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Plant evolution: Building nodules from borrowed parts

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Root nodules are distinct organs assembled from ancient developmental components. A new study shows that rhizobial Nod factors activate a conserved auxin module controlling lateral root formation, revealing how symbiotic signals can recruit pre-existing programmes without reproducing lateral root development.

Evolution rarely starts from a blank page. New structures generally emerge through the duplication, modification and reconnection of existing developmental circuits. The nitrogen-fixing root nodule is a particularly striking example. This organ enabled plants to house bacteria that convert atmospheric nitrogen into a usable form, yet much of its developmental toolkit appears to have been borrowed from pathways that already operated in roots. A new study by Lesterps and colleagues, published in this issue of *Current Biology*, now identifies another component of this borrowed machinery: rhizobial Nod factors activate an evolutionarily conserved auxin-signalling module controlling lateral root formation, independently of the canonical pathway governing nodule organogenesis[1] (Figure 1).

The relationship between lateral roots and nodules has intrigued plant biologists for decades, but it should not be reduced to simple morphological homology. Both are post-embryonic lateral organs initiated within the root, and both require coordinated cell proliferation across several tissue layers. In legumes, lateral root initiation begins in the pericycle, but also involves mitotic activation of the endodermis and cortex, a pattern now recognised as an ancestral and widespread feature of seed-plant root branching rather than an exception to an *Arabidopsis* rule[2,3]. Nodule organogenesis, likewise, engages divisions in inner root tissues, with the relative contributions of the cortex and pericycle varying among legume species and nodule types.

These shared cellular features nevertheless lead to organs with markedly different architectures. A lateral root re-establishes a root-like radial organisation, including a central vascular cylinder connected to that of the parent root. By contrast, the indeterminate nodules of *Medicago truncatula* contain a central symbiotic tissue surrounded by several peripheral vascular bundles, an organisation that is in some respects more reminiscent of an aerial organ than of a root[4]. Nodules also acquire specialised tissues for bacterial infection, nutrient exchange and oxygen control. A nodule is, therefore, not merely a lateral root diverted towards symbiosis. It is a distinct organ that combines selected components of the root developmental toolkit with new tissue identities, a different vascular pattern and a specialised physiological function.

The strongest relationship between the two organs may consequently lie not in their final anatomy, but in the regulatory modules used to initiate organogenesis. The transcription factor NODULE INCEPTION, or NIN, is indispensable for nodulation, and provided an early example of how a new developmental programme can be assembled from older components[5]. In *M. truncatula*, NIN promotes the expression of the lateral-organ regulator LBD16, thereby linking

cytokinin perception to local auxin biosynthesis and cortical cell division[6]. In *Lotus japonicus*, the closely related LBD16/ASL18 gene contributes to both lateral root formation and nodule development, further illustrating the sharing of regulatory components between the two pathways[7]. NF-Y transcription factors provide another example: members of this conserved family contribute to root growth and branching, but have also acquired prominent functions in nodule initiation and meristem development.

Auxin occupies a central position in this evolutionary patchwork. It controls virtually every phase of lateral root formation, from founder-cell specification and formative divisions to primordium growth and emergence. Auxin responses are gated by AUX/IAA repressors, whose degradation releases AUXIN RESPONSE FACTOR transcription factors to activate downstream developmental genes. In *Arabidopsis*, modules involving IAA14, ARF7, ARF19 and LBD proteins are central to the progression of lateral root organogenesis[8–10]. Auxin redistribution, biosynthesis and signalling are also required during nodulation, where they support cortical cell proliferation and nodule vascularization[6,11,12]. Auxin thus represents a shared developmental currency, but one that can be spent differently in a lateral root and a nodule.

Nod factors add another layer to this relationship. These lipo-chitooligosaccharide molecules are produced by rhizobia and perceived at the root surface, where they initiate the signalling cascade required for infection and nodulation. Yet, purified Nod factors do not simply reproduce nodule organogenesis. In *M. truncatula*, they primarily stimulate lateral root formation, and related microbial signals can promote root branching in a broad range of plants[13,14]. This raises a deceptively simple question: when Nod factors stimulate lateral roots, do they activate part of the nodulation programme, or do they gain more direct access to an ancestral root-development pathway?

Lesterps and colleagues answer this question by showing that Nod factor-induced lateral root formation does not require either the cytokinin receptor CRE1 or NIN, despite their central roles in nodule organogenesis. Instead, Nod factors influence auxin biosynthesis and signalling in inner root tissues. The authors identify the AUX/IAA protein MtIAA7 as a negative regulator of lateral root development and show that it interacts with ARF proteins related to the *Arabidopsis* lateral-root regulators ARF7 and ARF19. Their results support a model in which Nod factor signalling promotes local auxin production in the pericycle, relieving AUX/IAA-mediated repression and allowing lateral root primordia to progress.

Our understanding of the mechanism is not yet complete. Nod factors are perceived in the epidermis, whereas the developmental response occurs in the pericycle, implying the existence of one or more secondary signals between the two tissues. Direct evidence that Nod factors or auxin promote MtIAA7 destabilisation, however, remains to be obtained. The proposed sequence from local auxin biosynthesis to MtIAA7 degradation and ARF activation therefore remains a plausible model rather than a fully resolved molecular chain. Nevertheless, the genetics clearly separate this response from the NIN-dependent route that activates auxin production in cortical cells during nodule formation. The distinction is spatial as well as regulatory: the same hormone is recruited through different upstream pathways and in different tissues to produce different developmental outcomes.

The evolutionary conservation of IAA7 function makes the result particularly compelling. The corresponding proteins from tomato and *Arabidopsis* retain roles in lateral root development, although tomato forms arbuscular mycorrhiza but not nodules, whereas *Arabidopsis* has lost the capacity to establish either of these endosymbioses. The auxin module identified in *Medicago* therefore did not arise with nodulation. Rather, Nod factor signalling appears to have connected to a developmental circuit that was already present in the common ancestors of these plants.

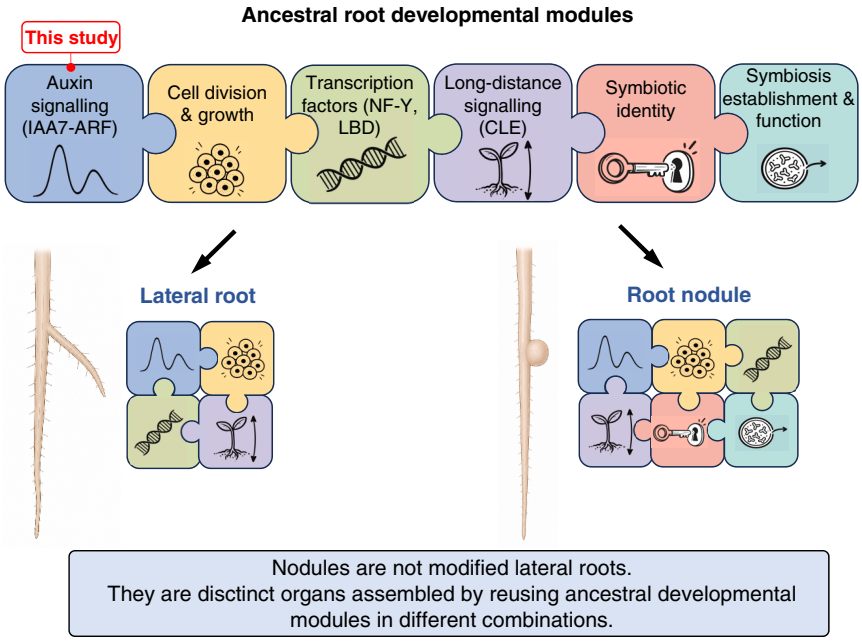

Figure 1. A modular view of root nodule evolution.
Root nodules are not modified lateral roots, but distinct organs assembled through the progressive recruitment and recombination of ancestral developmental modules. The present study identifies auxin signalling as one such conserved module that can be directly activated by rhizobial Nod factors during lateral root development. Other modules involved in cell division, transcriptional regulation, long-distance signalling, symbiotic identity and symbiotic function were likely recruited at different stages during the evolution of nodulation. This schematic represents a simplified conceptual model and is not intended to depict the complete set of developmental modules contributing to root nodule organogenesis. Selected graphical elements were generated using ChatGPT (OpenAI), while the overall figure design, scientific content, layout and final artwork were created by the author.

This finding argues against viewing nodulation as the product of a single act of developmental co-option. A more likely scenario is a stepwise assembly of modules that differ in age and function. Ancient lipo-chitooligosaccharide signals and the common symbiosis signalling pathway were already associated with arbuscular mycorrhizal interactions before nitrogen-fixing nodules evolved[15]. These signals may have gained access to conserved hormonal programmes affecting root branching. Later, the emergence of a nodulation-specific NIN network enabled cytokinin signalling to redirect auxin biosynthesis and lateral-organ regulators towards cortical nodule organogenesis. Further innovations then integrated infection, vascular development, nutrient exchange and control of nodule number.

This modular recruitment was not restricted to local organogenesis. Because nodules consume substantial photosynthate, their production must be coordinated with the nitrogen status of the entire plant. Legumes achieve this through long-distance autoregulation pathways involving shoot receptors such as HAR1, SUNN and NARK. Recent work in white lupin showed that the related receptor CCR1 controls not only nodulation but also non-symbiotic root development, including the production of specialised cluster roots[16]. This suggests that systemic circuits coordinating root architecture were also recruited into nodulation. Local auxin signalling and whole-plant regulation may thus represent two different scales of the same evolutionary process: the incorporation of pre-existing root-development mechanisms into a new symbiotic programme.

The parallels may extend beyond mutualistic symbioses. Plant-parasitic nematodes, together with other plant-associated organisms such as pathogenic bacteria and gall-inducing insects, manipulate auxin- and cytokinin-regulated developmental pathways to redirect plant cell proliferation[17]. Similar hormonal pathways can, therefore, support lateral roots, nodules or parasitic feeding structures, depending on where, when and by whom they are activated. The identity of a new organ cannot be inferred from the developmental module alone; it emerges from the regulatory context into which that module is embedded.

Several questions now come into focus. What signal carries the Nod factor response from the epidermis to the pericycle? Is the IAA7 module involved in root responses to mycorrhizal signals, or has it acquired a more specific connection to rhizobial Nod factors? How many AUX/IAA–ARF combinations contribute to the response? And which additional modules transformed a transient stimulation of root branching into the organised development of a vascularised, infected and systemically regulated nodule?

Lesterps and colleagues do not show that nodules are modified lateral roots. They reveal something subtler and arguably more informative: a symbiotic signal can directly recruit one of the ancient regulatory modules used to build lateral roots, while a distinct pathway uses related components to construct a morphologically different organ. Evolution did not borrow a lateral root. It borrowed developmental modules and rewired their connections to build an entirely new organ.

DECLARATION OF INTERESTS

The author declares no competing interests.

DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES

Selected graphical elements were generated using ChatGPT (OpenAI), while the overall figure design, scientific content, layout and final artwork were created by the author, who takes full responsibility for the content of the publication.

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Plant tropisms: pH-guided saprotropism enables roots to avoid decay zones

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Plants use tropisms, directional growth responses, to navigate diverse environmental cues such as light, gravity, water, temperature and salinity. A recent study shows roots avoid microbial decay zones by sensing pH gradients generated by decomposition, uncovering a new tropism — saprotropism.

Plant roots continuously adjust their growth according to chemical, physical and biological cues they experience in the soil[1]. For example, gravity directs roots downward, water gradients guide roots towards moisture, salinity causes roots to bend away and nutrient distributions influence root angle and branching to optimise soil exploration (Figure 1A)[1–3]. However, soils are not just shaped by physical and chemical heterogeneity, they are also biologically dynamic ecosystems populated by microbes that decompose organic matter and shape root system development[4]. A new study by Bao, Wang *et al.*[5] reveals that roots can detect nearby decaying plant material and actively grow away from it. The authors identify a previously unknown root tropism, termed saprotropism, in which roots respond to microbial decomposition by sensing local pH gradients generated during decay[4]. This discovery adds a new dimension to our understanding of how plants navigate underground environments. Typical tropisms, such as gravitropism, hydrotropism and halotropism are generally viewed as responses to abiotic stimuli (Figure 1A)[2]. Saprotropism is different, as the directional cue originates from biological activity and roots are responding to the chemical landscape created by this activity[4]. Hence, the finding by Bao, Wang *et al.*[5] extends the concept of root tropisms, highlighting the importance of biological soil activity directing root growth.

Soil is a very heterogenous environment[1]. Leaf and root litter, wooden debris, as well as soil faunal and microbial necromass are continuously decomposed by soil organisms ranging from fungi, bacteria, archaea and soil fauna (e.g., earthworms or arthropods), which collectively drive nutrient cycling and ecosystem productivity (Figure 1B)[4]. However, these decay zones are also hotspots of microbial activity, and can harbour potentially harmful pathogens and spoilage organisms[2]. Although decaying organic matter represents a nutrient-rich component of soil ecosystems, it may also pose risks to growing roots. Until now, little was known about whether plants can distinguish between organic-rich patches and potentially hostile decomposition zones before physical contact occurs. The work from Bao, Wang *et al.*[5] shows that roots can sense decay from a distance. When roots encountered decaying organic material, their growth was strongly inhibited, indicating that decomposition zones can be detrimental to plant fitness. More surprisingly, when roots were placed near, but not touching, the decaying material, they consistently bent away from it[5]. This avoidance response was observed across several species, suggesting that saprotropism may be broadly conserved among flowering plants[5].

A key advance reported by Bao, Wang *et al.*[5] is the identification of the environmental signal that informs this saprotropic behaviour. The authors show that fungal-driven decomposition released abundant organic and phenolic acids into the surrounding environment. As these compounds diffuse through the soil, they establish stable local pH gradients characterised by increased acidity near the decay source (Figure 1B)[5]. Remarkably, these gradients function as spatial information, demonstrating that local pH asymmetry is both necessary and sufficient to guide saprotropic growth. In this respect, saprotropism may resemble navigational strategies that occur throughout biology. Bacteria follow nutrient gradients through chemotaxis[6], while animals use chemical cues and odour gradients to locate resources or avoid danger[7]. Plants, lacking mobility, solve the same problem differently. Rather than moving their bodies through space, they alter their developmental trajectories[3]. Saprotropism illustrates how plant roots transform environmental information into long-term growth decisions, effectively allowing them to map their subterranean surroundings (Figure 1)[5].

Bao, Wang *et al.*[5] also report the molecular machinery that converts