The impact of root exudates, volatile organic compounds, and common mycorrhizal networks on root system architecture in root-root interactions

Xiu Zhang\textsuperscript{a,b}, Jingfan Yan\textsuperscript{a,b}, Muhammad Khashi u Rahman\textsuperscript{a,b} and Fengzhi Wu\textsuperscript{a,b}

\textsuperscript{a}Department of Horticulture, Northeast Agricultural University, Harbin, People’s Republic of China; \textsuperscript{b}Key Laboratory of Cold Area Vegetable Biology, Northeast Agricultural University, Harbin, People’s Republic of China

**ABSTRACT**

Plants constantly communicate with coexisting neighbors and adjust their physiological and morphological characteristics, including changes in root system architecture (RSA). Increased or decreased biomass accumulation, horizontal and vertical asymmetric distribution are the main behavioral performances. Some evidence has shown that these performances are associated with plant plasticity such as secretion of root exudates and release of volatile organic compounds (VOCs) and describe the role of common mycorrhizal networks (CMNs) as a communication pathway during belowground interplant interaction. Here, we highlight the direct role of root exudates as cues and signals and the indirect effects via regulating soil nutrients and soil microorganisms of these media in root-root interactions on RSA have been taken into consideration. At last, the existing knowledge gaps and potential research directions have been outlined for a better understanding of plant belowground interactions via RSA.

**Introduction**

The sessile nature gives plants a passive characteristic that makes them inevitable to interact with coexisting neighbors in natural and agricultural systems (Schandry and Becker 2020; Bilas et al. 2021; Ninkovic et al. 2021). Plants often grow together, and change traits above- and belowground to avoid the worst ecological consequences and challenges (Crepý and Casal 2015; Chen et al. 2021a). For example, plants can eavesdrop on volatile organic compounds (VOCs) signals emitted from herbivore-attacked neighbors and prime defenses (Baldwin et al. 2006). Similarly, the unstressed plants perceived and responded to osmotic and drought stress cues from their stressed neighbors and closed stomata (Falik et al. 2012). Due to the accessibility of aerial tissues facilitating shoot research, the aboveground interactions have been established in detail. In the last two decades, plant belowground interactions gain ever-increasing attention in contexts of root-root interactions (Semchenko et al. 2007b; Belter and Cahill 2015), root-soil interactions (Cahill et al. 2010; Yang et al. 2018), and root-soil-microbe interactions (Hellequin et al. 2021; Yu et al. 2021; Xu et al. 2021a).

Root-root interactions occur belowground, where roots can detect and respond to their neighbors which is conducive to plant performance and fitness (Liu et al. 2015; Rogers and Benfey 2015; Li et al. 2016b; Guo et al. 2020; Wang et al. 2020). Plant roots are plastic, resulting in alterations of root growth and distribution when growing with other plants. Root system architecture (RSA), the spatial configuration with some functional significance to the root system, serves pivotal role in obtaining water and mineral nutrients (Lynch 1995; McKay Fletcher et al. 2020; Liu 2021). There are different classifications of root systems, including tap roots (primary roots), lateral roots, basal roots (seminal roots) and shoot-borne roots (Lynch 2013; Satbhai et al. 2015; Hochholdinger et al. 2018). Root hairs, the tubular structure formed by the outwardly protruding epidermal cells, are also important for the root system (Leavitt 1901; Dolan 2017; Bienert et al. 2021). In addition, root hairs can increase the contents of exudates to enhance the nutrient absorption and rhizosphere interactions (Holz et al. 2018).

The mechanisms involved in the root-root interactions on RSA are well sophisticated. The action of root exudates, VOCs, and common mycorrhizal networks (CMNs) in plant-plant interaction is summarized in detail (Khashi u Rahman et al. 2019). In this review, we aim to shed light on our current knowledge of the role of root exudates, VOCs, and CMNs in root-root interaction on RSA, and to discuss potential directions to increase future research and understanding.

**Effect of root-root interactions on RSA**

Interaction between two roots can be studied as inter- or intraspecific considering the identity of neighbors (Faget et al. 2013). There are increasing evidence that interactions induce a range of changes in RSA (Munoz-Parral et al. 2017a; Colom and Baucom 2020; Bendes and Lincoln 2021). The root system has evolved different behavioral strategies, including adjustment of growth and allocation (Figure 1; Table 1), which are often characterized by root length, angle, and biomass (Waidmann et al. 2020; Xiong et al. 2020). The main outcomes of growth are increases, decreases and no changes in biomass accumulation. Plants usually over-proliferate their roots at the expense of reduced seed production when plants share soil resources, which is known as the tragedy of the commons (Gersani et al. 2001).
In a split-root experiment, sharing soybeans (with interplant root competition) produced 85% more root mass and 30% less reproductive yield when there was no interplant root competition (Gersani et al. 2001). More phenomena about the tragedy of the commons were reported later (Maina et al. 2002; O’Brien et al. 2005; Zhu et al. 2019). Plants also adjust the lateral root number, which increases when neighboring plants were present. Other examples are theophrasti plants interact with their kins and strangers (Palmer et al. 2016). Furthermore, plants also decrease the amount of root production in response to the presence of neighbors. Cahill et al. (2010) found that Abutilon theophrasti plants adopted restricted foraging strategies when neighboring plants were present. Other examples are consistent with this result (Mommer et al. 2012; Chen et al. 2015; Broadbent et al. 2018). However, other results show that the growth of the root system depends on the availability of soil nutrients rather than on neighboring plants, that is, the ideal free distribution (Semchenko et al. 2007a; McNickle et al. 2014; Chen et al. 2021a).

All else being equal, roots preferentially grow in areas where there are no other roots (Gersani et al. 2001). Plant species, therefore, have developed a wide variety of traits that allow species to occupy different niches in specific time and specific locations, which is called niche complementarity (Faget et al. 2013). Studies reported that plant avoidance or spatial segregation during growing with neighbors creates a phenomenon of ecological niche complementarity (Schmid et al. 2015; Yang et al. 2018; Cabal et al. 2020). Spatial niche differentiation in root architecture enhances nutrient capture and biomass production in ancient maize/bean and maize/bean/squash polycultures (Postma and Lynch 2012). Many studies also observed that the root length density of the upper or deeper layer is greater in the intercropping system (Streit et al. 2019; Gong et al. 2020). There are also some examples that roots aggregate beside neighboring plants or do not respond (Fang et al. 2011, 2013; Sattler and Bartelheimer 2018). Different species and genotypes have distinct responses to flexible neighbors. Yang et al. (2018) found that Oryza sativa roots invaded closely related cultivars and avoided distantly related cultivars. Moreover, Zea mays GZ1 roots invaded their roots but avoided Glycine max HX3 roots (Fang et al. 2011). Therefore, more research is needed to elucidate the effects of adjacent plants on focal plants.

**Pathways of interactions on RSA**

Plants can detect their neighboring plants (Cahill et al. 2010; Veits et al. 2019), and distinguish each other, including self/non-self (Falik et al. 2003, 2006), kin/non-kin (Callaway and Mahall 2007; Yang et al. 2018), and conspecific/heterospecific (Fang et al. 2011; Zhang et al. 2020). The alteration of RSA is one of the outcomes of response to plant interaction. Plants do not hear, see, smell or taste, instead, they secrete root exudates and release VOCs which directly affect RSA as cues and signals, establish CMNs for transmission of those cues and signals, or indirectly shape RSA by changing soil nutrients and soil microbial community composition (Figure 2; Table 2). The complex mechanisms of the effect of interplant interactions on RSA are discussed in detail below.

**Role of root exudates in interplant interactions**

Roots secrete different substances to their surrounding environment generally described as root exudates (Walker et al. 2003; Bais et al. 2006; Biedrzycki et al. 2010). Root exudates are composed of high molecular weight compounds such as polysaccharides and proteins, and low molecular weight compounds which are further categorized as primary metabolites (e.g. sugars, amino acids and organic acids) and secondary metabolites (e.g. terpenes, flavonoids, glucosinolates and alkaloids) (Bais et al. 2006; Canarini et al. 2019; Ehlers et al. 2020; Chai and Schachtman 2022). These metabolites perform essential functions in different biological processes (Bais et al. 2006; Badri and Vivanco 2009). There is also conclusive supporting evidence that root exudates are a kind of wireless signal in cross-plant communications (Sharifi and Ryu 2021). They exist in the soil for a long time and affect coexisting neighbors and future generations by changing soil properties described as plant-soil feedback (Karlovsy 2008; Hu et al. 2018; Delory et al. 2021).

**Root exudates directly affect RSA as cues and signals**

Coexisting plants perceive chemicals released from neighbors and perform an inhibitory or stimulatory response. There is reasonable evidence that root exudates signaling is one of the most common mediators of interactions among
functions of allelochemicals is further emphasized. Furthermore, root secreted phyto-toxic substances, such as gallic acid, ferulic acid, phytocyanic acid, vanillic acid, salicyclic acid, tannic acid and hydroquinone, from tomato plant inhibited the growth of lettuce and egg seedlings (Kim and Kil 1989). In addition, the e phytotoxin (--)-catechin secreted by Centaurea maculosa is considered a weapon for successful invasion (Bais et al. 2003).

Overall, the results of these recent studies demonstrate that both root exudates and biochemicals in root exudates are considerable cues and signals in terms of root-root interaction-induced changes in RSA. However, information on signaling substances in certain biological processes remains to be characterized due to methodological limitations (Pantigoso et al. 2021). New approaches are needed to clarify root-secreted specific signaling compounds.

**Root exudates indirectly affect RSA by changing nutrients**

Root exudates can mobilize soil nutrients, such as nitrogen (N), phosphorus (P), iron (Fe), that play a crucial role in modulating RSA (Li et al. 2014; Chai and Schachtman 2022). The regulation of soil nutrition by root exudates is hence worthy of attention in root interactions on RSA.

Plants rely on foraging major nutrients from the soil, especially N and P (Oldroyd and Leyser 2020). Root exudates at a certain growth stage have a positive effect on soil nutrient mineralization (Zhao et al. 2021). Both primary and secondary metabolites affect nutrient availability. Liu et al. (2022) demonstrated that carbohydrates and organic acids promote N transformations under low fertility conditions. Liu and Murray (2016) reviewed that the root secretion of flavonoids, including flavone, coumestan, isoflavonoid, flavonol, etc., is very important for nodulation and N fixation in the below-ground. Notably, different types of flavonoids have different effects on the mineralization of nutrients. For example, luteolin (flavone) and coumestrol (coumestan, isoflavonoid) act on the nod gene (nodulation gene), but the former is an inducer and the latter is an inhibitor (Cooper 2004).

### Table 1. The phenomena of root-root interaction on RSA.

| No | Focal species | Neighboring species | Behavioral strategies of focal plants | Ref. |
|----|--------------|---------------------|--------------------------------------|------|
| 1  | Glycine max  | G. max              | Increased amount of root production  | Gersani et al. 2001 |
| 2  | Arabidopsis thaliana | A. thaliana. | Increased number of lateral roots | Biedrzycki et al. 2011; Palmer et al. 2016 |
| 3  | Pisum sativum | P. sativum           | Increased or decreased amount of root production | O’Brien et al. 2005; Chen et al. 2018 |
| 4  | Cakile edentula | C. edentula         | Increased root allocation when growing with strangers but decreased root allocation when growing with siblings | Dudley and File 2007; Bhatt et al. 2011 |
| 5  | Zea mays     | Brassica campestris, Vicia faba, Cicer arietinum or G. max | Increased or decreased total root length and growth space | Xia et al. 2013 |
| 6  | Rumex palustris, A. graminea | R. palustris, A. stolonifera | Decreased root growth | Mommer et al. 2012 |
| 7a | V. faba/Triticum aestivum | T. aestivum/V. faba | Shallower roots within own row and deeper within neighboring’s row | Streit et al. 2019 |
| 8  | Panicum miliaceum | Vigna radiata         | Increased root biomass and greater root length density in the upper soil | Gong et al. 2020 |
| 9  | Glechoma hederacea | G. hederacea and Fragaria vesca | Root avoidance | Semchenko et al. 2007b |
| 10 | Z. mays      | G. max               | Root avoidance                        | Fang et al. 2011 |
| 11 | Hieracium pilosella | Capsella rubella or Cardamine hirsuta | Root segregation                     | Schmid et al. 2015 |
| 12 | Capsicum annuum | C. annuum            | Root exploitative segregation        | Cabal et al. 2020 |
| 13 | Oryza sativa | O. sativa            | Root avoidance or overlap             | Fang et al. 2013; Yang et al. 2018 |
| 14 | Abutilon theophrasti | A. theophrasti         | Decreased amount of roots towards neighboring plants | Callih et al. 2010 |
| 15a| Z. mays/G. max | A. theophrasti         | Root aggregation towards neighboring plants | Fang et al. 2011 |

*, the left and right of ‘/’ represent two combinations, respectively.
However, isoflavones did not affect rhizobia signaling in red clover in a recent study (Weston and Mathesius 2013), which suggested that species identity may be associated with the effect of flavonoids on N fixation. Root exudates can facilitate P uptake as well (Li et al. 2003). The release of protons, carboxylates, and enzymes are the main pathways that facilitate P capture (Li et al. 2014). For example, the exudation of organic acid and acid phosphatase from faba bean and chickpea roots enhanced the absorption of P in maize plants (Li et al. 2004, 2007; Zhang et al. 2020).

Trace elements, such as Fe, are also essential for plant growth (Gallego et al. 2012; Colombo et al. 2014). In Leguminosae/Gramineae intercropping, gramineous plants may be used to absorb Fe nutrition in alkaline soils (Dai et al. 2019). The reason could be that the gramineous plants release Fe carriers and bind Fe (III) to increase the effectiveness of Fe (Xiong et al. 2013). Similar results were obtained in A. thaliana (Sisó-Terraza et al. 2016a). Flavins exuded by Beta vulgaris can also improve the availability of Fe (Sisó-Terraza et al. 2016b). Furthermore, the acidification of the rhizosphere caused by proton efflux can increase the absorption of Fe by plants (Marschner and Römheld 1994). Moreover, the secretion of organic acids can alleviate the toxic effects of Al (Ma et al. 2001).

In short, the substances secreted by the roots can affect RSA, including root biomass (Zhang et al. 2016; van Dijk et al. 2021; Wang et al. 2021), root length (Kumar et al. 2020; Xia et al. 2020), lateral root number (Drew 1975; Pongrac et al. 2020), and root horizontal and vertical distribution (Liu et al. 2015; Zhang et al. 2020). Therefore, we speculate that root exudates can indirectly affect RSA by changing soil nutrients.

**Root exudates indirectly affect RSA by altering soil microbial community**

Plants can interact with neighboring plants and soil microorganisms by producing different chemical components. Another situation to be considered is that since root exudates are the main source of energy for microorganisms, they play a key role in the root recruitment and assembly of microorganisms (Berendsen et al. 2012; Carvalhais et al. 2015).
Root exudates can stimulate positive interactions with soil microorganisms, which contribute to plant resource absorption, stress tolerance and pathogen defense (Sasse et al. 2018). It has been proposed in the previous section that flavonoids are useful for N fixation, which is related to the interaction between roots and N-fixing bacteria (Liu and Murray 2016; Li et al. 2016a; Liu et al. 2017). Simultaneously, the symbiotic system of legumes usually requires a large amount of P, and the citrate secreted by the root chelates Ca\(^{2+}\) then P is released from the Ca-P complex, which improves the N fixation capacity of root nodules (Mei et al. 2012). Moreover, exudates of Michelia macclurei improved root growth and placement of Cunninghamia lanceolata through shaping microorganisms for P acquisition (Xia et al. 2016). Therefore, we conclude that microbes can mediate root foraging during interplant interaction. Furthermore, the composition and content of root exudates can change under biotic and abiotic stress conditions (Henry et al. 2007; Ksouri et al. 2007; Mithöfer and Boland 2012; Hoysted et al. 2018), and altered root exudates can further induce changes in soil microbial composition (Bezemier and van Dam 2005). For instance, plants release specific root exudates to promote the colonization of plant growth-promoting bacteria (PGPR), thereby stimulating plant growth (Vives-Peris et al. 2018). This is consistent with the view of Chen et al. (2019) who found that T. aestivum recruited PGPRs to trade off the growth and development at different stages. In addition, root exudates can also act on the pathogen that interferes with the defense system of the plant (Baetz and Martinoina 2014).

Previously, it has been reported that soil microbes, such as PGPRs, can improve root performance effectively (Alzate Zuluaga et al. 2021). Moreover, microbial community assembly is dependent on root exudates and its chemical structure (Yuan et al. 2018; Zhalina et al. 2018; Kudjordjie et al. 2019; Kawasaki et al. 2021; Wen et al. 2022). These results indicated that different components of root exudates may recruit different microorganisms to cause different root system responses under different growth conditions.

### Role of VOCs in interplant interactions

Root exudates are usually secreted in the form of water. In contrast, VOCs are typically released as airborne signals. Plants emit a large amount of VOCs into the surrounding environment when they encounter herbivorous animals, pathogens or mechanical damage, which mediates the plant-plant interactions (Sugimoto et al. 2014; Coppola et al. 2017; Ninkovic et al. 2019, 2021). VOCs as signals are important for the success of plants. For example, the parasitic plant Cuscuta pentagona makes use of VOCs for host location and host selection to adjust their growth (Runyon et al. 2006). Apart from these, Ninkovic (2003) found that volatile profiles also have an impact on biomass allocation. So, the question is raised whether VOCs can modulate RSA?

Increased interest has been found in the belowground plant-environment interactions. Munoz-Parrá et al. (2017b) found that VOCs may be perceived by neighboring plants and regulate root physiology and morphological behavior. Centaurea stoebe root VOCs are beneficial for the germination and growth of different neighboring plants in the same domain (Gfeller et al. 2019). However, different VOCs components and concentrations have different effects. For instance, the volatile 6-pentyl-2H-pyran-2-one promoted lateral root formation (Garnica-Vergara et al. 2016). The VOCs also have an impact on primary root growth. However, different VOCs components and concentrations have different effects. For instance, the volatile 6-pentyl-2H-pyran-2-one restrained primary root growth (Garnica-Vergara et al. 2016). The volatile N,N-dimethyl-hexadecylamine also regulated primary root length, enhancing at low concentrations but inhibiting at high concentrations in A. thaliana (Vázquez-Chimalhuah et al. 2021). Meanwhile, the physiological situations aboveground affect the secretion of VOCs belowground (Rostás et al. 2015). Root VOCs further reshape microbial

---

**Table 2. The examples of root-root interaction on RSA via root exudates, VOCs and CMNs.**

| No. | Passways of interactions on RSA | Description | Ref. |
|-----|--------------------------------|-------------|------|
| 1   | Root exudates: (-)-catechin | (-)-catechin exuded by Centaurea maculosa decreased the growth of Festuca idahoensis, Koeleria micrantha and Arabidopsis thaliana. | Bais et al. 2003 |
| 2   | Root exudates: benzoic, caffeic, chlorogenic, ferulic, salicylic acid | Benzoic, caffeic, ferulic and salicylic acid decreased fresh weight of Solanum lycopersicum, and chlorogenic, ferulic and salicylic acid discolored roots. | Jung et al. 2004 |
| 3   | Root exudates: meta-Tyrosine | Multiple fine fescue cultivars and related root exudates meta-Tyrosine decreased lettuce root length. | Bertin et al. 2007 |
| 4   | Root exudates | A. thaliana had more lateral roots in strangers (non-siblings) than in sibling root exudates, yet had shorter roots in the sibling or stranger root exudates than in its own root exudates. | Biedrzycki et al. 2010; Biedrzycki et al. 2011 |
| 5   | Root exudates | Deschampsia caespitosa had greater root length density; in the treatment with root exudates (comparing to the treatment with control solutions), in the treatment with root exudates of unrelated individuals from the same population (comparing to the treatment with root exudates of related individuals from the same population), in the treatment with root exudates of conspecifics from the same community (comparing to the treatment with root exudates of heterospecifics from the same community). | Semchenko et al. 2014 |
| 6   | Root exudates | A. thaliana Col-0 and LA-1 had more lateral roots in the stranger populations or corresponding root exudates than those in kin populations or relevant root exudates in the low nutrient conditions. | Palmer et al. 2016 |
| 7   | Root exudates | The root exudates from weeds induced Triticum aestivum or Oryza sativa to release certain root exudates that decreased the growth of weeds. | Kong et al. 2018; Yang et al. 2018 |
| 8   | Root exudates | The soil solution of four grass species or four forb species decreased root foraging of Dianthus deltoides. | Delony et al. 2021 |
| 9   | VOCs: sesquiterpenes (E)-β-caryophyllene | Root VOCs of Centaurea stoebe increased germination growth of sympatric neighbors. | Gfeller et al. 2019 |
| 10  | CMNs | Dicymbe corymbosa had greater growth and survivorship with access to an ECM network than which without such access. | McGuire 2007 |

VOCs: volatile organic compounds; CMNs: common mycorrhizal networks; RSA: root system architecture.
community assembly (Kong et al. 2021). The exposure of tomato leaves to Bacillus amyloliquefaciens strain GB03-released β-caryophyllene elicited the release of SA from the root, which reassembled the composition of the rhizosphere microbial community (Kong et al. 2021). These results suggest that VOCs have important implications for subsurface plant-microbe interactions.

It can be concluded from these findings that VOCs, both above- and belowground, can affect root architecture and soil microorganisms. However, whether VOCs can affect RSA of the neighboring plants by influencing microorganisms is not well understood.

**Role of CMNs in interplant interactions**

Researchers showed that the connection established by fungal hyphae through the root cells is known as CMNs (Genre et al. 2005; Bever et al. 2010). CMNs can promote plant growth, facilitate effective nutrient exchange and affect the composition of plants and soil microbial communities (Wipff et al. 2019; Sharifi and Ryu 2021).

Arbuscular mycorrhizal (AM) fungi, a class of microorganisms widely found in terrestrial ecosystems, can form symbiosis with most higher plants (Smith and Read 2008), which strongly regulates RSA and thereby promotes plant growth and development (Gutjahr and Paszkowski 2013). According to Sun et al. (2015), AM fungus Gigaspora margarita spores release volatiles and exudates that significantly affects lateral root formation in Lotus japonicus and A. thaliana. RNA-sequencing analysis revealed that AM regulates lateral root formation of Poncirus trifoliate and Camellia sinensis, associated with the hormone pathways and the nutrient pathways (Chen et al. 2017, 2021b). However, after AM fungal treatment, different hormones had different effects on lateral root formation, with auxin being positive and ethylene being negative (Chen et al. 2017, 2021b). Moreover, studies also showed that inoculation with AM fungi significantly increased the number of root hairs of Poncirus trifoliate, which was also associated with hormones and nutrient signaling (Wu et al. 2016). Some studies confirmed that AM fungal mycelium can obtain nutrients (such as N, P, etc.) from the soil and transmit them to the host plant (Ryan et al. 2012; Walder et al. 2012). Other reports also indicated the importance of hormone and nutrient signals for RSA (Giehl et al. 2014; McClure et al. 2017; Shahzad and Antmann 2017). Our existing knowledge also suggests that AM fungi can mobilize bacteria through fungal hyphae (Simon et al. 2015; Otto et al. 2017). A study found that AM fungal hyphae has dispersal networks that can transport phosphate solubilizing bacteria for the mineralization of organic phosphorus (Jiang et al. 2021). In addition, ectomycorrhizal (EM) fungi, another class of microorganisms that can form mycorrhizal networks belowground. Mycorrhizal network formed by EM fungi mediates interspecific communication between Betula papyrifera and Pseudotsuga menziesii (Simard et al. 1997). Another report showed that EM fungi stimulated lateral root production by synthesizing sesquiterpenes (Ditengou et al. 2015).

Combine mentioned information earlier, mineral nutrients and microorganisms affect RSA. Thence it has been noted that CMNs benefit from the reprogramming of RSA through releasing chemicals or reshaping nutrients and microorganisms in the soil.

**Conclusion and future directions**

As the work reviewed here shows that root-root interactions, to a large extent, dominate the fate of the plant’s success as a result of the central role of roots in foraging water and nutrients. Root-root interactions can be positive, neutral or negative and roots show outcomes of over-proliferation, decreased amount of root production, and vertical and horizontal asymmetry, etc. Root exudates, VOCs, and CMNs contribute important roles in the strategic processes of interactions on RSA directly or perhaps indirectly. However, some questions have not been answered yet and future studies are needed to investigate the detailed interactions among root exudates, VOCs, CMNs and RSA.

Social interactions usually exist in agriculture and natural ecosystems. So far, most of the studies of cross-plant interactions are carried out in greenhouses or controlled conditions. Therefore, a general universal understanding of interactions on RSA in the field remains to be found. Moreover, the composition of root exudates is complex and exudates are difficult to extract and characterize due to method and technical limitations (Canarin et al. 2019; Ehlers et al. 2020; Williams et al. 2021). Thus, what signal molecules and what functions in root exudates need to be further confirmed in the interactions on RSA. Furthermore, it is well understood that root exudates, VOCs and CMNs interact with each other (Li et al. 2020; Tian et al. 2021). Root structure and function affect plant exudation and nutrient absorption (McKay Fletcher et al. 2020; Sun et al. 2021). However, whether these interactions affect RSA requires further investigation.

**Disclosure statement**

No potential conflict of interest was reported by the author(s).

**Funding**

This work was supported by the National Natural Science Foundation of China [grant number 31872156].

**Notes on contributors**

- **Xiu Zhang** is a PhD student at the College of Horticulture and Landscape Architecture, Northeast Agricultural University, Harbin, P. R. China. She researches effects of root interactions on root architecture and the mediation of root exudates within it.

- **Jingfan Yan** is a postgraduate student at the College of Horticulture and Landscape Architecture, Northeast Agricultural University, Harbin, P. R. China. She researches the effects of root interactions on root system architecture under different nutrient conditions.
Muhammad Khashi u Rahman is a PhD student at the College of Horticulture and Landscape Architecture, Northeast Agricultural University, Harbin, P. R. China. He researches mediums of plant interactions, particularly chemistry and functioning of root exudates.

Fengzhi Wu, an Associate Professor at the College of Horticulture and Landscape Architecture, Northeast Agricultural University, Harbin, P. R. China, is specialized in the prevention and control of soil-borne diseases and efficient utilization of nutrients. Some key technologies for safe production have been well applied.

References

Alzate Zuluaga MY, Martinez de Oliveira AL, Valentinuzzi F, Tiziani R, Pii Y, Memmo T, Cesco S. 2021. Can inoculation with the bacterial biostimulant Enterobacter sp. strain 15S be an approach for the smarter P fertilization of maize and cucumber plants? Front Plant Sci. 12:7919873.

Badri DV, Vivanco JM. 2009. Regulation and function of root exudates. Plant Cell Environ. 32(6):666–681.

Bartz U, Martinioa E. 2014. Root exudates: the hidden part of plant defense. Trends Plant Sci. 19(2):90–98.

Bais HP, Vepachedu R, Gilroy S, Vivanco JM. 2003. Allelopathy and exotic plant invasion: from molecules and genes to species interactions. Science. 301(5638):1377–1380.

Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM. 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. Annu Rev Plant Biol. 57:233–266.

Baldwin IT, Hallitschke R, Paschold A, von Dahl CC, Preston CA. 2006. Volatile signaling in plant-plant interactions: “talking trees” in the genomics era. Science. 311(5762):812–815.

Belter PR, Caihlf JJ, Jr. 2015. Disentangling root system responses to neighbours: identification of novel root behavioural strategies. AoB Plants. 7:plv059.

Bendes MS, Lincoln NK. 2021. Impressions of underground competition and establishment on growth and root architecture of breadfruit (Artocarpus altissimus) and māmaki (Pipturus albidus). Rhizosphere. 18:100337.

Berendse RL, Pieterse CMI, Bakker PAHM. 2012. The rhizosphere microbiome and plant health. Trends Plant Sci. 17(8):478–486.

Bertin C, Weston LA, Huang J, Lamb EG, Orwin KH. 2018. Belowground competition drives invasive plant impact on native species regardless of nitrogen availability. Oecologia. 186(2):577–587.

Bilas RD, Bretman A, Bennett T. 2021. Friends, neighbours and enemies: an overview of the communal and social biology of plants. Plant Cell Environ. 44(4):997–1013.

Broadbent A, Stevens CJ, Pelzter DA, Ostle NJ, Orwin KH. 2018. Belowground competition drives invasive plant impact on native species regardless of nitrogen availability. Oecologia. 186(2):577–587.

Cabal C, Martinez-Garcia R, Auclair A, Vallades F, Pacala SW. 2020. The exploitive segregation of plant roots. Science. 370(6521):1197–1199.

Cahill JF, Jr, McNickle GG, Haag JJ, Lamb EG, Orwin KH. 2019. Root exudation of primary metabolites: mechanisms and their roles in plant responses to environmental stimuli. Front Plant Sci. 10:157.

Carvalhais LC, Dennis PG, Badri DV, Kidd BN, Schenk PM. 2015. Linking jasmonic acid signaling, root exudates, and rhizosphere microorganisms. Mol Plant Microbe Interact. 28(9):1049–1058.

Chai YN, Schachtman DP. 2022. Root exudates impact plant performance under abiotic stress. Trends Plant Sci. 27(1):80–91.

Chen BJ, During HJ, Vermeulen PJ, Kroon H, Poorter H, Anten NP. 2015. Correlations for rooting volume and plant size reveal negative effects of neighbour presence on root allocation in pea. Funct Ecol. 29:1383–1391.

Chen BJW, Huang L, During HJ, Wang X, Wei J, Anten NPR. 2021a. No neighbour-induced increase in root growth of soybean and sunflower in mesh-divider experiments after controlling for nutrient concentration and soil volume. AoB Plants. 13(3):plab020.

Chen S, Waghmode TR, Sun R, Kuramata EE, Hu C, Liu B. 2019. Root-associated microbiomes of wheat under the combined effect of plant development and nitrogen fertilization. Microbiome. 7(1):136.

Chen W, Li J, Zhu H, Xu P, Chen J, Yao Q. 2017. Arbuscular mycorrhizal fungus enhances lateral root formation in P. trifoliate (L.) as revealed by RNA-seq analysis. Front Plant Sci. 8:2039.

Chen W, Ye T, Sun Q, Niu T, Zhang J. 2021b. Arbuscular mycorrhizal fungus alters root system architecture in C. sinensis as revealed by RNA-seq analysis. Front Plant Sci. 12:777357.

Colombo SM, Baucom RS. 2020. Belowground competition can influence the evolution of root traits. Am Nat. 195(4):577–590.

Colombo C, Palumbo G, He JZ, Pinton R, Cesco S. 2014. Review on iron availability in soil: interaction of Fe minerals, plants, and microbes. J Soils Sediments. 14:538–548.

Cooper JE. 2004. Multiple responses of rhizobia to flavonoids during legume root infection. Adv Bot Res. 41(18):1–62.

Coppola M, Cascione P, Madonna V, Lelio ID, Esposito F, Avitabile C, Romaneli A, Guerrieri E, Vittiello A, Pennacchio F. 2017. Plant-to-plant communication triggered by systemin primes anti-herbivore resistance in tomato. Sci Rep. 7(1):13522.

Crepy MA, Casal JJ. 2015. Photoreceptor-mediated kin recognition in plants. New Phytol. 205(3):329–338.

Dai J, Qiu W, Wang NQ, Wang TQ, Nakashishi H, Zuo YM. 2019. From Leguminosae/Graminaceae intercropping systems to see benefits of intercropping on iron nutrition. Front Plant Sci. 10:605.

Delory BM, Schempp H, Spachmann SM, Störzer L, van Dam NM, Temperton VM, Weinhold A. 2021. Soil chemical legacies trigger species-specific and context-dependent root responses in later arriving plants. Plant Cell Environ. 44(4):1215–1230.

Ditengou FA, Muller A, Rosenkranz M, Felten J, Lasok H, van Doorn EB. 2018. Plant secondary metabolites in rhizosphere interactions with plants and other organisms. Annu Rev Plant Biol. 57:233–266.

Drew MC. 1975. Comparison of e...

Ehlers BK, Berg MP, Staudt M, Holmstrup M, Glavind M, Maders B, Eilers J, Tomillo M, Sadsen RB, Slotsbo S, Madsen PA. 2020. Plant secondary compounds in soil and their role in belowground species interactions. Trends Ecol Evol. 35(8):716–730.
Faget M, Nagel KA, Walter A, Herrera JM, Jahnke S, Schurr U, Tempeerton VM. 2013. Root–root interactions: extending our perspective to be more inclusive of the range of theories in ecology and agriculture using in-vivo analyses. Ann Bot. 112 (2):253–266.

Falik O, de Kroon H, Novoplansky A. 2006. Physiologically-mediated self/non-self root discrimination in Trifolium repens has mixed effects on plant performance. Plant Signal Behav. 1(3):116–121.

Falik O, Mordoch Y, Ben-Natan D, Yanunu M, Goldstein O, Novoplansky A. 2012. Plant responsiveness to root-root communication of stress cues. Ann Bot. 110(2):271–280.

Falik O, Reides P, Gersani M, Novoplansky A. 2003. Self/non-self discrimination in roots. J Ecol. 91:525–531.

Fang SQ, Clark RT, Zheng Y, Iyer-Pascuzzi AS, Weitz JS, Kochian LV, Edelsbrunner H, Liao H, Beney PN. 2013. Genotypic recognition and spatial responses by rice roots. Proc Natl Acad Sci U S A. 110 (7):2670–2675.

Fang SQ, Gao X, Deng Y, Chen XP, Liao H. 2011. Crop root behavior coordinates phosphorus status and neighbors: from field studies to three-dimensional in situ reconstruction of root system architecture. Plant Physiol. 155(3):1277–1285.

Gallego SM, Pena LB, Barcia RA, Azpilicueta CE, Iannone MF, Rosales EP, Zawoznik MS, Groppa MD, Benavides MP. 2012. Unravelling cadmium toxicity and tolerance in plants: insight into regulatory mechanisms. Environ Exp Bot. 83:33–46.

García-Vergara A, Barrera-Ortiz S, Muñoz-Parra E, Raya-González J, Méndez-Bravo A, Macias-Rodríguez L, Ruiz-Herrera LF, López-Bucio J. 2016. The volatile 6-pentyl-2H-pyran-2-one from Trichoderma atroviride regulates Arabidopsis thaliana root morphogenesis via auxin signaling and ETHYLENE INSENSITIVE 2 function. New PhytoL. 209(4):1496–1512.

Genre A, Chabaud M, Timmers T, Bonfante P, Barker DG. 2005. Interspecific discrimination of root system architecture to improve performance and resistance. Trends Plant Sci. 10(7):267–274.

Gersani M, Brown JS, O’Brien EE, Abramsky MZ. 2001. Tragedy of the commons as a result of root competition. J Ecol. 89(4):660–669.

Geffler V, Huber M, Forster C, Huang W, Kollner TG, Erb M. 2019. Root volatiles in plant-plant interactions: I. High root sesquiterpene release is associated with increased germination and growth of plant neighbours. Plant Cell Environ. 42(6):1950–1963.

Giehl RF, Gruber BD, von Wirén N. 2014. The volatile ethylene nonyl glycolic acid in barnyardgrass-induced rice allelopathy. J Exp Bot. 65(679):778–788.

Gong XW, Dang K, Lv S, Zhao G, Tian LX, Luo Y, Feng BL. 2020. Interspecific root interactions and water-use efficiency of intercropped proso millet and mung bean. Eur J Agron. 115:126034.

Gupta C, Paszkowski U. 2013. Multiple control levels of root system remodeling in arbuscular mycorrhizal symbiosis. Front Plant Sci. 4:204.

Helleviun E, Binet F, Klärzyński O, Hallin S, Juhanston J, Daburon V, Monard C. 2021. Shaping of soil microbial communities by plants does not translate into specific legacy effects on organic carbon mineralization. Soil Biol Biochem. 163:108449.

Henry A, Doucette W, Norton J, Bugbee B. 2007. Changes in crested wheatgrass growth caused by drought, flood, and nutrient stress. J Environ Qual. 36(3):904–912.

Hochholdinger F, Marcon C, Baldauf JA, Yu P, Frey FP. 2018. Proteomics of maize root development. Front Plant Sci. 9:143.

Holz M, Zarebanadkouki M, Kuzaykov Y, Pausch J, Carminati A. 2018. Root hairs increase rhizosphere extension and carbon input to soil. Ann Bot. 121(1):61–69.

Hoysta GD, Bell CA, Lilley CJ, Urwin PE. 2018. Apidiph colonization affects the root exudate composition and the hatching of a soil borne pathogen. Front Plant Sci. 9:1278.

Hu LF, Robert CAM, Cadot S, Zhang X, Ye M, Li BB, Manzo D, Chervet N, Steinger T, van der Heijden MGA, et al. 2018. Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. Nat Commun. 9(1):2738.

Jiang F, Zhang L, Zhou J, George TS, Feng G. 2021. Arbuscular mycorrhizal fungi enhance mineralisation of organic phosphorus by carrying bacteria along their extraradical hyphae. New Phytol. 230 (1):304–315.

Jung V, Olsson E, Caspersen S, Asp H, Jensén P, Alsanius B. 2004. Response of young hydroponically grown tomato plants to phenolic acids. Sci Hortic. 100(4):23–37.

Karlovsky P. 2008. Secondary metabolites in soil ecology. Berlin Heidelberg: Springer.

Kawasaki A, Dennis PG, Forstner C, Raghavendra AKH, Mathiesus U, Richardson AE, Delhaize E, Gillimath W, Matt M, Ryan PR. 2021. Manipulating exudate composition from root apices shapes the microbiome throughout the root system. Plant Physiol. 187 (4):2279–2295.

Khatri u Rahman M, Zhou XG, Wu FZ. 2019. The role of root exudates, CMNs, and VOCs in plant–plant interaction. J Plant Interact. 14 (1):630–636.

Kim YS, Kil BS. 1989. Identification and growth inhibition of phytotoxic substances from tomato plant. Korean J Bot. 32 (1):41–49.

Kong CH, Zhang SZ, Li YH, Xia ZG, Yang XF, Meiners SJ, Wang P. 2018. Plant neighbor detection and allelochemical response are driven by root-secreted signaling chemicals. Nat Commun. 9(1):3867.

Kong HG, Song GC, Sim HJ, Ryu CM. 2021. Achieving similar root microbiota composition in neighbouring plants through airborne signalling. ISME J. 15(2):397–408.

Kouni R, Meglièche W, Debea A, Faléh H, Grignon C, Abdelly C. 2007. Salinity effects on polyphenol content and antioxidant activities in leaves of the halophyte Cakile maritima. Plant Physiol Biochem. 45 (3-4):244–249.

Kudjordjie EN, Sapkota R, Steffens SK, Fomsgaard IS, Nicolaisen M. 2019. Maize synthesized benzoazoxinoids affect the host associated microbiome. Microbiome. 7(1):59.

Kumar A, Duijnen RV, Delory BM, Reichel R, Tempeerton VM. 2020. Barley shoot biomass responds strongly to N:P stoichiometry and intraspecific competition, whereas roots only after their foraging. Plant Soil. 453:515–528.

Leavitt RG. 1901. Predetermined root-hair cells in Azolla and other plants. Science. 13(339):1030–1031.

Li B, Li YY, Wu HM, Zhang FF, Li CJ, Li XX, Lambers H, Li L. 2016a. Root exudates drive interspecific facilitation by enhancing nodulation and N2 fixation. Proc Natl Acad Sci U S A. 113(23):6496–6501.

Li L, Li SM, Sun JH, Zhou LL, Bao XG, Zhang HG, Zhang FS. 2007. Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. Proc Natl Acad Sci U S A. 104(27):11192–11196.

Li L, Tang CX, Rengel Z, Zhang FS. 2003. Chickpea facilitates phosphorus uptake by intercropped wheat from an organic phosphorus source. Plant Soil. 248(2):297–303.

Li L, Tilman D, Lambers H, Zhang FS. 2014. Plant diversity and over-yielding: insights from belowground facilitation of intercropping in agriculture. New Phytol. 203(1):63–69.

Li LL, Zhao HH, Kong CH. 2019. (-)-Loliolide, the most ubiquitous lactone, is involved in barnyardgrass-induced rice allelopathy. J Exp Bot. 71(4):1540–1550.

Li SM, Li L, Zhang FS, Tang C. 2004. Acid phosphatase role in chickpea/maize intercropping. Ann Bot. 94(2):297–303.

Li XG, Yang Z, Zhang YN, Yu L, Wang XX. 2020. Atractyloides lancea volatiles induce physiological responses in neighboring peanut plant during intercropping. Plant Soil. 453:409–422.

Li X, Zeng BS, Liao H. 2016b. Improving crop nutrient efficiency through root architecture modifications. J Integr Plant Biol. 58 (3):193–202.

Li YH, Xia ZC, Kong CH. 2016c. Allelobiosis in the interference of allelopathic weed with weeds. Pest Manag Sci. 72(11):2146–2153.

Liu CW, Murray JD. 2016. The role of flavonoids in nodulation host-range specificity: an update. Plants (Basel). 5(3):33.

Liu D. 2021. Root developmental responses to phosphorus nutrition. J Integr Plant Biol. 63(6):1065–1090.

Liu Y, Evans SE, Friessen ML, Tiemann LK. 2022. Root exudates shift effects on organic carbon mineralization contribute to the plant-available N supply in low fertility soils. Soil Biol Biochem. 165:108541.

Liu YC, Qin XM, Xiao JX, Tang L, Wei CZ, Wei JJ, Zheng Y. 2017. Intercropping influences component and content change of flavonoids in root exudates and nodulation of Faba bean. J Plant Interact. 12(1):187–192.
Liu YX, Zhang WP, Sun JH, Li XF, Christie P, Li H. 2015. High morphological and physiological plasticity of wheat roots is conducive to higher competitive ability of wheat than maize in intercropping systems. Plant Soil. 397(1-2):387–399.

Lynch J. 1995. Root architecture and plant productivity. Plant Physiol. 109(1):7–13.

Lynch JP. 2013. Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. Ann Bot. 112(2):347–357.

Ma JF, Ryan PR, Delhaize E. 2001. Aluminium tolerance in plants and the complex role of organic acids. Trends Plant Sci. 6(6):273–278.

Maina GG, Brown JS, Gersani M. 2002. Intra-plant versus inter-plant root competition in beans: avoidance, resource matching or tragedy of the commons. Plant Ecol. 160(2):235–247.

Marschner H, Römheld V. 1994. Strategies of plants for acquisition of iron. Plant Soil. 165:261–274.

McCleery WT, Mohd-Radzman NA, Grieneisen VA. 2017. Root branching plasticity: collective decision-making results from local and global signalling. Curr Opin Cell Biol. 44:51–58.

McGuire KL. 2007. Common ectomycorrhizal networks may maintain monodominance in a tropical rain forest. Ecology. 88(3):567–574.

McKay Fletcher DM, Ruiz S, Dias T, Petresolii C, Roose T. 2020. Linking root structure to functionality: the impact of root system architecture on citrate-enhanced phosphate uptake. New Phytol. 227(2):376–391.

McNichol GG, Brown JS, Schwinnin S. 2014. An ideal free distribution explains the root production of plants that do not engage in a tragedy of the commons game. J Ecol. 102(4):963–971.

Mei P-P, Gui L-G, Wang P, Huang J-C, Long H-Y, Christie P, Li L. 2012. Maize/faba bean intercropping with rhizobia inoculation enhances productivity and recovery of fertilizer P in a reclaimed desert soil. Field Crops Res. 130:19–27.

Mithöfer A, Boland W. 2012. Plant defense against herbivores: chemical aspects. Annu Rev Plant Biol. 63:431–450.

Mommer L, van Ruijven J, Cansen C, van de Steeg HM, de Kroon H. 2012. Interactive effects of nutrient heterogeneity and competition: implications for root foraging theory? Funct Ecol. 26(1):66–73.

Munoz-Parras E, Pelagro-Flores R, Raya-Gonzalez J, Salmeron-Barrera G, Ruiz-Herrera LF, Valencia-Cantero E, Lopez-Bucio J. 2017a. Plant-plant interactions influence developmental phase transitions, grain productivity and root system architecture in Arabidopsis via auxin and PFT1/MED25 signalling. Plant Cell Environ. 40(9):1887–1899.

Munoz-Parras E, Salmeron Barrera G, Ruiz-Herrera LF, Valencia-Cantero E, Lopez-Bucio J. 2017b. Self-plant perception via long-distance signaling. Plant Signal Behav. 12(12):e140218.

Nettan S, Thelhoff M, Lepik A, Semchenko M, Zobel K. 2019. Manipulation of vegetation with activated carbon reveals the role of root exudates in shaping native grassland communities. J Veg Sci. 30(6):1056–1067.

Ninkovic V. 2003. Volatile communication between barley plants affects biomass allocation. J Exp Bot. 54(389):1831–1839.

Ninkovic V, Markovic D, Rensing M. 2021. Plant volatiles as cues and signals in plant communication. Plant Cell Environ. 44(4):1030–1043.

Ninkovic V, Rensing M, Dahlin I, Markovic D. 2019. Who is my neighbor? Volatile cues in plant interactions. Plant Signal Behav. 14(9):1887–1899.

O’Brien EE, Gersani M, Brown JS. 2005. Root proliferation and seed yield in relation to spatial heterogeneity of below-ground competition. New Phytol. 168(2):401–412.

Oldroyd GED, Leyser O. 2020. A plant’s diet, surviving in a variable nutrient environment. Science. 368(6486):eaab0196.

Otto S, Bruni EP, Harms H, Wick LY. 2017. Catch me if you can: disentangling root foraging patterns in two clonal species. New Phytol. 204(3):631–647.

Postma JA, Lynch JP. 2012. Complementarity in root architecture for nutrient uptake in ancient maize/bean and maize/bean/squash polycultures. Ann Bot. 110(2):521–534.

Rogers ED, Benfey PN. 2015. Regulation of plant root system architecture: implications for crop advancement. Curr Opin Biotechnol. 32:93–98.

Rostás M, Cripps MG, Silcock P. 2015. Aboveground endophyte affects root volatile emission and host plant selection of a belowground insect. Oecologia. 177(2):467–497.

Runyon J, Mescher M, De Morais C. 2006. Volatile chemical cues guide host location and host selection by parasitic plants. Science. 313(5795):1964–1967.

Ryan MH, Tibbett M, Edmonds-Tibbett T, Suriyagoda LD, Lambers H, Cawthray GR, Pang J. 2012. Carbon trading for phosphorus gain: the balance between rhizosphere carbohydrates and arbuscular mycorrhizal symbiosis in plant phosphorus acquisition. Plant Cell Environ. 35(12):2170–2180.

Sasse J, Martinieva E, Northen T. 2018. Feed your friends: do plant exudates shape the root microbiome? Trends Plant Sci. 23(1):25–41.

Sattah SB, Ristova D, Busch W. 2015. Underground tuning: quantitative regulation of root growth. J Exp Bot. 66(4):1099–1112.

Sattler J, Bartelheimer M. 2018. Root responses to legume plants integrate information on nitrogen availability and neighbour identity. Basic Appl Ecol. 27:51–60.

Schandry N, Becker C. 2020. Allelopathic plants: models for studying plant-interkingdom interactions. Trends Plant Sci. 25(2):176–185.

Schmid C, Bauer S, Bartelheimer M. 2015. Should I stay or should I go? Roots segregate in response to competition intensity. Plant Soil. 391:283–291.

Semchenko M, Hutchings MJ, John EA. 2007a. Challenging the tragedy of the commons in root competition: confounding effects of neighbour presence and substrate volume. J Ecol. 95(2):252–260.

Semchenko M, John EA, Hutchings MJ. 2007b. Effects of physical connection and genetic identity of neighbouring ramets on root-placement patterns in two clonal species. New Phytol. 176(3):644–654.

Semchenko M, Saar S, Lepik A. 2014. Plant root exudates mediate neighbour recognition and trigger complex behavioural changes. New Phytol. 204(3):631–637.

Shahzad Z, Amtmann A. 2017. Food for thought: how nutrients regulate root system architecture. Curr Opin Plant Biol. 39:80–87.

Sharifi R, Ryu CM. 2021. Social networking in crop plants: wired and wireless cross-plant communications. Plant Cell Environ. 44(4):1095–1110.

Simard SW, Jones MD, Durall DM, Perry DA, Myrold DD, Molina R. 2012. Maize/faba bean intercropping with rhizobia inoculation enhances productivity and recovery of fertilizer P in a reclaimed desert soil. Field Crops Res. 130:19–27.

Simon A, Bindschedler S, Job D, Wick LY, Filippidou S, Kooli WM, Runyon J, Mescher M, De Morais C. 2020. Volatile chemical cues guide host location and host selection by parasitic plants. Science. 313(5795):1964–1967.

Smith SE, Read FD. 2008. Mycorrhizal symbiosis. 3rd ed. San Diego (CA): Academic Press.

Streit J, Meinen C, Rauber R. 2019. Intercropping effects on root distribution of eight novel winter faba bean genotypes mixed with winter wheat. Field Crop Res. 235:1–10.

Sugimoto K, Matsui K, Jijima Y, Akakabe Y, Muramoto S, Ozawa R, Uefune M, Sasaki R, Alamgir KM, et al. 2014. Intake of phosphorus by wheat and barley presence and substrate volume. J Ecol. 95(2):252–260.

Stephens GM, Postma JA, Lynch JP. 2012. Complementarity in root architecture for nutrient uptake in ancient maize/bean and maize/bean/squash polycultures. Ann Bot. 110(2):521–534.

Streit J, Meinen C, Rauber R. 2019. Intercropping effects on root distribution of eight novel winter faba bean genotypes mixed with winter wheat. Field Crop Res. 235:1–10.

Sudhakar K, Matsui K, Jijima Y, Akakabe Y, Muramoto S, Ozawa R, Uefune M, Sasaki R, Alamgir KM, Akitake S, et al. 2014. Flavins secreted by roots of iron-deficient Beta vulgaris enable mining of ferric oxide via reductive mechanisms. New Phytol. 209(2):733–745.

Smith SE, Read FD. 2008. Mycorrhizal symbiosis. 3rd ed. San Diego (CA): Academic Press.
Sun XG, Bonfante P, Tang M. 2015. Effect of volatiles versus exudates released by germinating spores of *Gigaspora margarita* on lateral root formation. Plant Physiol Biochem. 97:1–10.

Tian B, Pei YC, Huang W, Ding JQ, Siemann E. 2021. Increasing flavonoid concentrations in root exudates enhance associations between arbuscular mycorrhizal fungi and an invasive plant. ISME J. 15(7):1919–1930.

van Dijk JR, Kranchev M, Blust R, Cuypers A, Vissenberg K. 2021. *Arabidopsis* root growth and development under metal exposure presented in an adverse outcome pathway framework. Plant Cell Environ. 45(3):737–750.

Vázquez-Chimalhua E, Barrera-Ortiz S, Valencia-Cantero E, López-Bucio J, Ruiz-Herrera LF. 2021. The bacterial volatilite *N*,N-dimethyl-hexadecylamine promotes *Arabidopsis* primary root elongation through cytokinin signaling and the AHK2 receptor. Plant Signal Behav. 16(4):1879542.

Veits M, Khait I, Obolski U, Zinger E, Boonman A, Goldshtein A, Saban RM. 2018. *Mycorrhizal networks: common goods of soil-microbe-nutrient feedbacks in response to plant growth*. Plant Cell Environ. 41(3):823–831.

Walker TS, Bais HP, Grotewold E, Vivanco JM. 2003. Root exudation dynamics of root length and distribution and shoot biomass of maize as affected by intercropping with different companion crops and phosphorus application rates. Field Crops Res. 150:52–62.

Xia Z, He Y, Yu L, Lv R, Korpelainen H, Li C. 2020. Sex-specific strategies of phosphorus (P) acquisition in *Populus cathayana* as affected by soil P availability and distribution. New Phytol. 225(2):782–792.

Xia ZC, Kong CH, Chen LC, Wang P, Wang SL. 2016. A broadleaf species enhances an autototoxic conifers growth through belowground chemical interactions. Ecology. 97(9):2283–2292.

Xiong HC, Kakei Y, Kobayashi T, Guo XT, Nakazono M, Takahashi H, Nakanishi H, Shen HY, Zhang FS, Nishizawa NK, Zuo YM. 2013. Molecular evidence for phyto siderophore-induced improvement of iron nutrition of peanut intercropped with maize in calcareous soil. Plant Cell Environ. 36(10):1888–1902.

Xiong R, Liu S, Considine MJ, Siddique KHM, Lam HM, Chen Y. 2020. Root system architecture, physiological and transcriptional traits of soybean (*Glycine max* L.) in response to water deficit: a review. Physiol Plant. 172(12):405–418.

Xu L, Dong Z, Chiniqv D, Pierroz G, Deng S, Gao C, Diamond S, Simmons T, Wipf HM, Caddell D, et al. 2021a. Genome-resolved metagenomics reveals role of iron metabolism in drought-induced rhizosphere microbiome dynamics. Nat Commun. 12:3209.

Xu Y, Cheng HF, Kong CH, Meiners SJ. 2021b. Intra-specific kin recognition contributes to inter-specific allelopathy: a case study of allelopathic rice interference with paddy weeds. Plant Cell Environ. 44(12):3479–3491.

Yang XF, Kong CH. 2017. Interference of allelopathic rice with paddy weeds at the root level. Plant Biol (Stuttg). 19(4):584–591.

Yang XF, Li LL, Xu Y, Kong CH. 2018. Kin recognition in rice (*Oryza sativa*) lines. New Phytol. 220(2):567–578.

Yu P, He XM, Baer M, Beirinckx S, Tian T, Moya YAT, Zhang XC, Deichmann M, Frey FP, Bresgen V, et al. 2021. Plant flavones enrich rhizosphere Oxalobacteraceae to improve maize performance under nitrogen deprivation. Nat Plants. 7:481–499.

Yuan J, Zhao J, Wen T, Zhao M, Li R, Goossens P, Huang Q, Bai Y, Vivanco JM, Kowalchuk GA, et al. 2018. Root exudates drive the soil-borne legacy of aboveground pathogen infection. Microbiome. 6(1):156.

Zalhina K, Louie KB, Hao Z, Mansoori U, da Rocha UN, Shi SJ, Cho H, Kar ao z U, Loque D, Bowen BP, et al. 2018. Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. Nat Microbiol. 3:470–480.

Zhang D, Zhang C, Tang X, Li H, Zhang F, Rengel Z, Whalley WR, Davies WJ, Shen J. 2016. Increased soil phosphorus availability induced by Faba bean root exudation stimulates root growth and phosphorus uptake in neighbouring maize. New Phytol. 209(2):823–831.

Zhang DS, Lyu Y, Li HB, Tang XY, Hu R, Rengel Z, Zhang FS, Whalley WR, Davies W, Cahill JE, Jr., Shen JB. 2020. Neighbouring plants modify maize root foraging for phosphorus: coupling nutrients and neighbours for improved nutrient-use efficiency. New Phytol. 226(1):244–253.

Zhao ML, Zhao J, Yuan J, Hale L, Wen T, Huang QW, Vivanco JM, Zhou JZ, Kowalchuk GA, Shen QR. 2021. Root exudates drive soil-microbe-nutrient feedbacks in response to plant growth. Plant Cell Environ. 44(2):613–628.

Zhu YH, Weiner J, Li FM. 2019. Root proliferation in response to neighbour ing roots in wheat (*Triticum aestivum*). Basic Appl Ecol. 39:10–14.