



Root signals that mediate mutualistic interactions in the rhizosphere

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A recent boom in research on belowground ecology is rapidly revealing a multitude of fascinating interactions, in particular in the rhizosphere. Many of these interactions are mediated by photo-assimilates that are excreted by plant roots. Root exudates are not mere waste products, but serve numerous functions to control abiotic and biotic processes. These functions range from changing the chemical and physical properties of the soil, inhibiting the growth of competing plants, combatting herbivores, and regulating the microbial community. Particularly intriguing are root-released compounds that have evolved to serve mutualistic interactions with soil-dwelling organisms. These mutually beneficial plant-mediated signals are not only of fundamental ecological interest, but also exceedingly important from an agronomical perspective. Here, we attempt to provide an overview of the plant-produced compounds that have so far been implicated in mutualistic interactions. We propose that these mutualistic signals may have evolved from chemical defenses and we point out that they can be (mis)used by specialized pathogens and herbivores. We speculate that many more signals and interactions remain to be uncovered and that a good understanding of the mechanisms and ecological implications can be the basis for exploitation and manipulation of the signals for crop improvement and protection.

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Introduction

It has been estimated that between 20 and 80% of the total photosynthates enters the rhizosphere as root exudates [1]. These exudates are primarily composed of carbon-containing compounds, including the respired CO₂, but also of non-carbon-containing compounds including ubiquitous H⁺, inorganic ions, water, and electrons [2]. A large

fraction of the rhizodeposition also involves compounds such as phytosiderophores for improving nutrient acquisition [3,4], or polysaccharides, that, in association with rhizospheric microbial cells and clay particles, form a mucigel [5,6]. This mucigel provides protection and lubrication, and can create a suitable environment for symbiotic microorganisms. In this environment other exudates can operate as signals to mediate the interactions with plant-beneficial organisms [7,8,9*].

Indeed, a rapidly increasing number of studies is revealing that plant roots exude a variety of organic compounds that are not directly associated with plant nutrition or growth [9*,10,11*]. These may include sugars and simple polysaccharides (such as arabinose, fructose, glucose, maltose, mannose, oligosaccharides), amino acids (such as arginine, asparagine, aspartic, cysteine, cystine, glutamine), organic acids (such as acetic, ascorbic, benzoic, ferulic, malic acids), and phenolic compounds [2]. In addition, roots may exude higher-molecular-weight compounds such as flavonoids, enzymes, fatty acids, growth regulators, nucleotides, tannins, carbohydrates, steroids, terpenoids, alkaloids, polyacetylenes, and vitamins [12–14]. Many of these compounds are thought to mediate interactions with other organisms in the rhizosphere.

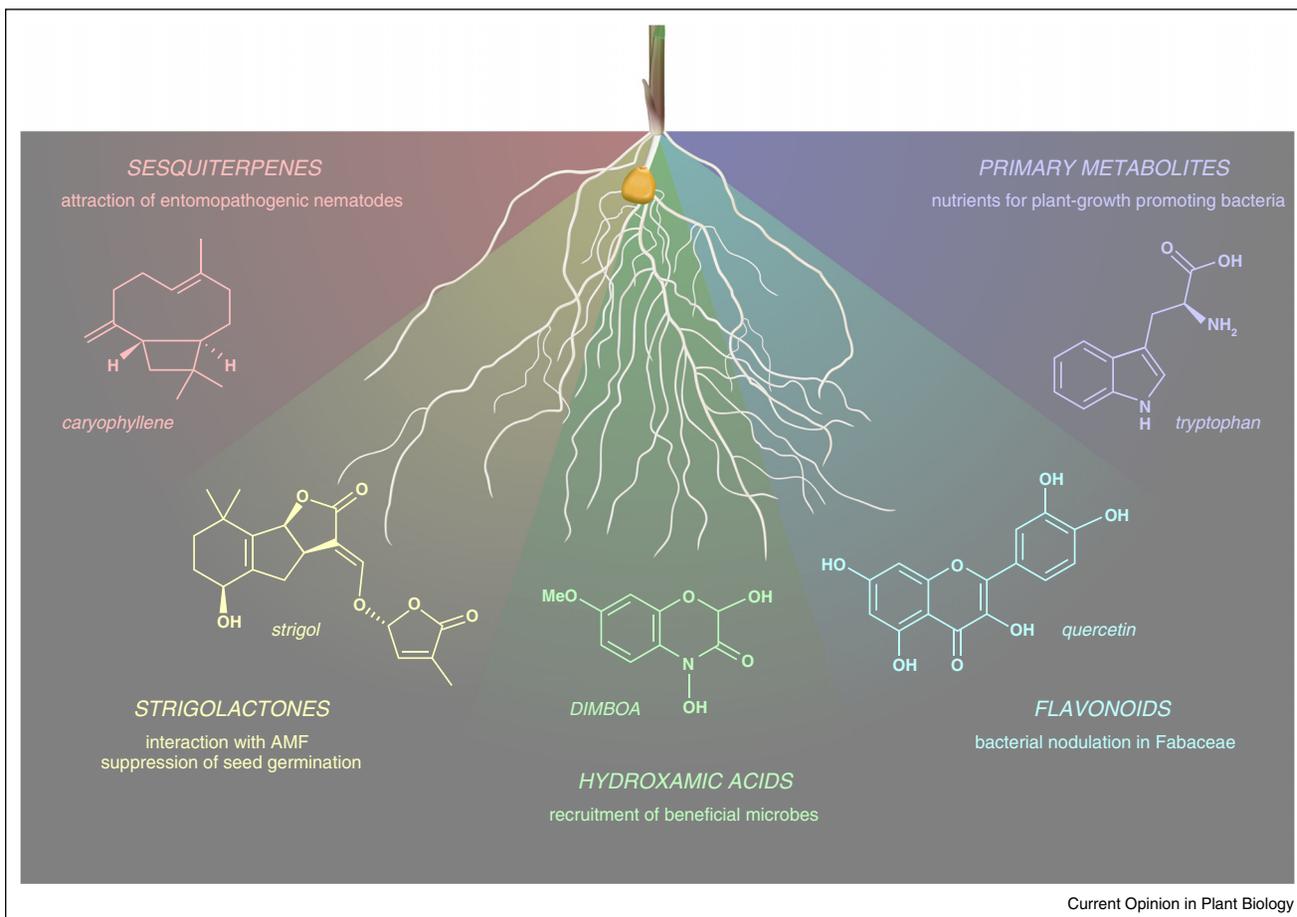
Below, we review how root-produced signals may mediate mutualistic interactions (Figure 1), but also stress that the same signals may be opportunistically used by plant antagonists. We point out gaps in the literature and reiterate that root-emitted signals might be exploited for application, for instance in crop protection [15].

Plants send chemical cues to other organisms Plant–plant interaction

Chemically mediated plant–plant interactions have been extensively studied for aboveground tissues, particularly in the context of herbivore-induced volatiles that can be perceived by neighbouring plants and ‘warn’ them for imminent attack [16*,17]. Specific volatiles are essential for this plant-to-plant signalling [18,19*] and may be exploitable for crop protection [20,21]. This should also be explored for belowground plant–plant signalling.

Indeed, it has been shown that when *Vicia faba* (broad bean) plants are subjected to aphid attack, they release root exudates that induce the release of volatiles in undamaged neighbouring plants, which in turn attracts aphid parasitoids [22]. Similarly, *Phaseolus lunatus* (lima bean) plants under attack by spider mites produce root

Figure 1



Examples of the diverse range of root exudates that are implicated in mutualistic rhizospheric interactions as outlined in the text.

exudates that induce the release of volatiles in other plants that attract predatory mites [23]. For now, the only other known mutually beneficial underground interaction involves fungal networks via which neighbouring plants can be informed of impending insect attack [24^{*}]. The specific signals that are involved in these interactions remain to be elucidated. Although for one type of plant-produced secondary metabolites (iridoid glycosides from *Plantago lanceolata*) it is known that they can be transferred to the fungal hyphae, protecting them against fungivore attack [25^{*}], and potentially affecting soil-dwelling herbivores too.

Considerably more is known about the chemicals involved in belowground plant–plant interactions that have negative, allelopathic, effects. Allelopathy involves the release of chemicals by a plant that inhibits seed germination or growth in other plants. Allelopathic root exudates are worth mentioning here because they are also available as signals that may be exploited by plant mutualists. This appears to be the case for the benzoxazinoids, like DIMBOA, released by maize, wheat and other

grasses roots. Like many other plant produced toxins, DIMBOA has allelopathic properties [12], but it is also induced upon root feeding by insects [26], and may have several signalling functions (Box 1).

Plant–arthropod interaction

Soil arthropod communities are largely composed of immature stage of insects (particularly in the case of Coleoptera and Diptera), collembolan, and mites. They can be involved in positive interactions (such as through the indirect positive effects of decomposers), but also in negative interactions, since many of the soil insect larvae feed on roots [11^{*}].

In the context of mutualistic root-produced signals, decomposers have not yet been considered. Decomposition by arthropods and other invertebrates, such as earthworms, have profound effects on nutrient cycling, which in turn affects plant performance [27], and defence [28]. It might therefore be highly advantageous for plants to send cues into the soil to attract specific decomposers. This

Box 1 Benzoxazinoids — Benzoxazinoids (BXs) are natural hydroxamic acids that are best known as the main chemical defence in many grasses, including important cereals like maize, rye and wheat. In the plants, the BXs are typically glycosidically bound and stored in the vacuole. The toxic and protective aglycones are only liberated upon exposure to β -glucosidases during tissue damage and/or ingestion by herbivores [64–66]. Specialized herbivores may detoxify the aglycones [67–69] and even use them for their own benefit [33*]. The best known of the BXs is DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one), which has been implicated in resistance against insect pests, as well as a number of pathogens [70]. The concentrations of BXs are typically higher in younger plants [71], and can be released in the rhizosphere [72]. The implications of this are still largely unknown, but it is increasingly clear that BXs have an effect on microbiota in the soil. For example, it was shown that DIMBOA and MBOA affected the soil microbial community structure near wheat plants to their competitive advantage through changes in fungal community composition [73]. Similarly, DIMBOA, the dominant BX in the exudates of maize roots, provokes chemotactic responses in *Pseudomonas putida* KT2440, a bacterium with plant-beneficial traits. The role of BXs in the recruitment of *P. putida* was elegantly confirmed with the use of maize mutants impaired in the production of BXs [47]. A complete understanding of these interactions will greatly facilitate their conceivable application in agriculture.

remains to our knowledge unexplored and merits further investigation.

Chemically mediated host location by root-feeding insects has been extensively reviewed by Johnson and Nielsen [29], showing that several dozens of compounds in root exudates can serve as foraging cues [30]. Such negative consequences of releasing these particular exudates are likely to be counter-balanced by interactions with positive effects for the plant. For instance, adult soil-dwelling arthropods are often predatory and may use plant exudates to find herbivore preys [31]. Therefore, similar to what has been described for aboveground plant–herbivore interactions [32], co-evolutionary adaptations of defence and counter-defence between plants and their herbivores appear to also take place belowground. An illustrative example is the highly specialized larvae of *Diabrotica virgifera virgifera* that exploit maize-produced benzoxazinoids, that are toxic to most herbivores, to identify the most suitable roots [33*] (Box 1). The same larvae also use an inducible root volatiles involved in indirect (see below) to aggregate, as they develop better when multiple larvae feed on the same root system [34]. But this same compound, the sesquiterpene (*E*)- β -caryophyllene, also benefits the plant by attracting entomopathogenic nematodes (see below and Box 2).

Signalling between plants and microbes (bacteria and fungi)

Plant associations with soil mutualistic microbes are largely mediated by root exudation. Three specific groups of organisms can be identified: mycorrhizal fungi, nitrogen fixing bacteria, and growth promoting bacteria [35].

Box 2 Terpenoids — Several root-produced compounds in the chemical class of the terpenoids are involved in numerous belowground mutualistic processes, such as the sesquiterpenes (*E*)- β -caryophyllene and pregeijerene, that attracts entomopathogenic nematodes (EPN) [56,58], and strigolactones that facilitate root associations with arbuscular mycorrhizal fungi (AMF) [44].

The role of terpenoids in EPN attraction was first shown when we investigated EPNs as potential biological control agents against the western corn rootworm (WCR), *D. virgifera virgifera*, a major pest of maize roots. In response to WCR-feeding maize roots release (*E*)- β -caryophyllene [58]. The importance of (*E*)- β -caryophyllene as an EPN attractant was confirmed by restoring its release in a maize variety that has lost the ability to produce it [62,74]. It should be noted that in combination with CO₂, (*E*)- β -caryophyllene is considerably more attractive [75]. This strong synergistic effect may also be true for other interactions, or other exudates that are commonly released from roots. Similarly, EPNs have been considered for the biological control of weevil larvae (Coleoptera: Curculionidae) attacking *Citrus* trees. Upon weevil damage the tree roots release several terpenes that recruit EPN to the site of wounding [56,57]. Enhancing the production of these root exudates can improve crop protection by EPNs (Degenhardt *et al.* [62]), but also the EPNs themselves can be selected to respond better to the root-produced attractants [60].

Strigolactones have been particularly well studied in the context of plant-beneficial interactions, but also in the recruitment of antagonists. These terpenoid lactones are carotenoid-derived plant hormones that regulate developmental processes, but they are also excreted into the rhizosphere where they recruit symbiotic fungi, but also root parasitic plants [76,77]. Strigolactones are a wonderful example of how mutualistic signalling can be abused by the plants' enemies, in this specific case they serve as germination stimulants for parasitic plants of the genus *Striga* from which they derive their name [(e.g. 78,79)]. In an evolutionary context, belowground strigolactone production is likely to be subject to diffuse selection, as is the case for aboveground emitted compounds [80]. Therefore, their production can only be maintained if other beneficial functions outweigh the detrimental effects. We argue that the fact that strigolactones trigger seed germination in parasitic *Striga* plants [76] is a case of 'leavesdropping' on a beneficial interaction of the plants with mutualistic fungi. If these negative effects could be minimized, strigolactones represent a wonderful example of how root-produced chemical cues could be enhanced to increase plant production in concomitance with the application mutualists. Strigolactones may also have a function as direct chemical defences against pathogens and herbivores, and efforts are underway to explore their overall potential for crop protection [81*].

Arbuscular mycorrhizal fungi (AMF) and plant roots form associations in more than 80% of terrestrial plants [36]. These symbiotic relationships facilitate nutrient uptake by the plant, and in turn, the associated fungi extract lipids and carbohydrates from the host root. AMF have also been shown to indirectly benefit plants, by increasing plant resistance against herbivores and pathogens in several systems [37,38*,39,40], but not all [41]. As obligate biotrophs, the survival of these fungi depends on their ability to rapidly establish a symbiotic relationship with plant roots. The growth and branching of germinating hyphae before root infection require the presence of compounds released by roots [42]. Among the diversity of molecules present in root exudates and active in hyphal branching, flavonoids have often been proposed to switch

AMF from non-symbiotic to pre-symbiotic growth [43]. Strigolactones, which are carotenoid-derived terpenoids, have been found to stimulate cell proliferation in the AM fungus *Gigaspora rosea*, and spore germination in *Glomus intraradices* and *Gl. claroideum* [43], and they induce branching in *G. margarita* [44]. Strigolactones are also involved in several other belowground interactions, again showing complex ecological and evolutionary dynamics at play (see Box 2).

Plants may also release root exudates to recruit nitrogen fixing and growth promoting bacteria (e.g. Rhizobia). A large number of plant species, mainly in the Fabaceae family profit from the intimate association with nitrogen-fixing bacteria and again plant-produced flavonoids are involved in the establishment of these associations [45] (Figure 1). Interestingly, because most legume species mainly produce their own specific isoflavonoids, it enables the Rhizobia to selectively colonize their specific host plants [10]. Finally, plants may produce exudates to attract plant-growth-promoting bacteria into their rhizosphere [46]. These free-living bacteria have been shown to be attracted to root-produced carbohydrates and amino-acids, including the primary metabolite tryptophan [10]. Recent evidence shows that benzoxazinoids may act similarly [47] (Box 1).

Whether root exudates can also attract the highly ubiquitous soil protists and how this may affect plant–microbe interactions is to our knowledge unknown. Protists have obvious associations with plants [48]. Several guilds of protists are microbial feeders, and should be attracted to locations with high-energy sources, generating a microbial loop that affects plant performance [49]. It is therefore highly likely that root exudates also mediate protist orientation.

Interaction between plants and herbivore-killing predators and pathogens

Plants can benefit from attracting predators and pathogens to the sites where they are attacked by herbivores. Indeed, root-feeding insects have plenty natural enemies, including arthropods such as predatory mites (Acari), ants (Formicidae), carabid beetles (Carabidae), staphylinid beetles (Staphylinidae), and spiders (Aranea), predatory nematodes, entomopathogenic nematodes (EPNs), entomopathogenic fungi, and insect-pathogenic bacteria [50].

As yet, there is limited evidence that root exudates can attract soil-dwelling predatory arthropods, but clearly this has potential to improve biological control [31,50]. For example, it was found that the predatory mite *Neoseiulus cucumeris* is attracted to tulip bulbs infested with rust mites (*Aceria tulipae*). No such attraction was found for mechanically damaged bulbs, strongly suggesting that the bulbs produce a specific exudate in response to rust mite infestation [51], but this remains to be elucidated. Similarly, we

are not aware of evidence for chemically mediated mutualistic interactions between entomopathogenic microbes and plants [11^{*}]. Besides releasing attractants, it is plausible that plants have evolved mechanisms, such as maintaining a nutrient-rich rhizospheric zone, in order to retain mutualistic microbes in the rhizosphere, which would represent an evolutionary advantage for both partners [52].

Much more is known about the chemically mediated interactions between roots and entomopathogenic nematodes (EPN). The underlining idea is that EPN use root exudates in their efforts to find hosts, which are predominantly arthropod root herbivores [53,54]. Once found and penetrated, EPNs rapidly kill their hosts, and thereby ultimately increase plant fitness [55]. Indeed, a combination of behavioural assays and metabolomics analyses has revealed the role for root-produced volatiles in the foraging success of EPNs [56–61]. To our knowledge the successful manipulation of the release of such an EPN attractant represents the only attempt so far to enhance a mutualistic rhizosphere interaction (Box 2). The manipulation greatly improved the protection that maize roots receive from EPN [62], but, as mentioned above, follow-up work also revealed potential negative effects of such an approach, as the root signal is also used by herbivores to locate host plants [33^{*},34]. This attraction may be dose-dependent [33^{*}], implying that the intensity of the root signals can be a key factor in determining whether the produced compound benefit the plant or not. This example illustrates the importance of studying all consequences of the signal production in order to optimize their possible application in crop improvement.

Conclusions and perspectives

We here presented the highlights of what is currently known about how root exudates can benefit plants via interaction with other soil-dwelling organisms. Methodological limitations to studying belowground processes are slowly vanishing, opening the way for many new chemically mediated interactions to be discovered [8^{*},9^{*},11^{*}]. With these new discoveries come new opportunities to study plant exudates and gain further insights into their importance in structuring ecological communities, and, from an applied perspective, to exploit the interactions that mediate to enhance crop yields.

To achieve this we need to understand the relative magnitude of the effects of root exudates on plant fitness across a wide range of natural conditions [63]. This relates to the new frontier in ecological research, which focuses on assessing habitat-mediated intra-specific and inter-specific variation of root exudation, and subsequent soil ecology effects.

From an applied perspective further insight into the signals that are needed to attract soil-dwelling beneficial organisms is badly needed. Specifically, unravelling the

mechanisms that are involved in the synthesis and exudation of these signals should make it possible to breed for crops with enhanced capacities to exploit the soil biota for optimal plant health and yields.

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- Nice synthesis of the advancement in different areas of the strigolactone domain and the implications for agronomical applications.