The role of root exudates, CMNs, and VOCs in plant–plant interaction

Muhammad Khashi u Rahman, Xingang Zhou and Fengzhi Wu

ABSTRACT
In the last few decades, incredible advances have been made in understanding the way of communication among members of kingdom plantae. Some plants fight for their existence and try to suppress the growth of other plants, while some share resources to benefit each other for their survival. During all these processes, plants use several biotic and abiotic mediums such as root exudates, volatile organic compounds (VOCs), and light for the interactions. Plant can change its physiological behaviors, such as change in gene regulation and induction of defense mechanism, when linked with neighboring plant through common mycorrhizal networks (CMNs). Root exudates are also critical in plant–plant interaction, since they share information, shape microbial community, and mediate recourse competition. Moreover, plants have been found warning their neighbors about pathogen attack and herbivory through the release of VOCs. This review will advance the understandings of roles of various communication media from the prospective of intra- and interspecific interactions as well as kin recognition.

1. Introduction
Plants recognize their neighboring species and interact with other plants in order to create and/or maintain suitable living conditions. Basically, plant–plant interaction can be positive or negative (Kuebbing and Nuñez 2015). The example of positive plant–plant interaction is the release of volatile compounds to warn other plant about possible near future danger, and an example of negative plant–plant interaction is allelopathy (Bais et al. 2006; Dicke and Baldwin 2010; Friedman 2017). Interaction between two plants can be studied as interspecific or intraspecific. A fine example of interspecific interaction is when plant release chemicals to inhibit the growth of plant from another species (Chen et al. 2017). For example, Phragmites australis suppresses the growth of other species plants in surroundings by releasing a phytotoxin compound (Rudrappa et al. 2009). Recently, researchers have track down the release of allelochemicals in some invasive plants, like Centaurea stoebe (Gfeller et al. 2019), Canada goldenrod (Wang et al. 2018), C. stoebe, and Melilotus officinalis (Siyar et al. 2017), that may inhabit native plants.

Kin recognition is a kind of intraspecific interaction in which the ability of the plant to recognize its kin is studied. It is considered as a mysterious phenomenon, and is well studied in the recent decade (Biedrzycki and Bais 2010). According to a study, Cakile edentula, which is an annual plant, produced more roots when planted in a pot with a stranger and less roots when grown with a kin (Dudley and File 2007). These findings have given researchers many interesting future study directions such as neighbor detection, mechanisms behind the signal exchange, the role of belowground community and resource partitioning. After this study, many scientists took interest and tried to explore the chemistry behind this mysterious behavior (Klemens 2008; Biedrzycki and Bais 2010; Bhatt et al. 2011; Crepy and Casal 2016; Yang et al. 2018; Pennisi 2019).

Root exudates play an important role in plant communication not only by increasing nutrient availability but also directly affecting outcomes of the interaction between roots in the rhizosphere (Van Der Heijden et al. 2008). The interaction between plant and mycorrhizal fungus is a symbiosis in which fungus increases nutrient acquisition and induces resistance against biotic and abiotic stress of plants; in return, plants provide carbon in the form of sugar (Bücking et al. 2016; Gilbert and Johnson 2017). Studies have found belowground transportation of warning signals through CMNs between plants (Babikova et al. 2014; Song et al. 2015), which has been a highlighted part of recent research on the role of CMNs in plant–plant interaction. Although plant VOC have been studied mostly as aboveground chemical signals, an increasing trend of studies revealed that VOCs also play an integral part in belowground plant–plant interactions (Gfeller et al. 2019). Root VOCs can affect the belowground microbial community, soil nematodes (Rasmann et al. 2005) and the behaviors of herbivorous insects (Robert et al. 2012).

The aim of this review is to shed light on background and recent advances in plant–plant interaction; to describe media of interactions involved in plant communication; and to suggest potential future directions to increase research and solve mysteries in this budding area.

2. Interspecific and intraspecific interaction
Plants have been evolving for years in mechanisms like producing offspring and resource competition for their survival. Some parasitic plants completely depend on their hosts for survival. Such kind of plants have gradually developed...
advance mechanisms for locating and sensing their hosts. For example, strigolactones secreted by maize, pearl millet, and sorghum attract *Striga* which is a parasite (Awad et al. 2006). Another parasitic plant *Cuscuta pentagona* can recognize a volatile compound secreted by tomato (a host plant) and directs its growth accordingly (Runyon et al. 2006). Some plants work as beneficial neighbors in positive plant-plant interaction by warning the plant of same or other species about possible future harm (Babikova et al. 2010). For example, leaf damage in maize leads to emit (Z)-3-hexen-1-ol (Z-3-ol), which may warn plants in surrounding about the herbivore attack (Heil and Bueno 2007; Heil and Karban 2010).

Talking about the difference between interspecific and intraspecific interaction, it is observed that plant roots with more relatedness show more growth toward each other compared with plants with less relatedness (Fang et al. 2011, 2013). Recently, the interaction of commercial soybean, with some of other cultivars of the same species and some leguminous species, was examined to check interspecific and intraspecific interaction (Murphy et al. 2017). In this experiment, soybean responded differently according to genetic relatedness. The OAC Wallace (a commercial soybean cultivar) increased leaves’ allocation in the presence of wild soybean and white beans and showed no change when grown with other soybean cultivars (Murphy et al. 2017). The result of the interaction between sorghum (*Sorghum vulgare*) and soybean (*Glycine max*) during intercropping suggests that soybean increased N uptake and sorghum increased root allocation in the competition.

Allelopathy is a fine example of negative interaction between plants in which one plant secretes chemicals to inhibit the growth or to kill another plant either from the same species (autotoxicity) or different species (Friedman 2017). Many plants have allelopathic characteristics. An invasive plant *P. australis* releases a phytotoxin compound (gallic acid) into the soil which suppresses plants in surroundings (Rudrappa et al. 2009). In another study, an invasive weed (*C. stoebe*) was grown with the same as well as different species plants. Results showed that *C. stoebe* significantly up-regulated its defensive mechanism when grown with the same species plants as compared to those grown with different species plants. It reflects that *C. stoebe* can modify its growth and defensive strategy according to the nature of plants in neighbor, which shows the importance of biochemical processes in the sensing and responding mechanism of plants, and plant grown with same species could be more resistant to pathogen than when cultured with different species plants (Broz et al. 2010). Results of another study, conducted by Chaill et al. (2010), showed that the interaction between plants from different species was highly governed by the nutrient resource availability in soil, which is conflicting with the data of Broz et al. (2010). *Impatiens glandulifera* (an invasive species) produces 2-methoxy-1, 4-naphthoquinone (2-MNQ), which is reckoned as an important allelochemical (Ruckli et al. 2014). Recently, it was found not only negatively affecting native plants but also the plants from the same species in neighbors (Bieberich et al. 2018).

3. Kin recognition

Kin recognition is simply the ability of an individual to distinguish between genetically close related kin and non-kin. The ability of recognizing kin is really an advantage for an individual to survive in this barbarous world. Kin recognition ability of a plant can be indicated by the changes in its functional traits such as plant size and root allocation during the competition (Dudley et al. 2013). In a plant diversity, kin recognition could affect the allocation of resource harvesting, because plants with more similar traits are supposed to compete more than non-kin individuals. However, these individuals can benefit its kins by improved fitness, as they share some of their genes (Chen et al. 2012). The evolution of kin recognition may help individuals to secure resource by cooperating with kin while competing with non-kin (Callaway and Mahall 2007). Finally, the discrimination of kin and non-kin could help individuals to cooperate with each other which is an important constituent of any ecosystem.

Studies were conducted to examine the root response of desert shrub (*Ambrosia dumosa*) grown with the same plant, different plants but from the same population, and with a clone (Mahall and Callaway 1991, 1992, 1996). Results of these studies showed that the root growth of desert shrub was inhibited when it came in contact with roots of a different plant, or clone, but no effect was found when it came in contact with roots of the same plant. Another study conducted on peas found that the behavior between roots of two separate individuals was different from that when came in contact with detached clones (Falik et al. 2003). In the above-mentioned studies, it was determined that the desert shrub and pea roots do not recognize roots from plants of different genotype; therefore, recognition can only occur in closely related plants, so kin/non-kin recognition may exist. Pakkasmaa and Laurila (2004) found *Rana temporaria* was grown better with kin than with a mixed population under a favorable environment. They also found unchanged results in an unfavorable growing environment because the survival cost was extremely high for kin discrimination in those stressful conditions. Dudley and File (2007) studied the response of root from sea rocket (*C. edentula*) growing in pots. They found that the root allocation of sea rocket increased with the presence of a stranger as compared with the presence of a kin.

Unlike previous studies, Murphy and Dudley (2009) examined changes in aboveground traits of *Impatiens pallida* during a kin recognition experiment. They found that *I. pallida* grown with a stranger significantly increased in stem allocation, leaves allocation, number of branches and plant height than when it was grown with a kin. These findings of competition in various traits and the response of species to a stranger and a kin reflects the differences in responses and mechanisms in animal species. However, the results from the above studies, disclosing a clear evolutionary tradeoff, have been difficult to pinpoint. According to Karban and Shiojiri (2009), sagebrush (*Artemisia tridentate*) emits volatile organic compound (VOC) cues as a result of herbivory or wounding. Interestingly, sagebrush plants found less damage that received cues from non-self-cuttings than the plants that received cues from non-self-cuttings (Karban and Shiojiri 2009; Masclaux et al. 2010). This was the first study to show the benefit for plants interacting with a kin and a non-kin.

Biedrzycki and Bais (2010) used a model plant *Arabidopsis thaliana* for the kin recognition study with a different methodology. Instead of growing in pots, they grew plant wells of tissue culture plates in liquid growth media. They found results that supported the results of Dudley and File (2007)
that *A. thaliana* plant produced more lateral roots when exposed to secretions of a stranger as compared to when exposed to kin secretions (Biedrzycki and Bais 2010). These studies also support the theory which states that some plants indeed have the ability to recognize other plants within the same species based on their relatedness. Furthermore, Biedrzycki and Bais (2010) applied sodium orthovanadate (Na₃VO₄) to plants, which is a root secretion inhibitor. This addition ended up the changes in root growth, suggesting that somehow root secretions are responsible for kin recognition in *A. thaliana*. After a series of studies in recent decade, researchers have come to know that kin recognition does also exist in several other plants including *Artemisia tridentata* (Karban et al. 2013), *Oryza sativa* (Fang et al. 2013; Yang et al. 2018), *Cycas edentata* (Gorelick and Marler 2014), *Distichlis spicata* (Mercer and Eppley 2014), *G. max* (Murphy et al. 2017), *Moricandia moricandioides* (Torices et al. 2018), and *S. vulgare* (Li et al. 2018).

### 4. Mechanism of interaction

The interaction between plants has been a burning topic for researchers in the recent decade, especially kin recognition. The mechanisms involved in the interaction between plants can be aboveground or belowground.

#### 4.1. Role of root exudates

Root secret a mixture of many molecules generally known as root exudates. Root exudates are complex in nature with thousands of different kinds of substances, which are further grouped into organic acids, amino acids, fatty acids, sugars, proteins and many more (Bais et al. 2006; Dennis et al. 2010). These substances perform different functions for plant and soil in the rhizosphere (Badri and Vivanco 2009). Root exudates mainly depend on external factors such as photosynthetic activity, the condition of soil and the size of the plant, also it is genotype or species dependent (Micallef et al. 2009; Semchenko et al. 2014). Hence, neighbors can get much information about an individual from its exudates (Mommer et al. 2016). This mechanism of getting information from an individual’s root exudates is largely unknown. Although recently some researchers have illustrated the role and importance of root exudates in underground plant–plant interaction (Figure 1), many root exudates have the ability to mediate resource competition because they can affect the availability of nutrients (Dotaniya and Meena 2015; Canarini et al. 2019). For example, the concentration of some ions (P and Zn) increases with exudation of carboxylates and acid phosphatase (Duffner et al. 2012). Keiluweit et al. (2015) illustrated that the mineralization of organic matter is stimulated by root exudates which may lead N cycling in the rhizosphere. This also gives a hint for the role and importance of root exudates which can be involved in stimulating N availability in the root zone.

Root exudates not only increase nutrient availability but also directly affect the outcomes of the interaction between roots in the rhizosphere (Bais et al. 2006). The most prominent example is allelopathy in *Centaurea maculosa* because it releases a compound (–catechin) in root exudates, which inhibit the neighboring plants (Thorpe et al. 2009; Carvalho and Martins 2018). Mostly, these allelopathic species are resistant to self-produced phytotoxins, but some non-allelopathic neighbors may be resistant as well. For example, in a study, the same plant (*C. maculosa*) found less resistant to –catechin than 8 out of 23 other species of neighborhood. It is true that root exudates have a big influence on nutrient availability, but one cannot evaluate it without considering the role and importance of rhizobiome. Soil microbiota have the ability to govern the root exudates by changing their composition and amount. Root exudates and rhizobiome also have another relationship in the root zone that plants choose their microbiota via exudates (Broeckling et al. 2008; Badri et al. 2013). Recently, Yang et al. (2018)
found that a nitrogen-rich allantoin component from root exudate is responsible for kin recognition in rice (O. sativa). All these findings suggest that the role of root exudates in plant–plant interaction is critically important.

4.2. Role of Common Mycorrhizal/Mycelial Networks (CMNs)

The roots of almost 80% of all higher plants interact with Arbuscular Mycorrhizal Fungi (AMF) through symbiosis (Smith and Read 2008). The hyphae length of fungi in the soil could be very vast (Leake et al. 2004). These lengthy hyphae of fungi have the ability to make various points of entry to root for the trade of nutrients with plants (Johnson and Gilbert 2015). When they come in contact with roots of more than one plant, they form a network called CMN in the root zone (Lin et al. 2015). CMNs play an important role in nutrient facilitation, transportation of water, stress signals, and allelochemicals between plants of the same or different species (Barto et al. 2011; Babikova et al. 2013, 2014; Weremijewicz and Janos 2013; Gorzela et al. 2015; Teste et al. 2015; Murphy and Dudley 2009). Moreover, studies revealed that CMNs can transport compounds from 12 (Barto et al. 2011) to 20 cm (Babikova et al. 2013). According to Babikova et al. (2013), plants produced VOCs (i.e. methyl salicylate) when they were infested with aphids. These volatile exudates are repellent to aphids but attract parasitoid wasps (a natural enemy of aphids). The neighboring plant that was connected with the infested plant through CMN released the same VOCs with the same effects on aphids and its predator. On the contrary, the neighboring plant that was not connected with an infested plant through CMNs showed the opposite phenomenon by not releasing such VOCs (Babikova et al. 2013). Another study (Song et al. 2014), in which tomato plants were attacked by caterpillar Spodoptera litura, also suggested that CMNs can be the signaling pathway between plants during herbivory. When infested plants (donor) are attacked by herbivores, they transfer signals to non-infested plants in neighbor through CMNs (Figure 1). In response to these rapidly transmitted signals, non-infested plants (receiver) up-regulate the genes of the defense pathway i.e. jasmonate (Song et al. 2014). The possible mechanisms behind the transfer of signals with CMNs can be through cytoplasmic streaming within hyphae, capillary action, root exudates (triacylglycerol (Bago et al. 2002), amino acids (Jin et al. 2005)), microbes and conduits for wound-induced electrical signals (Johnson and Gilbert 2015).

4.3. Role of VOCs

Several events must transpire for the aboveground plant–plant communication. For example, some kind of signals, such as signal cues or signal markers, must be generated by a plant (sender). Then, the other plant (receiver) must detect those signals and choose if the receiver and the signal are matching. At the end, the receiver must make a final decision, whether to accept or reject signals; and/or whether to work accordingly or against the sender. In kin recognition, this is called kin bias or kin discrimination (Hamilton 1964; Liebert and Starks 2004; Biedrzycki and Bais 2010). According to the basic concept developed by some early studies (Baldwin and Schultz 1983; Rhodes 1983; Fowler and Lawton 1985), researchers believed that the interaction between plants is a phenomenon that had been compiled, examined, and at the end debunked, just like cold fusion (Dicke and Bruin 2001). However, these series of evidence from the early studies suggest that study on plant–plant interaction was nothing more than compelling. Compared to the earliest studies, in the 1990s, studies were designed properly and found some indications about the exchange of volatile signals between plants (Farmer and Ryan 1990; Engelberth et al. 2004). After finding the exchange of these volatile signals, many ecologists disbelieved that this phenomenon could be seen in the field since previous studies were conducted in artificial settings of the laboratories (Fowler and Lawton 1985; Dicke and Bruin 2001).

During the late 1990s, the findings of some field experiments illustrated that wild tobacco (Nicotiana attenuata) and alder (Alnus glutinosa) experienced less herbivory damage when grown together (Dolch and Tscharntke 2000; Karban et al. 2000). Another study found that when barley (Hordeum vulgare) plants were exposed to air coming from thistle (Cirsium), they showed less attraction to aphids (Glinwood et al. 2004). As mentioned earlier, sagebrush (A. tridentate) emits VOC cues as a result of herbivory or wounding. These cues could be used by neighboring plants as warning signals (Karban and Shiojiri 2009). For example, it was observed that sagebrush plants that were less damaged received cues from self-cuttings (Karban and Shiojiri 2009; Masclaux et al. 2010). Another example of such interaction is the A. tridentate plants experience a less herbivorous attack when exposed to volatile cues (Karban et al. 2013).

In the recent decade, ecologists investigated the belowground exchange of VOCs which is now well documented (Ens et al. 2009; Jassbi et al. 2010; Rasmann et al. 2012; Eilers et al. 2015; Delory et al. 2016). These studies suggest the exchange of VOCs both aboveground and belowground between plants of the same and different species for facilitation as well as prevention of plant growth in an ecosystem.

4.4. Role of light and phenomenon of shade avoidance in plant

The most common features during the interaction between plants are shade avoidance and light sharing (Casal 2012). Light environment is modified through cryptochrome1 and phytochrome B by neighboring plants (Keller et al. 2011). The responses from a plant during shade avoidance include elongation of internode, petioles, and hypocotyl, elevated leaf angles, early flowering, and reduced canopy (Pierik and De Wit 2013). These responses mainly rely on combined actions of several plant hormones such as gibberellins, auxin, ethylene, and brassinosteroids (Franklin 2008; Casal 2012). The neighbor detection process starts with the detection of horizontal reflection of far-red light (700–800 nm Waveband of the light spectrum) by neighboring plants. This far-red enrichment occurs just prior to the onset of actual shading and is signaled by the phytochrome of photoreceptors (Pierik and De Wit 2013). An experiment conducted by Crepy and Casal (2015) indicated that the plant showed kin recognition by growing their leaves horizontally reoriented. This phenomenon was not observed when plants were planted in the presence of non-kin neighbors (Crepy and Casal 2015). In this study, the authors suggested that photosensory receptors (cryptochrome1, phytochrome B, and shade avoidance3) are involved in perceiving from kin
neighbors. It is argued that the airborne signals generated by neighboring plants are perceived by photoreceptors such as cryptochrome and phytochrome. Although a lot of work has been performed to understand the function of these receptors in plant communication, it is not fully clear yet (Bais 2015). It is argued that the change in aerial growth, such as leaf orientation, mediated by photosensory signals adds fitness cost to the individual.

5. Conclusion

It is obvious from the previous studies that plants share information through various channels and they do have the ability of neighbor detection and kin recognition. Plants also integrate information about nutrient availability and thus grow their roots accordingly (Bisseling and Scheres 2014). Initially, it was thought that kin selection is impossible in plants because of a lack of sensors like in animal kingdom (Till-Bottraud and De Vilmereuil 2016), but recent studies have found various responses from individuals i.e. allocation of roots and branches to the individuals according to relatedness. These studies have provided more opportunities to explore a new prospective of kin recognition. The exchange of warning signals, during herbivory or pathogen attack signals between plants through CMNs, is a worth finding of the last decade. The symbiotic relationship between AMF and plant is not all about give and take but it also mediates inter-plant nutrient-based competition. However, our knowledge about how plants compete with each other for nutrient resources that are available for their CMNs and how AMF allocates infochemicals and nutrient resources within their CMNs is very little.

6. Challenges and future directions

Since root exudates are composed of thousands of substances, the absolute characterization of molecules facilitating beneficial microbes and inducing resistance against pathogen is a big challenge. Studies also suggest that not only aboveground parts of plants emit VOCs but also roots release VOCs, which can act as signaling molecules in mediating belowground biotic interactions (i.e. plant–plant and plant–microbiome). However, the diversity, nature, and functions of specific VOCs and mechanisms involved in the exchange of VOCs still need a number of studies. Although several studies confirmed intra- and interspecific exchange of these chemical signals through CMN, still nature and factors affecting degree and speed of these signals need more controlled experimental studies. Thus

(1) Further investigations are required to find whole inventory of root exudates, specific signaling molecules and VOCs, their nature and mechanisms of their distribution both through soil and through CMNs during belowground plant–plant communication, and whether the belowground exchange of VOCs and chemical signals have any effects on aboveground traits?

(2) The work on the responses of individual against different relatedness levels i.e. clone, siblings, half siblings, a distant relative, and a stranger in more species would be more interesting and explanatory for the mysterious behavior of kin recognition in plants.

(3) More research is required to find a detailed chemistry of inter-plant as well as inter-fungal competition and how the costs and benefits are controlled within CMN during the symbiotic relationship. Furthermore, almost all the studies were conducted on a few specific strains of AMF and a small number of plant species. Hence, studies on more AMF strains and more plant species will explore the functions and mechanisms of this symbiotic partnership in more detail.

Finally, these studies will enhance our understanding of interactions between plants and the role of different biotic and abiotic factors in plant communications, which will eventually support food security, integrated agriculture, and environment-friendly farming.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by National Key Research and Development Program [grant number 2018YFD1000800]; China Agricultural Research System [grant number CARS-23-B-10]; National Natural Science Foundation of China [grant number 31772361] and Natural Science Foundation of Heilongjiang Province [grant number YQ2019C009].

Notes on contributors

Muhammad Khashi u Rahman is a PhD student at College of Horticulture and Landscape Architecture, Northeast Agricultural University, Harbin, P. R. China. His research focuses on mediums of interactions between plants, particularly chemistry and functioning of root exudates.

Xingang Zhou is Associate Professor at College of Horticulture and Landscape Architecture, Northeast Agricultural University, Harbin, P. R. China. His research examines how intercropping can be a useful tool in alleviating soil sickness. His main research areas include allelochemicals, plant-microbe interactions and rhizosphere ecology.

Fengzhi Wu is Professor at College of Horticulture and Landscape Architecture, Northeast Agricultural University, Harbin, P. R. China. Her main research expertise includes soil sickness in horticultural crops and soil health maintenance technology.

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