mechanisms whereby the cell types generated by root-tip stem cells make up the cell layers from which the cambium will form. They show that cambial precursor cells, also known as procambium cells, are specified by a complex molecular network of plant hormones, transcription-factor proteins and microRNAs.

Miyashima *et al.* report that, during an initial growth phase that precedes radial expansion, certain phloem cells at the periphery of the vascular tissue act as ‘organizers’ — cells that promote the division of nearby cells; in this case, the procambial cells. Miyashima



**Figure 1 | Development of plant cambial tissue.** Miyashima *et al.*<sup>3</sup> and Smetana *et al.*<sup>4</sup> studied the plant *Arabidopsis thaliana*, and report their analysis of the development of a tissue called the cambium, which generates cells of the water- and nutrient-transporting systems — the xylem and phloem, respectively. **a**, Miyashima and colleagues studied young roots to investigate how procambium cells proliferate. Smetana and colleagues studied older roots to investigate how cambial stem cells arise. **b**, Miyashima *et al.* report that a type of cell called a protophloem-sieve-element precursor contains high levels of the hormone cytokinin, and expresses transcription factors called PEAR proteins that can drive cell division and that are transported (red arrows) into adjacent cells. The authors report that procambial cells divide adjacent to these protophloem-sieve-element precursor cells. However, cells at a more-interior position in the root have a high level of the hormone auxin. The presence of auxin and PEAR proteins in these cells drives the expression of a type of transcription factor called HD ZIP III that inhibits the action of PEAR proteins. **c**, Smetana *et al.* studied how cambial stem cells arise in older regions of the root. They find that these stem cells form adjacent to xylem organizer cells that have high levels of auxin and HD ZIP III transcription factors.

and colleagues show that a type of developing phloem cell called a protophloem-sieve-element precursor responds to the hormone cytokinin by expressing proteins of a family of transcription factors that the authors term PEAR proteins (Fig. 1). PEAR proteins were also found in the neighbouring developing procambial cells, and the authors suggest that they reached this location from protophloem-sieve-element precursors through a cell-to-cell transport mechanism.

The presence of PEAR proteins can give cells the ability to divide; however, such division competency is limited to cells at the periphery of the vascular tissue. The authors report that this is because, towards the root interior, the hormone auxin, aided by PEAR proteins, causes HD ZIP III transcription factors to accumulate, inhibiting PEAR function. This combination of mobile and non-mobile components enables a dynamic yet robust spatial patterning of cell fate, and lays down the cellular foundation for the establishment of the cambium during the initial phase of the process leading to radial growth.

Focusing on later stages of root thickening,

Smetana and colleagues analysed how root procambial cells, which are kept in a dormant state, develop to form the actively dividing cambium; they focused particularly on how cambial stem cells arise. The authors conducted cell-lineage-tracing experiments, which revealed that only cells adjacent to the xylem can generate cambial stem cells. They also discovered that a single individual cambial stem cell can give rise to both xylem and phloem daughter cells, which resolves a nearly 150-year-old debate<sup>6</sup> over whether this occurs. By producing daughter cells of distinct fates towards the interior and exterior of the cambium, respectively, cambial stem cells differ substantially from those in root and shoot tips. In the root tip, stem cells generally produce daughter cells in one direction only. In the shoot tip, cells acquire their fate depending on their relative final position after they have left the shoot-tip region.

Smetana and colleagues report that cambial stem cells need to receive signals from neighbouring xylem cells that are acting as organizers. The division of cambial stem cells leads to the generation of xylem and phloem daughter

cells towards the root interior and periphery, respectively. This means that xylem cells acting as organizers do so only transiently, before another cell replaces them in the position adjacent to the cambial stem cell and assumes organizer function. Smetana *et al.* show that the cue that determines organizer function is provided by the local accumulation of auxin, which promotes the expression of HD-ZIP III transcription factors. These, in turn, maintain the organizer cells in a non-dividing state called quiescence, which is a hallmark of this type of cell.

Another discovery made by Smetana and colleagues from their lineage-tracing experiments is that organizer cells seem to differentiate without dividing, whereas cambial stem cells seem to have a fairly rapid cell-division cycle. This goes against the dogma<sup>7</sup> that plant and animal stem cells usually have a lower cell-division rate than do their most recently generated daughter cells (which in this case would be organizer cells). The team's finding that a single stem cell can give rise to xylem and phloem cells is particularly intriguing, considering that the relative rates of xylem and phloem production are not uniform, and that the generation of these tissues is subject to developmental and environmental regulation<sup>8,9</sup>.

Future research should investigate what determines whether a cambial stem cell produces phloem or xylem, how the ratio between the two cell types is coordinated across all of an organ's cambial stem cells, and how this process results in differential tissue growth. Also unresolved is whether the determination of cell fate and cell-division activity are interdependent in the developing cambium. Understanding the mechanisms underlying any such connection might lead to the development of biotechnological approaches to enhance the production of plant biomass.

The studies by Smetana, Miyashima and their respective colleagues analysed the root procambium, which originates in the embryo. By contrast, the shoot cambium is derived post-embryonically from stem cells at the top of the shoot stem. It will be exciting to discover whether there are similarities between the molecules that drive cambial development at these two different locations in the plant. Similar molecular comparisons between cambial development in *A. thaliana* and in woody species might reveal the key molecules that underlie radial plant growth, and provide clues about how this growth mechanism evolved. Moreover, such work could provide a definitive answer to the highly debated question of whether *A. thaliana* provides a good model system for studying wood formation<sup>10</sup>. ■

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## IMAGING TECHNIQUES

# Shadows used to peer around corners

The perception range of an ordinary camera can be extended by analysing information contained in shadows. This finding could have technological implications for robotic, automotive and medical sensing. [SEE LETTER P.472](#)

MARTIN LAURENZIS

Seeing around corners is difficult, but not impossible. When light scatters off an object that is hidden from view, it carries information about the object that can be reconstructed computationally. This imaging method, known as non-line-of-sight imaging, typically requires expensive, specialized equipment. But on page 472, Saunders *et al.*<sup>1</sup> report an approach that needs only a single photograph captured using a standard digital camera. The technique can reconstruct the position of an opaque object, as well as the scene behind the object, when both the object and the scene are out of direct sight.

There are two types of reflection: specular and diffuse. In specular reflection, incident light is deflected by a specific angle, whereas in diffuse reflection, it is scattered in many directions. In a conventional periscope — such as those once widely used by submerged submarines to scan the sea surface — specular reflection at the surface of a mirror is used to deflect the path of light onto areas outside the observer's line of sight.

Advances in computer science over the past few years have enabled optical-imaging systems to use information collected from diffusely reflecting surfaces to look around corners and to view scenes that are out of direct sight. In this case, the optical path is not simply deflected by mirrors, and all of the imaging information is destroyed by diffuse reflection. The information has to be reconstructed computationally from a series of measurements, in a similar way to that used in the X-ray imaging method known as computed tomography.

Pioneering experiments<sup>2,3</sup> demonstrated that the surface geometries of objects hidden from direct view could be reconstructed. In these experiments, a diffusely reflecting 'relay' surface is irradiated with ultrashort laser pulses to indirectly illuminate a target that is behind an obscuring structure. This

light is reflected from any surface back towards the relay surface and detected by a specialized optical sensor.

For certain types of imaging, known as transient and time-resolved imaging, such a sensor can measure the arrival times of photons with extremely high precision. This timing information, together with the angles at which the photons hit the sensor and details about the relay surface, can be used to deduce the locations of reflecting surfaces by computational means. For example, the principle of non-line-of-sight transient imaging has been used to track objects in real time<sup>4</sup> and to reconstruct object shapes and textures<sup>5</sup>.

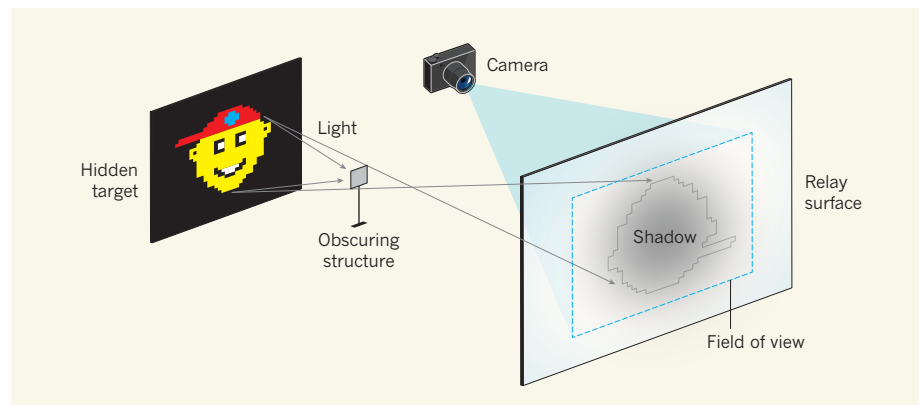
A more challenging task is non-line-of-sight imaging using an ordinary camera. In this case, photon arrival times are not recorded and therefore cannot be used to estimate a target's spatial properties. As a result, much more computation is needed. An ordinary camera equipped with a continuous light source has been used to track the position and

rotation of an object hidden from direct view<sup>6</sup>. However, the shape and size of the object had to be known in advance.

Another source of imaging information can be found in areas containing shadows or penumbræ — regions of shadows in which only some of the light source is obscured. In non-line-of-sight imaging, the obscuring structure can block certain optical paths and cast a shadow on the relay surface (Fig. 1). Therefore, information about the hidden scene is represented not only by the photons that arrive at the detector, but also by the photons that are blocked.

The idea of using shadows in non-line-of-sight imaging was first demonstrated by turning an ordinary camera into a corner camera<sup>7</sup>, in which shadows cast by the edge of a doorway or the corner of a wall were analysed. Small variations in intensity and colour in penumbræ were detected and used to observe the movement of people hidden around a corner. However, owing to the large size of the obscuring structures, only some of the spatial information could be reconstructed. The idea was later used in a more general approach to reconstruct a hidden scene from intensity variations in the penumbræ cast by relatively small structures, such as the leaves of a plant<sup>8</sup>. Nevertheless, a detailed calibration of the scene was needed to determine the photons' direction of propagation.

Saunders and colleagues present an approach in which light emanating from a hidden target is partially blocked by an obscuring structure of unknown position, producing a pattern of illumination and shadow on a relay



**Figure 1 | Non-line-of-sight imaging.** Saunders *et al.*<sup>1</sup> report a technique for imaging objects that are outside the direct field of view of a camera. In their approach, some of the light that is emitted from a hidden target is blocked by an obscuring structure of unknown position. The blocked light produces a shadow on a 'relay' surface, whereas the rest of the light illuminates this surface. Finally, a camera takes a photograph of the surface and feeds this information through a computer algorithm (not shown) that can reconstruct an image of the hidden target and give an estimate of the position of the obscuring structure.