Whispers in the dark: signals regulating underground plant-plant interactions

[1]Kaori Yoneyama and [2]Tom Bennett

Abstract

Plants are able to actively detect and respond to the presence in neighboring plants, in order to optimize their physiology to promote survival and reproduction despite the presence of competing organisms. A key, but still poorly understood mechanism for neighbor detection is through the perception of root exudates. In this review, we explore recent findings on the role of root exudates in plant-plant interactions, focusing both on general interactions, and also the highly specialized example of root parasite-host plant interactions.

Addresses

[1]Research and Development Bureau, Saitama University, Japan

[2]School of Biology, Faculty of Biological Sciences, University of Leeds, UK

Corresponding author: Yoneyama, Kaori (yoneyamak@mail.saitama-u.ac.jp)

Introduction: plant-plant signaling

For all the dangers posed by pathogenic organisms and herbivorous animals, it is neighboring plants, directly competing for light, water and mineral nutrients, that typically pose the single greatest biotic challenge in the life of a plant. As a significant body of work over the last two decades has revealed, plants therefore have multiple mechanisms to detect and respond to neighboring plants [1] (Figure 1). The role of light signaling in plant-plant interactions has been intensively studied and mechanisms by which reflected light quality regulates plant growth and development have been well-explained [1-3]. Touch is also a plant-plant signal, but a relatively simple one, which likely primes plants to respond to, or to emit other plant-plant signals [4]. Volatile organic compounds (VOCs) released by plants in response to herbivory or pathogen attacks can act as inter-plant signals, which play an important role to induce defense gene expression in neighboring plants [5-7]. Root exudates are also key chemical signals in plant-plant communications, and likely form the dominant plant-plant signals underground. However, methodological limitations have limited the discovery of detailed mechanisms of exudate-mediated plant-plant signaling [8]. Nevertheless, studies in the last few years have begun to identify some of the signals mediating plant-plant communication underground. In this review, we focus on this recent progress in understanding these 'whispers in the dark', first examining the specific example of root parasite-host plant interactions, before considering signals involved in more general plant-plant interactions.

Root parasitic plant-host plant interaction

Obligate root parasitic plants, such as those found extensively in the Orobanchaceae, largely or completely depend on host plants for water and nutrients and cannot survive without parasitizing host plants [9,10]. Root parasite seed are typically minute and their energy supply is sufficient only for germination; thus parasites need to attach host roots within a few days after germination. To find the living target roots, parasites detect and respond to 'germination stimulants' that are released from host roots. Strigolactones are the most ubiquitous germination stimulants for root parasites, and approximately 30 strigolactones have been isolated and characterized, primarily through their germination stimulant activities toward seeds of root parasitic plants [11]. Furthermore, recent study revealed that strigolactones also induce host tropism in the facultative root parasite *Phtheirospermum japonicum* [12]. Naturally, plants do not exude strigolactones for the benefit of root parasitic plants, but for initiating symbiotic relationship with arbuscular mycorrhizal (AM) fungi [13]. AM fungi supply mineral nutrients to host plants in exchange for photosynthetically derived sugars and lipids, and more than 80% of land plants form symbiosis with AM fungi. Strigolactones promote the hyphal branching of

AM fungi, a critical stage in the establishment of the symbiosis [13]. Exudation of these signals, however, leaves plants open to eavesdropping by parasites.

Strigolactones also act as a shoot branching inhibitor in planta [11,14,15], and now are widely accepted as a plant hormone regulating shoot and root architecture [11]. The receptors for strigolactones in a hormonal context are members of the DWARF14 (D14) family of α/β-hydrolases which are essential for suppression of shoot branching [16,17]. The D14 family is closely related to the KARRIKIN INSENSITIVE 2/HYPOSENSITIVE TO LIGHT (KAI2/HTL) family of α/β-hydrolases, which are presumed to act as receptors for an as-yet unidentified endogenous molecule called 'KAI2-ligand' (KL). KAI2 proteins also mediate seed germination in response to karrikins [18],butanolide compounds found in smoke, which trigger germination of many wild plant species after fire [19]. In root parasitic plants of the Orobanchaceae, seed-expressed *KAI2/HTL* homologs have been repurposed as receptors for strigolactone-induced germination, rather than D14 becoming expressed in the seed [20-23]. The model parasite *S. hermonthica* has 11 KAI2/HTL-derived putative strigolactone receptors. A crystal structure of a highly sensitive strigolactone receptor from *Striga* revealed a larger binding pockets of KAI2/HTL-derived putative strigolactone receptors than that of the *Arabidopsis* D14 receptor, which could explain the increased range of strigolactone sensitivity [21]. Depending on the plant species, different strigolactones structures can have greater or lesser activity as root parasite germination stimulants [24,25], suggesting some parasites are specialized to detect specific strigolactones emitted by their hosts. Conversely, the 11 KAI2/HTL receptors in *S. hermonthica* make it possible to detect structurally diverse strigolactones, consistent with the broad host range of this parasite [20-22] (Figure 2).

The formation of the specialized haustorium, by which parasitic plants attach to host roots, also depends on signals exuded from host plant [9]. Quinones, including 2,6-dimethoxy-p-benzoquinone (DMBQ), and cytokinin (CK), one of the canonical plant hormones, act as host-derived haustorium-inducing factors [26] (Figure 2). DMBQ was first isolated from root extracts of sorghum, one of the major host crops of *Striga* [27], but is only present in small amounts in root exudates of *Arabidopsis*, which nevertheless shows high haustorium-inducing activity [28]. Exudates of *Arabidopsis* CK-deficient mutant show significantly reduced haustorium inducing activity, but still retain substantial activity. DMBQ-responsive marker genes, which are not activated by CKs, are also highly expressed in response to *Arabidopsis* exudates. These results suggest that the host root exudates are likely to contain a mixture of quinone- and CK-type haustorium inducing factors [26].

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CARD1 (*CANNOT RESPOND TO DMBQ1, At5g49760*) isolated from *Arabidopsis* as a putative receptor of quinones encoding a leucine-rich-repeat receptor-like kinase, is highly conserved in land plants [29]. It contributes to immunity by the induction of defense-and/or stress-related genes, and by influencing stomatal immunity in response to DMBQ during bacterial infection. It has been demonstrated that *P. japonicum*, and the obligate hemiparasite *S. asiatica* have three *CARD1-LIKE (CADL)* homologs, which can complement in *Arabidopsis card1* mutants [29]. CADLs in *P. japonicum* were also shown to detect broader range of quinones. These suggest parasites are specialized to detect quinones more sensitively and/or a broader range of quinones. Moreover, analysis of both DMBQ-responsive (*ShQR2, ShPIRIN, ShYUC3, ShEXPB1*) and CK-responsive genes (*ShRR5* and *ShCKX2*) in *S. hermonthica* revealed that CK treatment upregulated the expression of *ShPIRIN* and *ShYUC3* but not *ShQR2b* and *ShEXPB1*, and DMBQ did not significantly affect the expression of CK signaling genes, indicating that CK-regulated haustorium formation overlaps with the DMBQ pathway at downstream targets [26] (Figure 2).

Signals mediating plant-plant interactions

Given that strigolactones act as signals between parasites and hosts, they are perhaps obvious candidates to act as more general plant-plant signals. Plants increase strigolactone exudation under phosphate deficiency to promote symbiosis with AM fungi [30], in order to obtain phosphate supplied by AM fungi. Strigolactone levels in roots are also elevated and suppression of shoot branching can be observed under phosphate deficiency [31], suggesting that plants also inhibit shoot branching to minimize the energy consumption under nutrient starvation. Although the identity of strigolactones that acts as hormonal signals remains unclear [32], recent studies have demonstrated that the canonical strigolactones exuded into the rhizosphere do not play this role [33,34]. Since plants are in effect always subject to phosphate deficiency [35], plants seem to constitutively exude canonical strigolactones, making them also available to act as constitutive plant-plant signals.

The possibility that strigolactones act as plant-plant signals has recently tested by using the strigolactone mutants of rice (*Oryza sativa*) and garden pea (*Pisum sativum*) [36,37]. When grown in the presence of neighboring plants, pea plants show a strong reduction in shoot growth between 3-5 weeks after germination. To test whether strigolactones could act as a signal mediating this response, pea strigolactone biosynthetic mutants were grown together, and were found to lack this characteristic shoot growth inhibition [37]. While this could in theory be a

result of an inability to regulate shoot growth in response to another signal, combinatorial growth of biosynthetic mutants with wild-type plants shows that biosynthetic mutants can respond to their neighbors, but cannot exert any effect on them, firmly supporting the role of strigolactones as the signal itself, rather in the response to the signal. Direct uptake of strigolactones from neighboring plants has also been demonstrated [36,37].

To better understand this signaling system, rice plants were placed into either a 1-, 2-, or 3-plant culture in the same volume of hydroponate, under phosphate deficiency [36]. Remarkably, levels of 4-deoxyorobanchol and orobanchol, major strigolactones in rice, were essentially identical irrespective of the number of plants in the system, indicating that the net strigolactone exudation in 1-, 2-, and 3-plant cultures is constant. These effects occurred before any changes in biomass, strongly suggesting that plants can detect other plants and homeostatically adjust their strigolactone exudation before physiological responses occur [36]. No corresponding decrease of 4-deoxyorobanchol levels in root tissues could be observed, but expression of strigolactone biosynthetic genes including *D27, D17, D10,* and *Os01g0701400* was significantly reduced, while expression of *D14* increased in 3-plant culture. Unlike in wild-type plants, there was no statistically significant reduction in per-plant strigolactone exudation in either 2- or 3-plant cultures relative to 1-plant cultures in *d14* mutants [36]. Similarly, wild-type plants grown in 2-plant culture with strigolactone synthesis mutants did not significantly reduce their exudation of strigolactones. Highly comparable effects were also seen in pea [37]. These results indicate that short exposure to neighboring plants triggers a density-dependent, D14-mediated reduction in strigolactone biosynthesis and exudation.

The role of strigolactones in angiosperms was presaged by work in the moss *Physcomitrium patens* [38]. Mosses do not form symbiotic associations with AM fungi but still exude unknown strigolactones, probably carlactone and its oxidized metabolites [39]. In *P. patens* and likely other mosses, these strigolactones seem to act as plant-plant signals instead. Wild-type *P. patens* colonies do not grow into each other, implying that they can detect each other and modulate their growth accordingly. Conversely, strigolactone synthesis mutant colonies fail to sense the proximity of neighboring colonies and grow into each other. However, neighboring wild-type colonies can inhibit the growth of synthesis mutant colonies [38]. These data imply that strigolactones are a mobile signal between colonies, although this has not been directly demonstrated. Given the evolution of strigolactone perception is likely convergent in mosses and angiosperms [40], it is also likely that the role of strigolactones as plant-plant signals is also convergent.

Several other low molecular weight exudates have been implicated in plant-plant interactions. A common form of competitive response is the release of allelopathic compounds that inhibit the growth of neighboring plants, which has been well-studied in crop-weed interactions [8,41,42]. In this context, (-)-loliolide has been implicated as a key molecule released by weed species that stimulates the release of allelochemicals such as DIMBOA (2,4-dihydroxy-7-methoxy- 1,4-benzoxazin-3-one) in wheat [43,44] and momilactone in rice [45]. The induction of allelopathic responses in crops appears to be a more specific version of a general response in plants; (-)-loliolide is exuded by plants upon both biotic and abiotic stress, and triggers the induction of defense responses in neighboring plants, including the production of defense-related secondary metabolites [46,47]. In this sense, (-)-loliolide seems like an exudate equivalent to VOCs, emitted by plants to trigger defense responses in both distal roots of the same plant, and neighboring plants as well.

Plants are also known to release jasmonic acid and ethylene into the soil, although these are technically volatiles, rather than exudates [43,48]. Like strigolactones, these molecules are plant hormones, with clearly defined perception mechanisms in plants. Thus, it is inevitable that their emission from a focal plant can be detected by any neighboring plants in the vicinity, and likely that these molecules are therefore also used as cues for the presence of neighboring plants (Figure 3). Further work is needed to directly test these hypotheses, but we certainly anticipate that more plant-plant cues will be confirmed over the next few years.

Perspectives

The identification of exudate signals mediating plant-plant interactions is an exciting development in our understanding of how plants interact each other using key elements of their biotic environment. However, significant gaps remain in our understanding of plant-plant interactions. While observed phenotypic responses can be interpreted as being competitive, cooperative or facilitative, the intentionality of these responses is usually unclear [1]. Are plants *deliberately* choosing to compete or cooperate with their neighbours, or are the apparently competitive/cooperate effects simply the unintentional result of hardwired growth responses to environmental stimuli? How can we tell, as external observers, what plants are attempting to achieve in the response to neighbor presence?

Another key gap in our understanding is whether plant-plant interactions are generic or specific. Can plants distinguish between neighbors on the basis of relatedness, and differentially respond

depending on the neighbor? And if so, how does this occur? The signals thus far identified are highly generic, and unlikely to allow specific kin/non-kin recognition. However, it is certainly theoretically possible that plants could distinguish between kin/non-kin neighbours (or between con/heterospecific neighbours), as long as the nature of the signals involved allowed plants to measure the genetic distance between themselves and their neighbour from themselves. In this context, we therefore hypothesize that there could be exuded peptide signals which allow plants to distinguish between close kin, distant kin and other species. The affinity of binding between such a peptide signal exuded by a neighbouring plant and the cognate receptor in a focal plant, could, at least in theory allow plants to distinguish between close kin (high affinity), distant kin (low affinity) and other species (no affinity). Such a signal might underpin the remarkable ability, previously reported, of closely related rice roots to spatially segregate in an agar medium, while more distantly-related rice roots do not [49]. Whether this idea is valid or not, we anticipate that the next few years will undoubtedly reveal more of the underground whispers that plants use to communicate with each other.

Acknowledgements

Declaration of interest

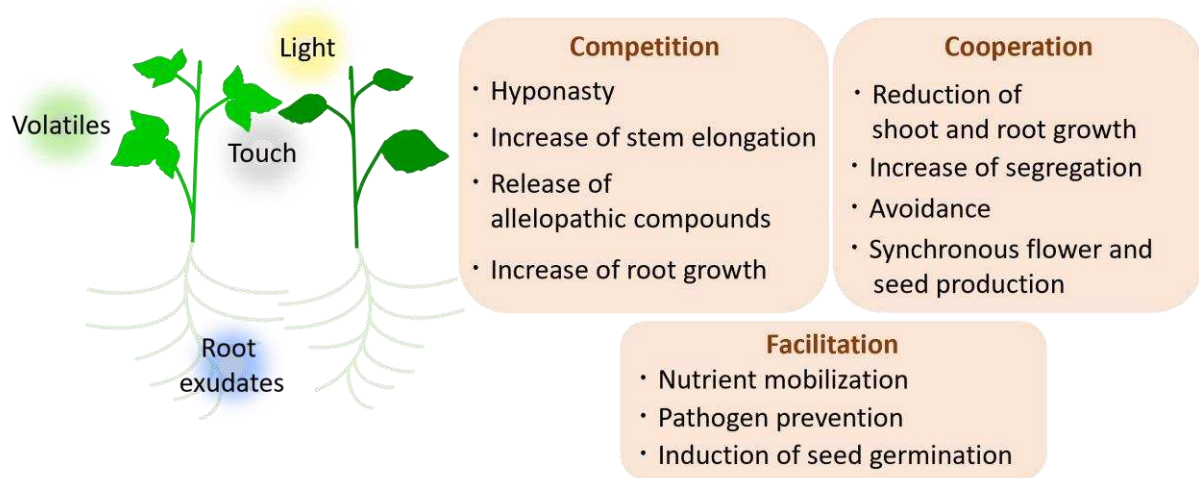The authors declare that they have no conflict of interests

Figures:

Figure 1: Mechanisms and consequences of neighbor detection in plants

Plants use multiple cues to detect the presence of neighboring plants, including reflected light, touch, emission of volatile organic compounds, and emission of root exudates. Characterized responses to these signals include competitive responses in which plants grow more strongly in the presence of neighbors, cooperative responses in which growth is reduced, and facilitation, in which plants inadvertently benefit each other.
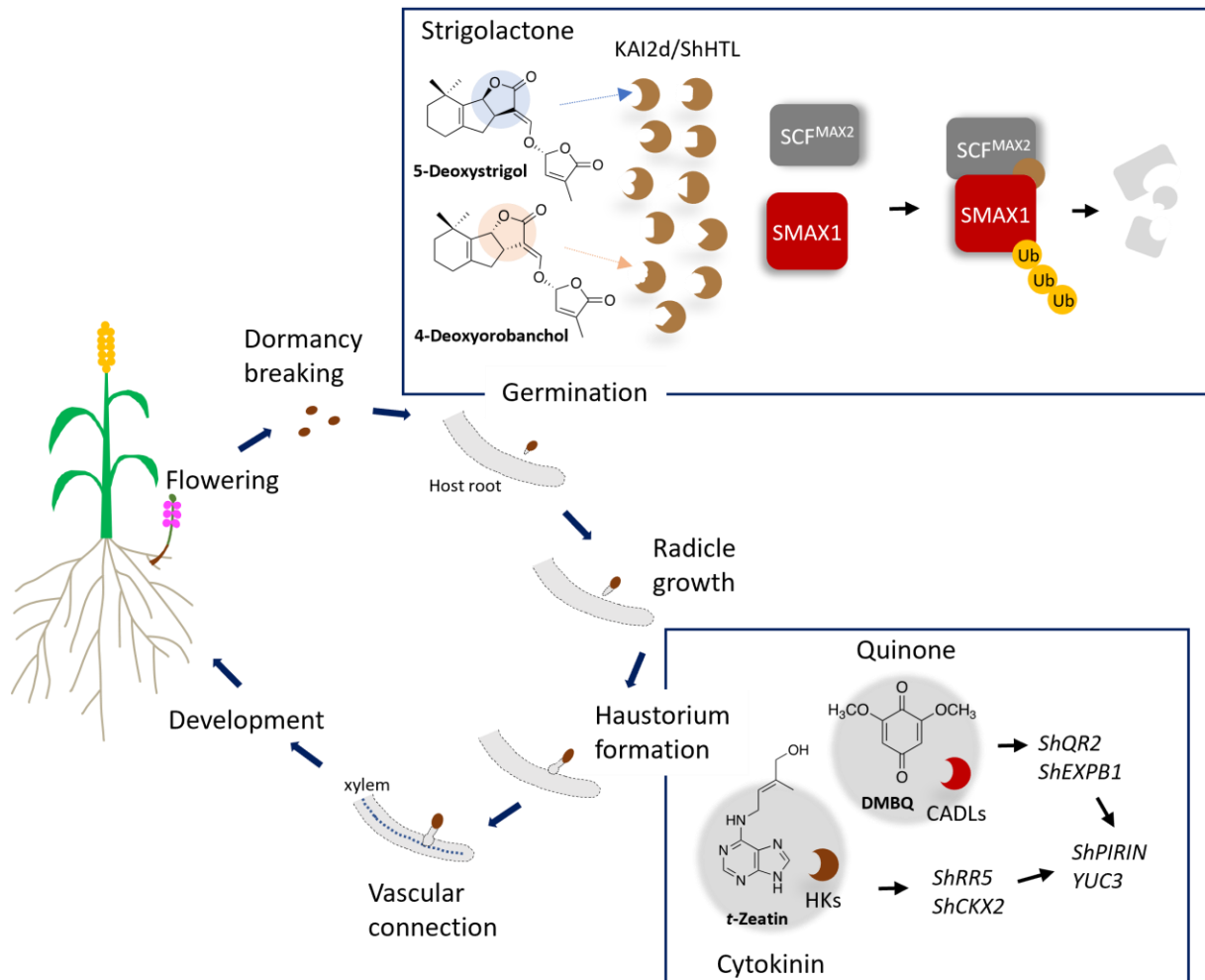
Figure 2: Root parasites respond to multiple cues emitted by host plants

Germination and haustorium formation of root parasites such as *Striga* species are induced by host-derived signals. Strigolactones emitted by host plants are detected by divergent KAI2/HTL receptors in parasite seed, resulting in degradation of SMAX1 proteins. Quinones and cytokinins emitted by host plants are detected by germinated parasites in order to regulate haustorium formation. These signal transductions are proposed from *Arabidopsis* and facultative root parasite *Phtheirospermum japonicum* and not yet confirmed in *Striga*.
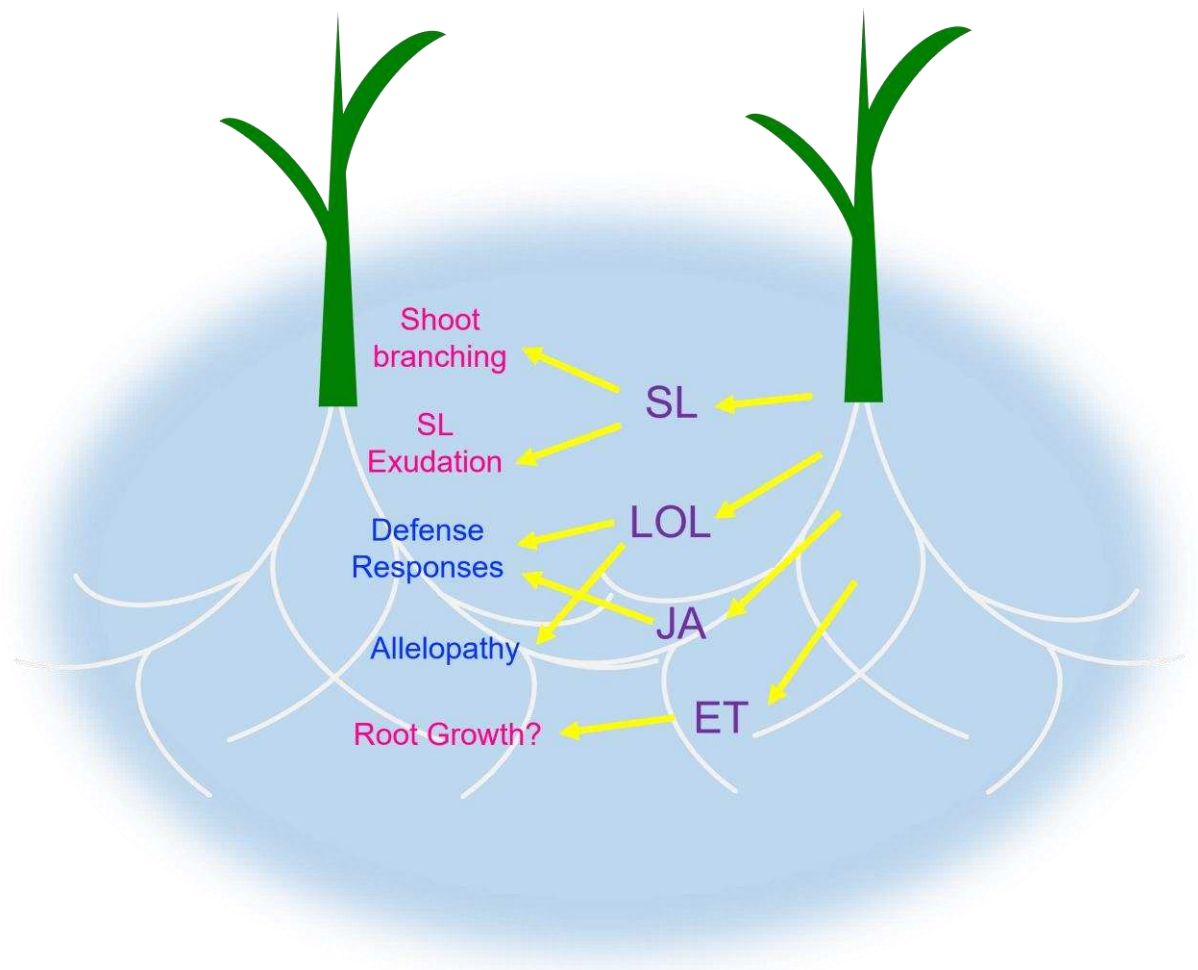
Figure 3: Root exudates in plant-plant interactions
Plants exude multiple low molecular weight compounds that can be detected by neighboring
plants, including strigolactones, loliolide, jasmonic acid and ethylene. Detection by
neighboring plants leads to up-regulation (blue text) or downregulation of physiological
responses.

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Special interest

Nelson DC: The mechanism of host-induced germination in root parasitic plants. *Plant Physiol* 2021, 185:1353-1373
This is an excellent and comprehensive review to understand the mechanism of strigolactone-induced germination in root parasitic plants.

Wheeldon CD, Hamon-Josse M, Lund H, Yoneyama K, Bennett T: Environmental strigolactone drives early growth responses to neighboring plants and soil volume in pea. *Curr Biol* 2022, 32:3593-3600 e3593.

The authors demonstrated that garden pea detect neighbors through their root systems early in life and strigolactone exudation by neighbors is needed for this response by using strigolactone biosynthesis and perception mutants as in the case of rice.

Ogawa S, Cui S, White ARF, Nelson DC, Yoshida S, Shirasu K: Strigolactones are chemoattractants for host tropism in Orobanchaceae parasitic plants. *Nat Commun* 2022, 13:4653.

The authors demonstrated that strigolactones function as host-derived chemoattractants and this function attenuates in ammonium rich conditions in facultative root parasitic plant *Phteirospermum japonicum*, implying this parasite infect hosts when the nitrogen source is limited.