



# How plants communicate using the underground information superhighway

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**The rhizosphere is a densely populated area in which plant roots must compete with invading root systems of neighboring plants for space, water, and mineral nutrients, and with other soil-borne organisms, including bacteria and fungi. Root–root and root–microbe communications are continuous occurrences in this biologically active soil zone. How do roots manage to simultaneously communicate with neighboring plants, and with symbiotic and pathogenic organisms within this crowded rhizosphere? Increasing evidence suggests that root exudates might initiate and manipulate biological and physical interactions between roots and soil organisms, and thus play an active role in root–root and root–microbe communication.**

Rhizosphere interactions are based on complex exchanges that evolve around plant roots. Root-based interactions between plants and organisms in the rhizosphere are highly influenced by EDAPHIC FACTORS (see Glossary); however, the belowground biological interactions that are driven by ROOT EXUDATES are more complex than those occurring above the soil surface [1] (Figure 1). These interactions include signal traffic between roots of competing plants [2], roots and soil microbes [3,4], and one-way signals that relate the nature of chemical and physical soil properties to the roots [5].

Many of the processes mediated by roots in the rhizosphere, such as the secretion of root border cells and root exudates, are not well understood [6]. In addition to the compounds that roots synthesize and accumulate [7,8], a remarkable diversity of micro- and macromolecular metabolites is also secreted into the rhizosphere as root exudates [8] (Figure 2). Root exudates play an active and relatively well-documented role in the regulation of symbiotic and protective interactions with microbes [4,9–11]. However, the role of root secretions in regulating other rhizospheric interactions is less clear. Through the exudation of a wide variety of compounds, it is suggested that roots can regulate the soil microbial community in their immediate vicinity, withstand herbivory, encourage beneficial symbioses, change the chemical and physical

properties of the soil, and inhibit the growth of competing plant species [12]. In this review, we explore the current knowledge relating to how root exudates mediate communication between plant roots and other components of the rhizosphere, and what these processes imply at both the plant and ecosystem level.

## Root–microbe communication as a means of establishing symbiotic relationships

Plants depend on the ability of roots to communicate with microbes. The converse is also true; many bacteria and fungi are dependent on associations with plants that are often regulated by root exudates. A chemotactic response towards root-secreted organic and amino acids is the first step in root colonization [13]. For instance, the motility required for *Pseudomonas fluorescens* to colonize tomato roots is driven by root exudate-influenced CHEMOTAXIS [14] and, in the presence of rice root exudates, endophytic bacteria show a fivefold increase in chemotaxis over other bacteria [15]. These relationships are influenced by soluble and non-soluble root exudates, border cells, and the large polysaccharide layer that surrounds roots [6,16]. Recently, Pieter van West *et al.* [17] have shown that electrical signals can augment or override chemotaxis in mediating short-range tactic responses of oomycete zoospores at root surfaces, which is the first demonstration that electro taxis plays a major role in a plant–microbe interaction under natural conditions. This investigation suggested that electro taxis augments other root-targeting mechanisms, overriding chemotaxis when the effector molecules are at concentrations normal to the rhizosphere, and that chemotaxis and electro taxis participate in the homing responses

## Glossary

**Allelopathy:** Chemical inhibition of one species by another.

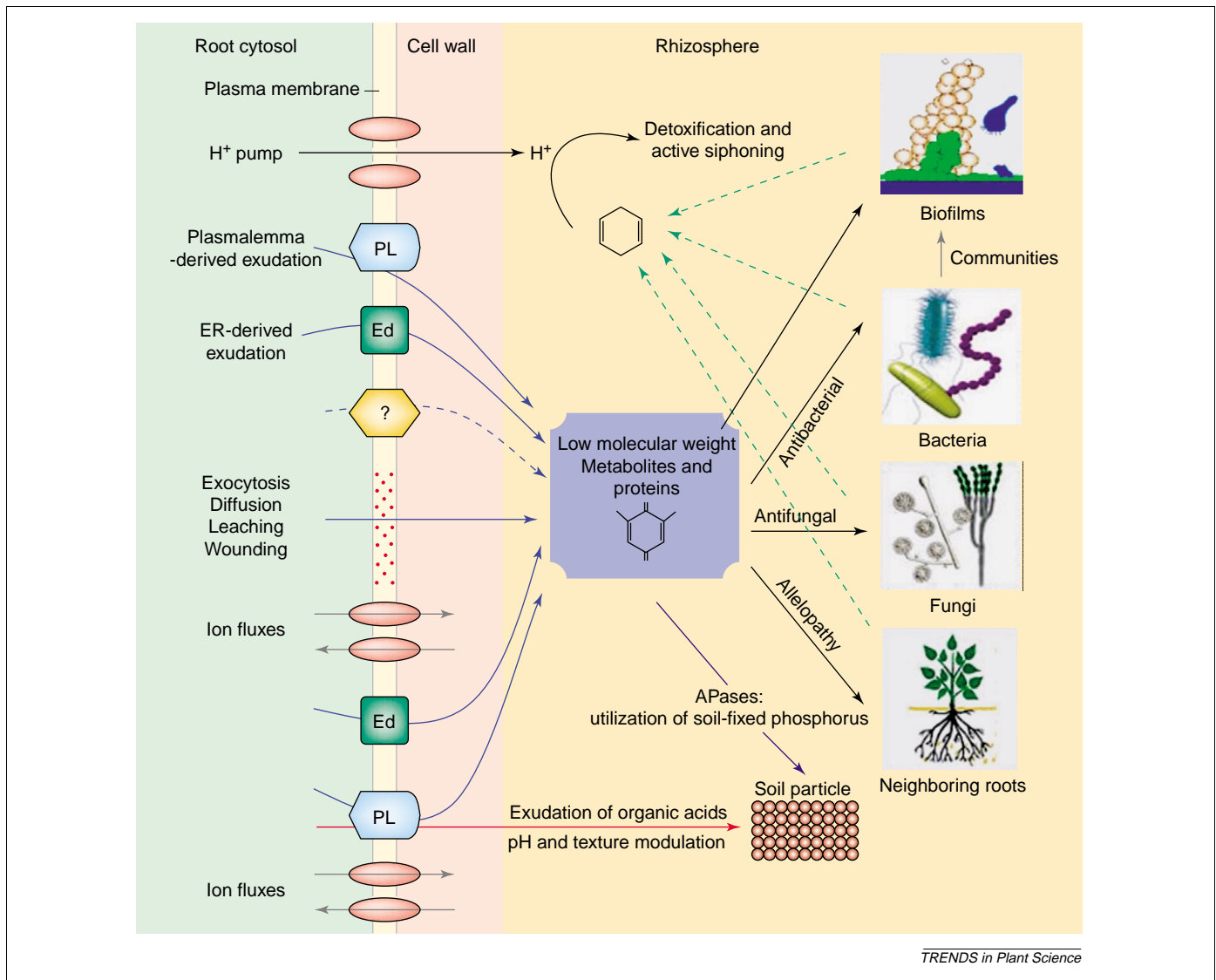
**Allelochemicals:** Small molecular weight phyto-inhibitory compounds produced by a plant to ward-off another plant.

**Chemotaxis:** Phenomenon by which a biotic adherence takes place by virtue of the production of a chemical signal.

**Edaphic factors:** Involve both biological and abiotic climatic conditions required to regulate a specific niche.

**Root exudates:** The chemicals secreted into the soil by roots.

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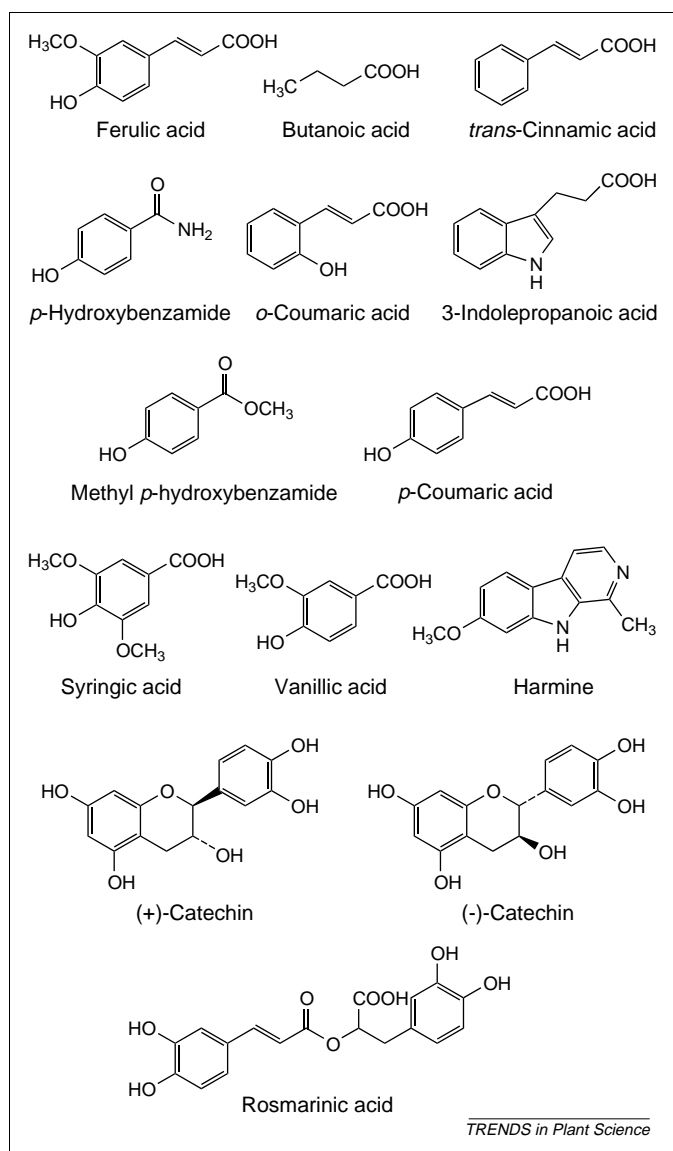
**Figure 1.** Model showing plausible mechanisms of root exudation and active rhizospheric interactions. The hexagon component in the detoxification process depicts the low molecular weight toxins produced by bacteria and fungi during the pathogen attack. Plant roots adopt a proton ( $H^+$ )-pumping mechanism to exclude the phytotoxins produced by bacteria and fungi. The green, broken arrows depict pathogen attacks against the plant. The blue, black and red arrows show the response of the host plant root to a pathogen attack. The blue, broken arrow represents an unknown mode of root exudation and host response against pathogen attack. On the right, the biofilm panel depicts bacterial communities that are much more resistant to plant-derived antimicrobials than planktonic bacteria are. Abbreviations: PL, plasmalemma-derived exudation; Ed, endoplasmic-derived exudation.

of zoospores toward roots. They also suggest that root surface charges, generated by the metabolism of living roots, ensure that zoospores colonize living rather than dead roots.

Not surprisingly, specific compounds identified in root exudates have been shown to play roles in root–microbe interactions (Figure 2). For example, isoflavonoids and flavonoids present in the root exudates of a variety of leguminous plants activate the *Rhizobium* genes responsible for the nodulation process and might be responsible for vesicular-arbuscular mycorrhiza (VAM) colonization [18–20]. Flavonoid profiles in root exudates differ considerably among legumes [21], and this specificity enables mutualists and beneficial bacteria such as rhizobia to distinguish their hosts from other legumes. How this specificity is accomplished is relatively well understood, at least within the limits of laboratory results [22].

### Root–microbe communication that can lead to defense responses

Root exudates also act as antimicrobials against rhizospheric microflora, providing the plant with defensive advantages. Collectively, plants produce a compositionally diverse array of > 100 000 different low-molecular-mass natural products, known as secondary metabolites [23]. The rich diversity of secondary metabolites arises partly because of selection for improved defense mechanisms against a broad array of microbes, insects and plants. Although such diversity has made it difficult to apply conventional molecular and genetic techniques to determine the functions of natural products in plant defense, examining gene expression in model plants and microorganisms should lead to a better understanding of the processes mediating plant–microbe recognition and communication.



**Figure 2.** Bioactive secondary metabolites isolated from plant-root exudates of *Arabidopsis thaliana*, *Ocimum basilicum*, *Oxalis tuberosa* and *Centaurea maculosa* exhibit a broad array of antibacterial and antifungal activities.

Related plant families generally make use of similar root-localized secondary metabolites for defense purposes (e.g. isoflavonoids in the Leguminosae and sesquiterpenes in the Solanaceae), although some chemically related defense compounds are shared across taxa (e.g. phenylpropanoid derivatives) [7,23]. Most antimicrobial plant secondary metabolites have relatively broad-spectrum activity, and specificity is often determined by whether or not a pathogen has the enzymatic machinery to detoxify a particular host product [24,25]. Root-microbe interactions studied to date are mainly confined to the accumulation of inducible antimicrobial compounds localized in roots [7,23]. *Arabidopsis*, rice, corn, soybean and the model legume *Medicago truncatula* have been subjected to intensive gene-sequencing efforts and are rich sources of the root-derived antimicrobials indole, terpenoid, benzoxazinone, flavonoid and isoflavonoid [23]. However, in contrast to root-sequestered compounds, there are as yet no profiles of the root exudates of

*Arabidopsis*, rice, corn, soybean and *M. truncatula* to enable the significance of these defense compounds in the rhizosphere to be determined.

Plant roots face relentless attack from pathogens with the potential for rapid and selective responses to plant defense mechanisms, and hence roots must continuously produce and secrete compounds into the rhizosphere [7,8]. One mechanism by which plants cope with pathogens is the production of a 'front line' of detached, living cells called border cells [6]. These border cells exude a diverse array of biological chemicals that influence the behavior of fungi and bacteria [26]. Border cells released in advance of the vulnerable root tip might protect plant health by inhibiting tip infection by pathogens, or by stimulating the development of beneficial associations. Under controlled conditions, border cells and their associated products can contribute up to 98% of the carbon-rich material that is released by plants as root exudates, so their potential impact on root-microbe interactions is large [27].

Although little is known about elicited compounds in root exudates, some recent work has shed light on the subject. A report on isoflavonoid (genistein) exudation from the roots of white lupine (*Lupinus luteus*) indicates that a specific elicitation regime is crucial for enhanced exudation of genistein [28]. Several recent papers have documented the antimicrobial and antifungal properties of elicited, root-secreted secondary metabolites [29,30]. Research has shown that chemical or biological elicitors, acting as natural stresses, stimulate roots to exude an array of compounds not detected in the constitutively expressed exudates of *Arabidopsis thaliana* and *Ocimum basilicum* (sweet basil) [31–34]. An elicitor triggers the production of different compounds in different plant species [31], and elicitation can dramatically increase the quantities of certain continuously expressed compounds in the exudates [31–34,30]. Because many of the compounds found in root exudates display both antifungal and antibacterial activity [35,36], it is likely that several secreted compounds act synergistically, accounting for the overall antimicrobial activity of root exudates. These results also show that roots can selectively sense a pathogen in the vicinity, resulting in tip-exudation of an antimicrobial to ward off the pathogen [31–34]. This observation of root-tip exudation agrees with the report by Lindy Brigham *et al.* [37]. Their observation revealed that pigmented naphthoquinone derivatives of shikonin were induced and exuded by roots upon pathogen challenge.

Plant roots also secrete a battery of proteins to defend the plant against potential soil-borne pathogens. The mechanism by which proteins are secreted is not completely understood, but it has been proposed that proteins are actively secreted from the root epidermal cells [7,38]. By generating transgenic tobacco (*Nicotiana tabacum*) with exogenous non-exuded proteins such as the green fluorescent protein (GFP), human placental secreted alkaline phosphatase (SEAP) and xylanase in the presence of the endoplasmic reticulum (ER) signal peptide, it was shown that recombinant GFP, SEAP and xylanase were secreted through the root systems of the transgenic tobacco [39]. The recombinant proteins that fused to the ER-targeting signal peptide were preferentially translocated



to the cell walls and extracellular space (apoplast), and subsequently secreted from the root cells [40]. These results indicate that the ER secretory pathway is closely linked with the root secretory pathway.

Recently, it has been reported that the hairy roots of pokeweed (*Phytolacca americana*) are able to secrete various defense proteins, including a ribosome-inactivating protein (RIP), PAP-H [38]. RIPs are widely distributed among higher plants and inhibit protein synthesis by virtue of their *N*-glycosidase activity, selectively removing an adenine residue at a conserved site of the 28S rRNA [41,42]. This root-exuded RIP has shown antifungal activity against fungi that cause root rot: *Rhizoctonia solani* and *Trichoderma reesei* [38,43]. Other pathogenesis-related (PR) proteins, including  $\beta$ -1,3-glucanase, chitinase, and protease, are also secreted from pokeweed roots [43]. These PR proteins are thought to play a crucial role in facilitating the entrance of PAP-H into the cells by disrupting the fungal cell walls [38,43]. Concomitantly, PAP-H actively penetrates into the cytoplasmic space of the fungal cells, depurinates ribosomes and causes protein synthesis to cease, resulting in cell death [38,43]. In addition, the plant root secretory mechanism of PAP-H is enhanced by abiotic stress, such as ethylene, which might be a signal that indicates pathogen-induced stresses in the roots [38,44]. Microscopic analysis showed that PAP-H is also localized in the cell walls of root border cells, indicating that it is released as a component of these cells [38]. These results demonstrate that the plant root-secretion system and its exuded bioactive-proteins and secondary metabolites are involved in root-microbe interactions, actively protecting themselves from the invasion of soil-borne pathogens.

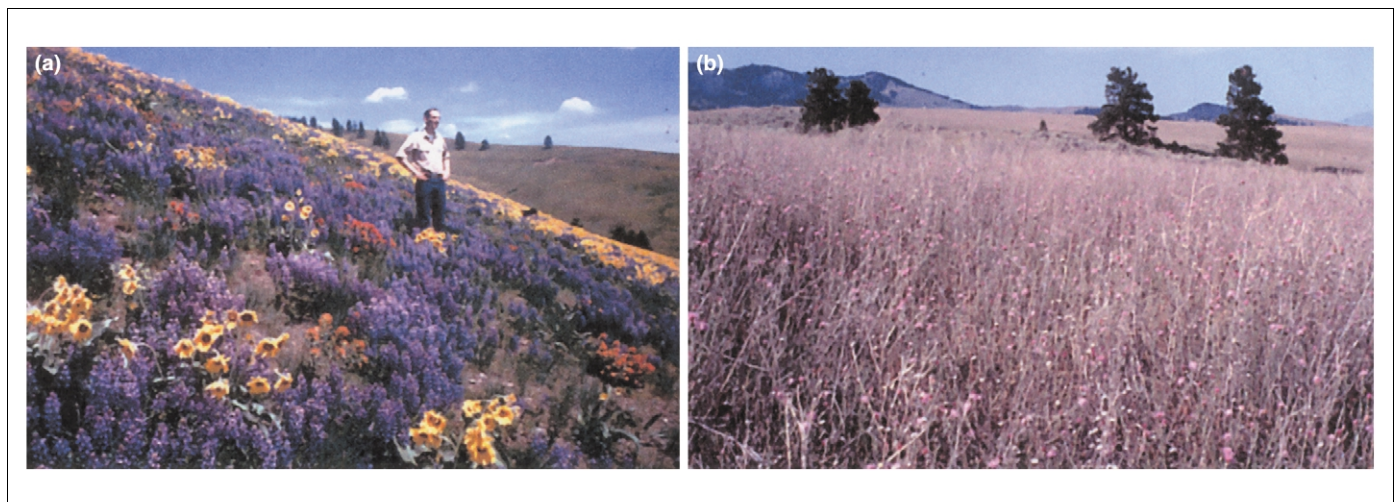
### Negative root-root communication

Root secretions can play a role in interactions among plants as well. Recognition of the importance of root exudates in plant interactions has fluctuated over the past 50 years [45], but acceptance of ALLELOPATHY (the release of phytotoxins by plants) has increased with recent studies of inter- and intraspecific root communication [46–48].

Allelopathy demonstrates how plants use root-secreted secondary metabolites to regulate the rhizosphere to the detriment of neighboring plants. Certain aspects of the general argument for plant interactions via root exudates are strong. First, as described above, plant roots produce an amazing array of chemicals, many of which appear to be species-specific [7,8,49]. Second, many of these chemicals are exuded into the rhizosphere and can move at least decimeters from their source [50,51]. Third, chemicals in root exudates have powerful and apparently non-controversial ecological effects on animals, bacteria, viruses and fungi [52,53]. Fourth, many compounds released from plant roots have been shown to have deleterious effects on other plants [7,54,55], although these effects have not been studied under completely natural conditions. Finally, substances with organic adsorptive capacity (activated carbon, gel filters) have been found to reduce the negative effects of the roots of some species on other plants [46,47,56]. In spite of a large body of evidence for root exudate-mediated allelopathy as an important plant interaction [57], the inability of experiments to separate the effects of root exudates from resource competition, and an intriguing historical legacy [45,57], has preserved skepticism among ecologists [58].

Callaway and Aschehoug [59] examined the effects of the root exudates of *Centaurea diffusa* on bunchgrass species that co-exist with *C. diffusa* in its native Eurasia and the effects of *C. diffusa* on bunchgrass species from North America. *C. diffusa* and *C. maculosa* had stronger negative effects on North American species than on Eurasian species (Figure 3a,b). However, addition of activated carbon, which binds organic compounds such as ALLELOCHEMICALS, to North American grasses growing with *C. diffusa* was positive, indicating strong root exudate effects. By contrast, no evidence was found for root-mediated allelopathy on the Eurasian natives. These results provide a case that root-secreted allelochemicals play a role in root-root communication in natural environments.

One convincing example of a root-secreted allelochemical was a study combining biochemical and molecular data with ecological experiments to link allelochemicals



**Figure 3.** Peculiar invasion patterns of *Centaurea maculosa*, which is replacing native plants in the fields of northwestern USA. (a) Non-invaded area. (b) Same area photographed 20 years later, by which time *C. maculosa* has invaded the area.

that have both field activity and were a direct cause of cell death in neighboring plants [60]. Recently, Bais *et al.* [34] isolated two enantiomers of catechin secreted from *C. maculosa* roots. One enantiomer, (+)-catechin, exhibited anti-bacterial functions, whereas the other enantiomer, (–)-catechin, had strong allelopathic effects on a variety of plant species. *Arabidopsis* and *C. diffusa* were chosen as target species for the phytotoxicity of (–)-catechin [34,60]. The addition of  $100\ \mu\text{g ml}^{-1}$  of (–)-catechin to the roots of *C. diffusa* and *Arabidopsis* led to a condensation of the cytoplasm, characteristic of cell death along with a rapid and transient elevations in root tip-localized  $[\text{Ca}^{2+}]_{\text{cyt}}$  levels in *C. diffusa* seedlings [60]. By contrast, *C. maculosa* showed no change in  $[\text{Ca}^{2+}]_{\text{cyt}}$  upon (–)-catechin treatment [60]. In summary, root-exuded allelochemicals have been identified, quantified in soil, and shown to be taken up by and cause damage to other plants when added to field soils [57–60]. This case challenges the conventional ecological perspective that the invasiveness of a species is mainly the result of enhanced resource competition after escape from natural enemies [45], and highlights that the biochemical potential of the plant is an important determinant of invasive success.

Recent studies on signals between the roots of parasites and hosts has increased the understanding of this unique rhizospheric interaction [2,4,61], which previously had received little attention. Parasitic plants often use secondary metabolites secreted from roots as chemical messengers to initiate the development of invasive organs (haustoria) required for heterotrophic growth [62]. Some of the most devastating parasitic plants of important food crops such as maize, sorghum, millet, rice and legumes belong to the Scrophulariaceae, which typically invade the roots of surrounding plants to deprive them of water, minerals, and essential nutrients [2]. It has been reported that certain allelochemicals such as flavonoids, *p*-hydroxy acids, quinones and cytokinins secreted by host roots induce haustorium formation [2,63], but the exact structural requirements of the secreted compounds for haustorium induction is not fully understood.

### Root exudate-mediated environmental feedback

Various mechanical functions have been attributed to root exudation including the maintenance of root–soil contact, lubrication of the root tip, protection of roots from desiccation, stabilization of soil micro-aggregates, and selective adsorption and storage of ions [6,27,64,65]. For example, plant roots have evolved a range of mechanisms for increasing the availability of phosphorous (P), including the increased exudation of organic acids, the release of enzymes (particularly acid phosphatases) and the production of root clusters (proteoid roots), allowing plants to survive in P-deficient soils [66]. The most thoroughly understood root-exuded proteins are acid phosphatases (APases), which facilitate and increase the availability of soil P for uptake by roots [67,68]. Plants absorb P from the soil in the form of soluble orthophosphate anions ( $\text{P}_i$ ,  $\text{H}_2\text{PO}_4^-$  or  $\text{HPO}_4^{2-}$ ), which are not readily available in the soil [69]. In response to P-deficiency, plant roots are capable of dramatically increasing the amount of various substrate-specific APases that they secrete [70].

For example, under P-deficient conditions, the secretion of APases from lupine roots increased up to 20 times compared with P-sufficient conditions [71], with large amounts of APase observed in the rhizosphere [72].

The ability of root surfactants to remove P adsorbed to the soil is important for extending roots seeking more nutrients, and offers an advantage over other organisms competing for P. Glycolipids and other phospholipids associated with plant cell membranes are expected to show marked surface activity [73]. Phospholipid surfactants increase the amount of P in the rhizosphere, and therefore available to the plant. However, plants have also developed a crucial root-secretion system to use the large amounts of insoluble organic and mineral P compounds found in the soil. Recently, it was reported that plant-released surfactants significantly affect the chemical and physical environment of the soil in the rhizosphere, modifying soil-water-release characteristics and hydraulic conductivity, and nutrient adsorption, availability and microbial turnover [5,74]. The root tip continuously releases surfactants into the surrounding soil and these root-exuded phospholipids profoundly influence the properties of the rhizosphere. Furthermore, the existence of microbially produced phospholipids reinforce the effects of decreased surface tension in the rhizosphere.

Taken together, these studies indicate that root exudation plays a major role in maintaining root–soil contact in the rhizosphere by modifying the biochemical and physical properties of the rhizosphere and contributing to root growth and plant survival. However, the exact fate of exuded compounds in the rhizosphere, and the nature of their reactions in the soil, remains poorly understood.

### Final remarks

Because of significant advances in root biology and the genomics of root-specific traits, roots can no longer be considered an unexplored biological frontier. However, our knowledge of the more complex rhizospheric processes mediated by root exudates has not developed at the same pace as our knowledge of roots overall. Nevertheless, our understanding of the importance of root exudates for plant interactions has increased substantially over the past decade. The integration of molecular tools with traditional ecological approaches holds great promise for more mechanistic advances. Whether or not plants interact via root exudates is not trivial. If even a small portion of the thousands of different chemicals produced by the roots of plants have effects on their neighbours, then species-specific interactions, natural selection, community integration, and community coevolution might proceed in different ways to those predicted by conceptual models based on resource competition. As highlighted here, several lines of evidence also indicate that root exudates, in their various forms, regulate microbial communities in the rhizosphere. Many microbes live in the soil, but only a few of these organisms have developed compatible interactions with specific plant species and developed into successful plant pathogens. The vast majority of microbes exhibit incompatible interactions with plants, which might be explained by the constant and diverse secretion of antimicrobial root exudates. Our rapidly expanding



understanding of the biology of root exudation should contribute to new strategies for improving the fitness of plants used by humans, understanding the processes that regulate the abundance and distribution of natural plant populations and the isolation of unique compounds found in the root exudates.

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