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Plant-microbe interactions

A receptor in symbiotic dialogue

Herman P. Spink

Proteins that help plants connect with symbiotic microbes have been identified. These proteins are related to receptors in animals and plants that function in the innate immune system and organ development.

Many plants can grow on soils that are poor in nutrients, and they do so by forming symbiotic associations with microbes. These associations require a molecular dialogue between the two partners. On pages 959 and 962 of this issue, Stracke *et al.*¹ and Endre *et al.*² describe how they have identified genes that encode a plant protein that is essential to the dialogue.

Important examples of microbes involved in symbiosis are bacteria called rhizobia and fungi — ‘arbuscular mycorrhizal fungi’ — that respectively supply the plant host with nitrogen- and phosphorus-containing nutrients^{3,4}. In return, the microbes receive carbohydrate nutrients from the plant. The genes identified by Stracke *et al.* and Endre *et al.* seem to belong to a large family of plant and animal genes that encode a particular class of receptor proteins. These proteins are characterized by having a repeated motif rich in the

amino acid leucine — called a leucine-rich-repeat (LRR) — in an extracellular domain^{5–7}. In animals the proteins comprise a group, known as the Toll-like receptors, that function in the innate immune system⁸. In plants they belong to a subfamily that has in common an intracellular serine/threonine kinase domain that triggers a signalling cascade inside the cell. Several members of this plant subfamily are involved in defence against pathogenic microbes, or in shoot development⁹ (Fig. 1).

It is not too surprising that receptors involved in plant-microbe symbiosis belong to the LRR receptor subfamily, given that it is one of the largest groups of receptors in the plant kingdom with, for instance, 174 members in the ‘model’ plant *Arabidopsis* alone¹⁰. But it is surprising that Stracke *et al.* and Endre *et al.* found a function for a highly similar LRR receptor in different plant species —

not only in the model legumes *Lotus japonicus*, *Medicago sativa* and *Medicago truncatula*, but also in the agriculturally important crop plant, pea (*Pisum sativum*). In all, the two groups carried out a genetic analysis of nine mutants that have defects in the early stages of symbiosis, discovering the involvement of a member of the LRR receptor family and by implication its key role in symbiosis.

For the rhizobium-plant interaction, various signal molecules produced by the microbial partner have been identified. One group — the Nod factors — has attracted much attention because Nod factors specifically trigger the host plants (belonging exclusively to the legume family) to produce a specialized microbe-accommodating organ, the root nodule³. But little is known of the plant factors that recognize rhizobial signal molecules. And even less is known of plant interactions with arbuscular mycorrhiza: for this microbe, no signal molecules have been identified.

In finding a receptor protein involved in recognizing signal molecules from both rhizobia bacteria and arbuscular mycorrhiza, Stracke *et al.*¹ and Endre *et al.*² have provided a long-awaited breakthrough. Identifying the genetic basis of microbial recognition in the plant hosts has been hampered by technical difficulties, which are especially acute for plants that form strong symbiotic relationships. As exemplified by legumes, such plants have relatively large genomes, which in some cases exceed the size of the human genome. That makes identification of point mutations — single-nucleotide changes in DNA — extremely difficult. Furthermore, in plants, gene-knockout techniques are still in their infancy^{11,12}. Stracke *et al.* and Endre *et al.* circumvented these difficulties by making optimal use of the advantages offered by classical plant genetics in legumes — the production of large numbers of mutants and genome-map-based cloning — and the increased availability of nucleotide sequence data.

The results open the way for detailed analysis of the direct binding partners, and downstream signalling pathways, that are associated with microbial recognition. Such analysis may soon provide further insight into the similarities with signal pathways involving other classes of LRR receptor, and could reveal connections with the recognition mechanism of factors produced by pathogenic microbes or signalling peptides involved in development.

The future bottleneck in studying this receptor family is our lack of knowledge about the signal molecules that are recognized by the receptors. Up to now, a triggering factor has been identified for only two plant LRR receptor proteins. These factors (microbial flagellin⁵ and the plant differentiation factor called CLAVATA3) are extracellular proteins. The structural evidence is consistent with the idea that LRR sequence

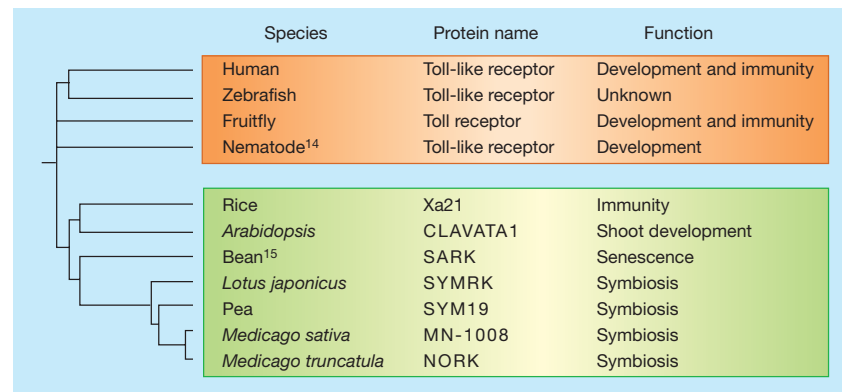


Figure 1 Comparison of members of the protein family of receptors containing extracellular leucine-rich-repeats (LRR). This tree of protein relatedness compares examples from various subfamilies in animals and plants, and indicates the breadth of species in which the receptors are found, and the variety of functions that they have. The receptors’ involvement in plant-microbe interactions, as a component of the plant side of the molecular dialogue in symbiosis, is described by Stracke *et al.*¹ and Endre *et al.*² in this issue. The plants concerned are the model legumes *Lotus japonicus*, *Medicago sativa* and *Medicago truncatula*, and the pea (*Pisum sativum*). The examples not referenced above are reviewed in refs 6 and 8. For zebrafish, the assignment is based on data (BG304206) submitted to Genbank by S. Johnson. CLAVATA1 is the receptor that recognizes CLAVATA3.

motifs have a general function in protein recognition⁷, indicating that LRR receptors are only indirectly involved in recognizing carbohydrate microbial factors (such as the Nod factors). Primary recognition could be performed by secreted extracellular molecules, lectins for instance, which are recognized by the LRR receptors after binding of microbial signals¹³.

The evolutionary relatedness of the plant and animal receptors shown in Fig. 1 is surprising if one considers that the last common ancestors of higher plants and animals separated more than 1.8 billion years ago. In animals, the relatives of the plant receptors are also involved in recognizing microbes, meaning that similar carbohydrate-recognition mechanisms could underlie the animal innate immune system. Carbohydrate recognition in the human immune system is still poorly understood, so unravelling microbe-recognition mechanisms in plants should also provide lessons for medical science. ■

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Earth science

How old roots lose their bounce

David James

Active mountain belts have crustal ‘roots’ that gravitationally balance the high topography. So why do old mountains that have been worn flat by erosion still have these roots?

Some mountain ranges form along the boundaries of colliding tectonic plates, and the classic account of their rise and fall runs as follows. In these ‘collisional belts’, the Earth’s crust is squeezed, thickened and uplifted by the forces that drive the plates together, and is also thickened by the addition of magmas from the underlying mantle. Where powerful mountain-building forces are at work today, as in the central Andes and Tibet, the mass of the mountains is gravitationally supported by a thick ‘root’ of buoyant low-density rock beneath them. When active uplift and crustal thickening cease, erosion begins the inexorable process of reducing once lofty mountains to low-lying plains. As the mountains are eroded, gravitational balance is maintained by continued uplift of the buoyant crustal root to compensate for mass loss at the surface.

As Fischer reports on page 933 of this issue¹, however, this classic balancing act seems not to apply to many old and deeply eroded collisional belts. In these places, disproportionately thick crustal roots have often survived for hundreds of millions — even billions — of years, and Fischer provides an explanation for why that should be so (Fig. 1).

She has examined collisional mountain belts of all ages worldwide. She finds that the ratio of elevation to crustal-root thickness decreases systematically from about 0.1–0.2

for the youngest mountain belts (root thickness 5–10 times greater than surface relief) to essentially zero for mountain belts several hundred million years old (still appreciable root thickness, but minimal surface relief; see Fig. 1a on page 933). This is perplexing because, given the mass balance between crustal roots and surface load in young mountain ranges, it would seem that removal of the mass at the surface should involve proportional loss of the buoyant root. Old mountains eroded to flat-lying plains should have no remaining roots.

It was triangulation anomalies, observed in the Himalayas during the Trigonometrical Survey of India in the mid-nineteenth century, that led to the realization that mountains are not simply loads piled onto the surface but are compensated by a comparable ‘mass deficit’ at depth. This gravitational balancing act is termed isostatic compensation. In its most common form, isostasy is simply Archimedes’ principle applied to the Earth: low-density crustal blocks ‘float’ in a higher-density ‘fluid’ mantle, much as an iceberg floats in water with its tip gravitationally balanced by a much greater volume of displaced water beneath the surface. Mountain ranges in isostatic equilibrium are held aloft by the buoyant forces of crustal roots, and the higher the mountains, the thicker the roots. Strictly speaking, the iceberg analogy is valid only if the crust and

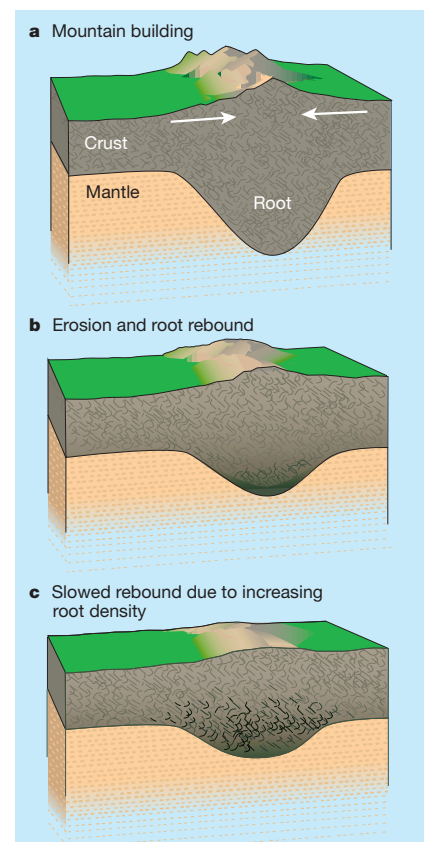


Figure 1 Mountain building at ‘collisional’ boundaries, and the fate of crustal roots. a, The collision of tectonic plates produces a thickened crust — a mountain range — which is gravitationally supported by an underlying crustal root of buoyant, low-density rock. b, When active mountain-building ends, the erosional loss of surface mass is gravitationally balanced by rebound of the buoyant root. The principle of isostasy suggests that continued uplift and exhumation — deep erosion — of the crust should continue until the buoyant crustal root is completely consumed. c, Fischer¹ finds, however, that older collisional belts tend to have disproportionately thick roots even when surface topography has been greatly reduced. She explains this as a result of reduced root buoyancy, caused by mineralogical reactions that increase root density relative to that of the surrounding mantle.

mantle are assumed to be sufficiently weak — deformable — that the crust really can ‘float’ in the dense ‘fluid’ mantle beneath. This assumption seems to be plausible for active mountain belts, but it might not be valid for older mountain ranges, for which progressive cooling may lead to an increase in rigidity.

Fischer assessed the role of isostatic balance by considering two hypotheses for how crustal roots could survive over geological time. The first was that the lithosphere — the crust and upper mantle — becomes increasingly rigid over time, impeding the buoyant rebound of low-density roots; the second was that the density contrast between crustal