

CURRENT REVIEW

Strigolactones in the Rhizosphere: Friend or Foe?

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Strigolactones are well-known endogenous plant hormones that play a major role in planta by influencing different physiological processes. Moreover, ex planta, strigolactones are important signaling molecules in root exudates and function as host detection cues to launch mutualistic interactions with arbuscular mycorrhizal fungi in the rhizosphere. However, parasitic plants belonging to the Orobanchaceae family hijacked this communication system to stimulate their seed germination when in close proximity to the roots of a suitable host. As a result, the secretion of strigolactones by the plant can have both favorable and detrimental outcomes. Here, we discuss these dual positive and negative effects of strigolactones and we provide a detailed overview on the role of these molecules in the complex dialogs between plants and different organisms in the rhizosphere.

Strigolactone, a versatile molecule.

Belowground as well as aboveground, plants encounter various organisms (Buée et al. 2009). In the soil, these interactions take place in the rhizosphere, the narrow zone of soil surrounding the root in which different microorganisms reside, including neutral, beneficial, and harmful ones (Raaijmakers et al. 2009). Plants need to be able to cope with all of them; they should defend themselves against pathogens, while simultaneously trying to establish mutualistic associations. To accomplish this challenging task, plant roots release a wide range of communication molecules in the rhizosphere, e.g., polysaccharides, amino acids, aliphatic acids, aromatic acids, fatty acids, sterols, phenols, and other secondary metabolites, including strigolactones (Bais et al. 2006; Steinkellner et al. 2007; Venturi and Keel 2016).

Strigolactones are present in root exudates of diverse monocotyledonous and dicotyledonous plant species at very low concentrations (picomolar and nanomolar) (Xie 2016). In the soil, these molecules are implicated in the communication between plants and a wide range of parasites belonging to the Orobanchaceae family (Cook et al. 1966; Yoneyama et al. 2010) but, also, in the communication with arbuscular mycorrhizal fungi (Akiyama et al. 2005) and, more recently, in the legume-rhizobia symbiosis (De Cuyper et al. 2015; Foo and Davies 2011; Peláez-Vico et al. 2016; Soto et al. 2010). In addition to their importance as rhizosphere molecules, strigolactones are also studied for their role as plant hormones that influence various physiological processes to adjust plant growth and development, such as shoot branching, secondary growth processes, leaf shape and senescence,

internode elongation, and environmental stress responses (Al-Babili and Bouwmeester 2015).

The presence of strigolactones in algae indicates that these molecules appeared in evolution before the first arbuscular mycorrhizal symbiosis, suggesting that their original function was to act as plant hormones that later evolved into rhizosphere communication signals (Delaux et al. 2012). Indeed, strigolactones stimulate rhizoid elongation of Charales, liverworts, and mosses, thereby increasing their anchorage ability, an essential trait for terrestrial colonization 460 million years ago (Delaux et al. 2012). By their action, both as phytohormones in planta and as rhizosphere signaling molecules ex planta, strigolactones allow plants to adapt flexibly to different biotic or abiotic stress conditions by establishing mutualistic interactions, by playing a potential role in plant-pathogen interactions, and, by coordinating root and shoot architecture. Here, we give a detailed overview on the role of strigolactones in the complex dialogs between plants and other rhizosphere members.

From synthesis to secretion.

Strigolactones are synthesized from carotenoids through the consecutive action of DWARF 27 (D27), CAROTENOID CLEAVAGE DIOXYGENASE 7 (CCD7), CCD8, and MORE AXILLARY GROWTH 1 (MAX1). In the plastids, the β -carotene isomerase D27 and carotenoid cleavage dioxygenases CCD7 and CCD8 convert the strigolactone precursor all-*trans*- β -carotene into the strigolactone biosynthetic precursor, carlactone (Alder et al. 2012; Booker et al. 2004; Bruno et al. 2017; Kohlen et al. 2012; Lin et al. 2009; Seto et al. 2014). In the cytosol, the cytochrome P450 enzyme MAX1 catalyzes carlactone oxidations to produce carlactonic acid, which is further methylated and, subsequently, is oxidized by LATERAL BRANCHING OXIDOREDUCTASE, an oxidoreductase-like enzyme of the 2-oxoglutarate and Fe (II)-dependent dioxygenase superfamily, into biologically active strigolactone-like compounds (Alder et al. 2012; Booker et al. 2005; Brewer et al. 2016; Kohlen et al. 2011; Seto et al. 2014; Zhang et al. 2014). Despite our understanding of strigolactone biosynthesis, it remains unclear whether canonical strigolactones or rather carlactone-derived molecules are synthesized in *Arabidopsis thaliana* and it is still unknown which ones act as endogenous hormones (Abe et al. 2014; Kohlen et al. 2011).

Today, at least 20 different natural canonical strigolactones have been structurally characterized, all consisting of four rings, designated A to D rings (Tokunaga et al. 2015). The A, B, and C rings carry a lactone group to which the D ring is connected via an enol ether bridge. The C-D ring is highly conserved among the different strigolactones and is essential for its bioactivity, whereas the A and B rings can have various modifications (Yoneyama et al. 2013; Zwanenburg and Pospíšil 2013). Different plant species produce different strigolactone

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blends. Structure-activity relationship (SAR) studies have indicated that the chemical characteristics might be correlated with specific outcomes; for instance, strigolactones with a hydroxyl group have the highest activity in parasitic weed seed germination (Cavar et al. 2015). Understanding the specificity of these structural modifications allows the selection of plant varieties with a favorable strigolactone ‘fingerprint’ that is not recognized by parasitic seeds but still promotes mutualistic interactions. Instead of natural strigolactones, the synthetic strigolactone *rac*-GR24 is widely used in strigolactone research. This racemic mixture consists of both 2′*R*-configured molecules that mimic the configuration of the natural strigolactones and the 2′*L* configurations that are not found in nature. Nevertheless, as discussed below in more detail, these noncanonical forms are perceived by plants, not via the strigolactone, but via the karrkinin signaling pathway (Scaffidi et al. 2014). Hence, studies with *rac*-GR24 should always be interpreted within this context.

Different expression studies and grafting experiments have revealed that strigolactones might not exclusively be produced in the root but might be more generally synthesized in the vascular tissues of many organs (Borghini et al. 2016). In contrast, a long-distance transport from the root to the shoot has been considered as well. Indeed, the discovery of both strigolactones and carlactone in the xylem sap of *Arabidopsis* and *Solanum lycopersicum* (tomato) hinted at a root-derived strigolactone trafficking to the shoot via the xylem (Kohlen et al. 2011, 2012). However, in another study, no strigolactones were detected in the xylem sap of various species, although a slow root-to-shoot transport was still observed, suggesting an active cell-to-cell transport instead of a fast movement via the xylem sap stream (Xie et al. 2015b).

Knowledge about the strigolactone secretion from the root into the soil is essential to fully understand the role played by strigolactones in rhizosphere communication. Thus far, the only well-characterized strigolactone transporter is PLEIOTROPIC DRUG RESISTANCE 1 (PDR1) in *Petunia hybrida* (petunia) (Kretschmar et al. 2012), belonging to the G-type subfamily of ATP-BINDING CASSETTE (ABC) transporters, known to be involved in the directional transport of several phytohormones, such as cytokinin, abscisic acid, and auxin (Borghini et al. 2015). Mutants are characterized by an enhanced branching phenotype and their root exudates induce less efficiently arbuscular mycorrhizal hyphal branching and parasitic seed germination. Moreover, *Arabidopsis* plants overexpressing *PDR1* of *Petunia axillaris* secreted larger amounts of the synthetic strigolactone analog *rac*-GR24 than the wild-type plants. Taken together, these findings support a role for PDR1 as a strigolactone exporter that mediates strigolactone transport in the plant as well as into the soil (Fig. 1). The asymmetrical localization of PDR1 at the plasma membrane is the reason for the strigolactone export out of the cell. Indeed, in the root tip, PDR1 is localized at the apical membrane of root hypodermal cells, indicative for an active strigolactone transport from the root tip to the shoot. In contrast, above the root tip, PDR1 is located at the outer lateral membrane of hypodermal passage cells, known to be specific entry sites for arbuscular mycorrhizal fungi that enable an active outward traffic into the rhizosphere (Sasse et al. 2015; Sharda and Koide 2008). In addition to the root, *PDR1* is also expressed in the stem nodes, close to the axillary buds. Interestingly, because the *PDR1* expression is regulated by different factors, such as colonization of arbuscular mycorrhizal fungi, treatment with *rac*-GR24 or auxin, and nutrient conditions (mainly phosphate) in the soil, this strigolactone exporter might synchronize plant growth with nutrient availability (Kretschmar et al. 2012). In addition to petunia, in *Nicotiana tabacum* (tobacco), a close *PDR1* homolog, *PDR6*, has been

identified that could be involved in strigolactone transport (Xie et al. 2015a). However, in *Arabidopsis*, the closest *PDR1* homolog, *AtABCG40*, has been described as an abscisic acid transporter, demonstrating that sequence information might not always correlate with the transporter’s substrate (Borghini et al. 2016; Kang et al. 2010).

Strigolactones are inherently unstable in the soil, due to the labile ether bond that spontaneously hydrolyzes in water environments and inactivates these molecules (Akiyama et al. 2010). The hydrolysis rate strongly depends on strigolactone structure and environmental conditions. For instance, under neutral conditions, the half-life of the synthetic strigolactone analog *rac*-GR24 was estimated to be 10 days (Akiyama et al. 2010), but natural strigolactones are much more unstable than synthetic ones; for instance, the half-life of 5-deoxystrigol has been reported to be only 1.5 days (Akiyama et al. 2010). Because strigolactones are short-living compounds, partners can only react to these fragile molecules in close vicinity of the root, i.e., in the rhizosphere. Furthermore, a concentration gradient is expected to be formed that can be used by different organisms as an indicator for the distance to their host.

A cue for arbuscular mycorrhizal and other fungi.

Originally, strigolactones were discovered as seed germination stimulants of parasitic weeds (Cook et al. 1966). Immediately, the question arose why plants would release molecules that induce germination of their parasites. Therefore, strigolactones have been suggested to possess other functions that outweigh the negative effects of parasitism, resulting in a selective pressure to maintain strigolactone biosynthesis in nature. Indeed, a beneficial role for strigolactones has been unveiled, more particularly, in enhancing arbuscular mycorrhization, which is an important fungal symbiosis with roots of approximately 80% of the vascular plants (Akiyama et al. 2005). Arbuscular mycorrhizal fungi belong to the phylum Glomeromycota and are obligate symbionts that rely on their hosts to complete their development. They enhance uptake by the plant of water and mineral nutrients, especially inorganic phosphate (Pi) and, in return, they receive carbohydrates from their host. Molecular data and fossil studies suggest that this symbiosis evolved 400 million years ago and is of major importance in the colonization of land by plants (Remy et al. 1994). Hence, this symbiosis is assumed to exist much longer than the association with parasitic plants. In other words, the primary role of strigolactones in rhizosphere communication has been to stimulate the interaction with arbuscular mycorrhizal fungi and, later on, parasitic plants have hijacked this system to detect their hosts (Leyser 2008).

Upon host recognition, one of the first responses of arbuscular mycorrhizal fungi involves the extensive branching of hyphae to ensure a good contact with the host root, necessary for the further establishment of symbiosis (Giovannetti et al. 1993, 1994). Host roots release signal molecules, referred to as branching factors, that stimulate hyphal branching of several arbuscular mycorrhizal fungi species (Buee et al. 2000; Giovannetti et al. 1996). This branching factor has been isolated and identified as 5-deoxystrigol (Akiyama et al. 2005). Other strigolactones have been reported to induce hyphal branching as well (Akiyama et al. 2005; Mori et al. 2016), thereby forming a large network of mycelia that reaches out far beyond the root rhizosphere, allowing the capture of nutrients from expanded soil areas. In agreement, the colonization rates of the arbuscular mycorrhizal fungi *Glomus intraradices* and *Gigaspora rosea* have been found to be reduced in strigolactone-deficient tomato and *Zea mays* (maize) mutants, respectively (Gomez-Roldan et al. 2007; Koltai et al. 2010). In addition to hyphal branching, *rac*-GR24 also

stimulates spore germination and boosts fungal metabolism (Besserer et al. 2006, 2008).

As arbuscular mycorrhizal fungi respond to strigolactones, they must be able to sense them. How this perception is established is still unknown. Inside plants, strigolactones are recognized by the α/β hydrolase DWARF 14 (D14), after which a signaling complex is made, consisting of the Skp1-Cullin-F-box (SCF) complex with the F-box protein MORE AXILLARY GROWTH 2 (MAX2), members of the SUPPRESSOR OF MAX2 1-LIKE (SMXL) protein family, and TOPLESS repressors (Arite et al. 2009; de Saint Germain et al. 2016; Gomez-Roldan et al. 2008; Hamiaux et al. 2012; Jiang et al. 2013; Marzec et al. 2016; Nakamura et al. 2013; Stimberg et al. 2007; Umehara et al. 2008; Zhao et al. 2015; Zheng et al. 2016; Zhou et al. 2013). Upon strigolactone binding, the SCF^{MAX2} complex is anticipated to ubiquitinate the SMXL proteins to send them for proteasomal degradation, thereby activating downstream signaling (Jiang et al. 2013; Liang et al. 2016; Soundappan et al. 2015; Wang et al. 2015; Zhou et al. 2013). MAX2 is also essential for karrikin-induced seed germination (Nelson et al. 2011). However, rather than through D14, these smoke-derived germination stimulants (Waters 2017) are perceived by the D14 paralog D14-LIKE (D14L)/KARRIKIN INSENSITIVE 2 (KAI2), whereafter the SCF^{MAX2} complex is expected to ubiquitinate

members of the SMXL family that differ from those targeted by the D14/SCF^{MAX2} complex (Guo et al. 2013; Soundappan et al. 2015; Stanga et al. 2013; Waters et al. 2012). The synthetic strigolactone analog, *rac*-GR24, which is ubiquitously used in strigolactone research, is a mixture of four isomers, of which two mimic natural strigolactones that activate mainly D14 signaling cascades and the other two preferentially activate KAI2 signaling (Scaffidi et al. 2014). Additionally, besides karrikins, also endogenous, still-unknown ligands for KAI2 are predictable, which are also mimicked by the *rac*-GR24 mixture (Conn and Nelson 2016).

Protein sequences of both MAX2 and D14 have been shown to match those of the translated genome of arbuscular mycorrhizal fungi, albeit with a low identity, implying that the ability to respond to strigolactones might have evolved separately in plants and fungi (Koltai 2014). Indeed, thus far, the identification of a real MAX2 or D14 ortholog has not been reported. Interestingly, inside rice (*Oryza sativa*) roots, the D14 paralog D14L is required to initiate the symbiosis with arbuscular mycorrhizal fungi (Gutjahr et al. 2015). Thus, karrikins or karrikin-like molecules might play a role in this symbiosis (Gutjahr et al. 2015). Whether these karrikin-like molecules are derived from the plant or from the fungus is currently unknown and would be interesting to investigate.

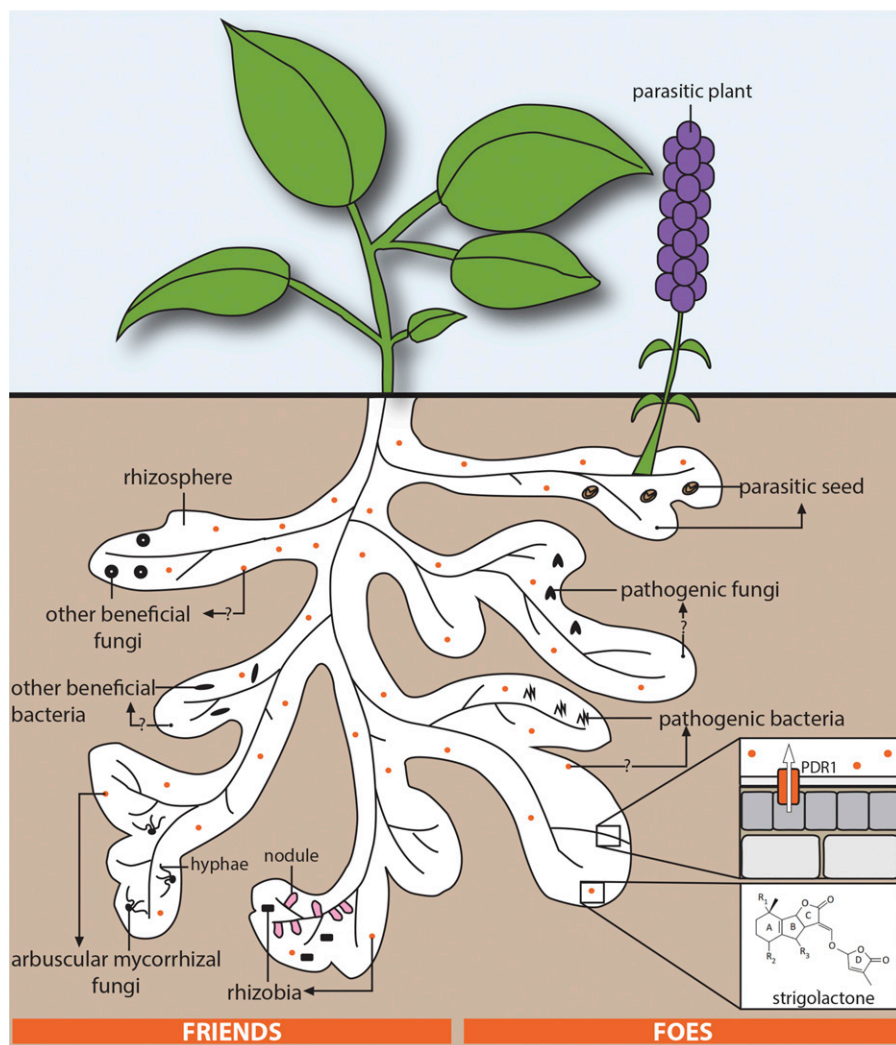


Fig. 1. Strigolactones as Janus-faced molecules in the rhizosphere. To interact with other organisms in the soil, plants secrete strigolactones in the rhizosphere through the strigolactone exporter PDR1. Rhizobia and arbuscular mycorrhiza have been shown to respond to strigolactones, favoring their interaction with the plant. However, parasitic weeds misuse the presence of strigolactones to recognize their hosts.

Intriguingly, nonhost plants for arbuscular mycorrhizal fungi, such as *Arabidopsis* and *Lupinus albus* (white lupin), also produce and secrete strigolactones, hinting at a more general function as communication signals in other rhizosphere interactions. Whether or not strigolactones can influence the growth and branching of pathogenic fungi and oomycetes is not clear. Indeed, although no influence of *rac*-GR24 [10^{-6} M] or natural strigolactones on the branching pattern or germination of various root-colonizing beneficial and pathogenic fungal or oomycete species, including *Fusarium oxysporum*, has been observed (Blake et al. 2016; Decker et al. 2017; Foo et al. 2016; Steinkellner et al. 2007), treatment with *rac*-GR24 [10^{-5} M] strongly inhibits the growth of several pathogenic fungi, among which, again, *Fusarium oxysporum* (Decker et al. 2017; Dor et al. 2011). As most effects occur with the application of high concentrations of strigolactones (50 μ M), highly exceeding the levels found in the rhizosphere, strigolactones might probably only have little or no effect on the tested pathogens in nature.

In contrast, strigolactones might act as plant endogenous hormones to influence defense responses against fungal intruders. The strigolactone-deficient tomato *Slccd8* RNA interference line has been shown to be more susceptible to the foliar fungal pathogens *Botrytis cinerea* and *Alternaria alternata*. This sensitivity correlates with reduced levels of the phytohormones jasmonate, salicylic acid, and abscisic acid, implying a role for strigolactones in plant defense (Torres-Vera et al. 2014). In agreement, strigolactone biosynthesis mutants of *Physcomitrella patens* have an enhanced disease susceptibility against various phytopathogenic fungi, possibly due to changes in defense responses rather than to direct effects on the pathogens (Decker et al. 2017). On the contrary, in pea (*Pisum sativum*), no changes in disease symptoms of *Pythium irregulare* or *Fusarium oxysporum* have been reported in various strigolactone synthesis and perception mutants (Blake et al. 2016; Foo et al. 2016) nor in the interaction between *Arabidopsis* strigolactone-deficient mutants and *B. cinerea* (Piisilä et al. 2015). Hence, the effects of strigolactones on diseases vary. Therefore, further research is required to better understand how strigolactones play a role in the interaction of plants with root-pathogenic fungi and oomycetes. Nevertheless, the impact of *rac*-GR24 on the colony growth of *B. cinerea* has been used to elucidate their mode of action. The analysis of *B. cinerea* mutants that are less sensitive to *rac*-GR24 suggests that responses rely on reactive oxygen species (ROS) and mitochondria (Belmondo et al. 2017).

A cue for rhizobia and other bacteria.

Besides the interaction between plants and arbuscular mycorrhizal fungi, another beneficial dialog in the rhizosphere is the rhizobia-legume symbiosis. Whereas the role of strigolactones in the communication with arbuscular mycorrhiza or parasitic plants is well-defined, their involvement in the communication with rhizobia is less clear and some discrepancies still exist. The symbiosis between legumes and rhizobia is generally referred to as nodulation, a process by which the soil bacteria invade the legume roots and form nodules in which the bacteria fix atmospheric nitrogen that is transferred to the plant in exchange for carbohydrates and a protective niche (Markmann and Parniske 2009).

Application of *rac*-GR24 positively affects the nodule number in *Medicago sativa* (alfalfa), with an increase of 30 to 40% compared with untreated controls (Soto et al. 2010). In agreement with these results, transgenic *Lotus japonicus* plants silenced for the strigolactone biosynthesis gene *CAROTENOID CLEAVAGE DIOXYGENASE 7* (*LjCCD7*) develop approximately 20% fewer nodules than the control plants, without alterations in nodule development or morphology (Liu et al. 2013).

Also in *ramosus 1* (*rms1*) mutants of pea, defective in the strigolactone biosynthesis gene *PsCCD8*, approximately 40% fewer nodules are produced, whereas treatment with *rac*-GR24 restores this hyponodulation phenotype (Foo and Davies 2011). In addition, the nodule number decreases significantly in *rms5* mutants, which are defective in *PsCCD7* (Foo et al. 2013), but it increases in the strigolactone-insensitive *rms4* mutant that is affected in the *Arabidopsis* ortholog *MAX2* involved in strigolactone signaling (Foo and Davies 2011). Although this observation contrasts with the data obtained for the *rms1* mutants and the *LjCCD7* lines, *rac*-GR24 treatment could affect the nodule number in a concentration-dependent manner in *Medicago truncatula* (barrel medic), with a stimulating effect at low *rac*-GR24 concentrations and a negative effect at high concentrations (De Cuyper et al. 2015).

As treatment with *rac*-GR24 has no impact on bacterial growth, nodulation factor production, or bacterial calcium spiking, *rac*-GR24 has been suggested to act on the plant side as a plant hormone and not directly on the bacteria, which is in contrast to their role as rhizosphere signaling molecules in the interaction with arbuscular mycorrhizal fungi (Moscatello et al. 2010; Soto et al. 2010). However, the crystal structure of the rice strigolactone receptor D14 resembles that of the *Bacillus subtilis* RsbQ protein that is a stress-response regulator with hydrolase activity (Kagiya et al. 2013), indicating that strigolactones might influence rhizobial cellular activity in a manner different from that tested above. Indeed, a role for strigolactones has been implied in the chemical dialog between plants and rhizobia (Peláez-Vico et al. 2016; Tambalo et al. 2014). For instance, extracts of the moss *Physcomitrella patens* stimulate the swarming motility, i.e., a rapid coordinated movement of bacteria across a surface, in *Rhizobium leguminosarum*, whereas this promoting effect is reduced by extracts from the strigolactone-deficient strain *Physcomitrella patens Ppccd8Δ* (Peláez-Vico et al. 2016; Tambalo et al. 2014). In addition, *rac*-GR24 triggers the swarming motility of *Sinorhizobium meliloti* in a dose-dependent manner (Peláez-Vico et al. 2016). Both studies also describe a correlation between increased surface motility and a stimulation of *flagellin flaA* gene expression in response to either moss extracts or *rac*-GR24, further providing evidence that rhizobia can, indeed, perceive and respond to strigolactones. Whether or not this effect causes the observed changes in nodule number needs further investigation, because changes in rhizobial swarming have been shown to influence nodulation in some cases and not in others (Bernabéu-Roda et al. 2015; Caetano-Anollés et al. 1988; Soto et al. 2002; Wei and Bauer 1999). Taken together, strigolactones might, besides controlling the optimal nodule number as a plant hormone, also act as host detection cues for rhizobia in the rhizosphere, by stimulating bacterial swarming motility and, very probably, the rhizobia-legume symbiosis as well. However, the ecological relevance of this swarming behavior is poorly described and needs to be investigated to better understand the impact on nodulation.

With the exception of their role in communication with rhizobia, no function in dialog with other soil bacteria has been reported for strigolactones until now, but strigolactones have been linked to interaction with different bacteria in the shoot. For instance, in *Arabidopsis*, the *MAX2* protein, implicated in strigolactone signaling, has contributed to plant disease resistance against the bacterial pathogens *Pectobacterium carotovorum* and *Pseudomonas syringae*. The reason for the increased susceptibility to both pathogens of the *max2* mutants might be an enhanced stomatal conductance, promoting pathogen entry into the plant apoplast, a decreased tolerance to apoplastic ROS, and alterations in hormonal balances (Piisilä et al. 2015). Moreover, because both strigolactone biosynthesis and signaling mutants display

enhanced symptoms upon infection with the pathogenic *Rhodococcus fascians*, strigolactones have also been proposed to act as a defense mechanism against leafy gall syndrome indirectly, by inhibiting the outgrowth of newly formed shoots from the leafy galls (Stes et al. 2015). Future studies need to clarify whether strigolactones can also directly interact with pathogenic bacteria and not only indirectly play a role in defense. Interestingly, in rice, grassy stunt disease, characterized by excessive tillering, provoked by the grassy stunt virus is correlated with the suppression of strigolactone biosynthesis and signaling genes (Satoh et al. 2013).

In silico analyses of the promoter regions of strigolactone biosynthesis genes have also revealed a role in biotic stress responses (Marzec and Muszynska 2015). Indeed, in *Arabidopsis* and rice, *cis*-regulatory motifs involved in defense reactions against viruses, bacteria, and fungi have been identified in the promoters of strigolactone biosynthesis genes (Dong et al. 2003; Gutha and Reddy 2008; Kalde et al. 2003; Liu et al. 2007). As a result, the strigolactone biosynthesis pathway could be regulated by specific biotic stress-related transcription factors to protect the plant. To gain more insight into the importance of strigolactones during biotic stress responses, comparative meta-genomics analyses that combine different genotypes (such as strigolactone-deficient and -overproducing lines) and various pathogens need to be done.

A cue for parasitic plants.

To prevent germination in the absence of suitable host roots, parasitic plants have established the need for germination stimulants released by their specific hosts. Strigolactones stimulate the germination of *Striga* spp. (witchweeds), *Orobanch* spp., *Phelipanche* spp., and *Alectra* spp. (broomrapes), all root-parasitic weeds that belong to the Orobanchaceae family and are considered as the most damaging plants for agriculture worldwide (Parker 2009). Indeed, *Striga* spp. parasitize important food crops such as sorghum (*Sorghum bicolor*), maize, millet (*Pennisetum glaucum*), and rice, with enormous yield losses in sub-Saharan Africa and parts of Asia as a consequence (Parker 2009). *Orobanch* and *Phelipanche* species are a major pest for crops growing under a more temperate climate, e.g., tomato, tobacco, carrot (*Daucus carota*), rapeseed (*Brassica napus*), and sunflower (*Helianthus* sp.), and cause huge problems in Europe, the Middle East, and North Africa. The millions of hectares infested by these parasitic plants generate enormous losses in crop yield, estimated to correspond with billions of US\$ (Parker 2009).

The survival and development of most parasitic plants depend fully on the nearby presence of a host plant, because of the slight, or lack of, photosynthetic capacity and of the small storage reserves of their thousands of small seeds (0.2 mm in diameter). The seeds can remain dormant (up to 10 years and more) until they sense specific host-derived germination stimulants, such as strigolactones, that ensure that the parasite germinates only when a host plant is within reach (Cardoso et al. 2011; Tsuchiya and McCourt 2009).

Parasitic plants germinate already in the presence of nanomolar concentrations of *rac*-GR24. Nevertheless, the molecular mechanisms of strigolactone perception and induction of seed germination in parasitic plants are now emerging. In *Arabidopsis*, D14 is characterized as the strigolactone receptor, whereas its paralog, KAI2, is involved in the perception of smoke-derived karrikin molecules (Waters et al. 2012). However, strigolactone perception by the parasites is most probably mediated through a divergent KAI2 receptor, from which the binding pocket has evolved to bind to strigolactones instead of karrikins (Conn et al. 2015). Interestingly, because the divergent parasitic plant KAI2 could complement the

Arabidopsis kai2 mutant and make it highly sensitive to *rac*-GR24-mediated germination but not to karrikin-induced germination, the other members of the signaling complex, in addition to KAI2, are expected to be conserved between parasitic and nonparasitic plants (Conn and Nelson 2016; Toh et al. 2015; Xu et al. 2016).

To be responsive to strigolactones, parasitic seeds need to pass through a conditioning period for a minimum of 4 days under appropriate humidity, temperature, and oxygen conditions (Joel et al. 2012; Lechat et al. 2012). This period is characterized by water uptake via the micropyle, followed by imbibition of the seed and two essential consecutive reductions in abscisic acid levels. The first one is caused by exudation of abscisic acid, whereas the second one results from strigolactone perception. Indeed, the abscisic acid catabolic gene *CYP707A1* catalyzes the breakdown of abscisic acid, and treatment with *rac*-GR24 results in a strong and fast upregulation of this gene in *Phelipanche ramosa*, whereas treatment with a combination of *rac*-GR24 and *CYP707A1* inhibitors blocks *CYP707A1* gene expression and prevents germination (Lechat et al. 2012, 2015). Interestingly, this *CYP707A1* induction depends on the DNA methylation level of its promoter as well as on the 26S proteasome, indicating that *rac*-GR24 can have an influence at both the RNA and protein levels (Lechat et al. 2012). After germination, the root emerges from the seed coat and forms a specialized structure, the haustorium, which fastens and penetrates the host root. Subsequently, this organ is linked with the host vascular system, from which water, carbon, and nutrients are obtained and are used to develop shoots and flowers that can produce seeds again (Cardoso et al. 2011; Press and Phoenix 2005). As a result of this interaction, the host plant will become severely weakened, growth will be impaired, and eventually the plant will die.

Different approaches to eliminate parasitic weeds from agricultural lands have been explored, such as soil treatment with synthetic strigolactones, use of mutants with limited strigolactone production or exudation, and cultivation of trap-and-catch crops, i.e., nonhost species that produce germination stimulants that lead to a suicidal germination of the parasitic plant seeds in the soil. By increasing the strigolactone production and exudation or by switching to more active strigolactone types, more effective trap crops might be created (Waters et al. 2017). Indeed, the search for cost-effective, practical, and targeted strategies still continues (Vurro et al. 2016). Interestingly, a well-established symbiosis with arbuscular mycorrhiza reduces strigolactone levels in the plant as a negative feedback mechanism to avoid excessive colonization (García-Garrido et al. 2009; López-Ráez et al. 2011; Mabrouk et al. 2007). Although it is still unknown whether this reduction in strigolactone levels is due to a direct effect on the strigolactone biosynthesis itself or indirectly through the improvement of the plant nutritional status by the symbiosis, this decrease in strigolactone levels might aid the plant to become less sensitive against parasitic plant infections. Moreover, other soil microorganisms can assist in preventing the germination of parasitic plants by acting as a physiological root barrier and by reducing the strigolactone content in the rhizosphere. For instance, the beneficial fungus *Trichoderma harzianum* detects and metabolizes strigolactones and might be of great value as a bioherbicide in parasitic weed management (Boari et al. 2016). In addition, different plant species produce a different blend of strigolactones, possibly with an impact on the sensitivities to parasitic plants (Čavar et al. 2015). Modification of the strigolactone secretion profile toward a blend to which parasitic plants are insensitive but arbuscular mycorrhizal fungi are not is a possible route to reduce parasitic plant infestations (Yoneyama et al. 2015).

Conclusion.

To establish an interaction between plants and surrounding organisms, a complex chemical dialog takes place, in which both partners exchange information by exudation and perception of different molecules. Here, we discussed strigolactones as plant-derived communication signals. Thus far, strigolactones are well-established communication molecules during arbuscular mycorrhization. As parasitic weeds have evolved to exploit the presence of strigolactones to recognize and infect their host, strigolactones behave as Janus-faced (god with two faces) molecules in the rhizosphere, i.e., they present the plant with a challenge, namely bonding with their friends while hiding from their foes (Fig. 1). Whether they also serve as plant signals toward other beneficial or detrimental rhizospheric microbes is currently less clear. Until now, single models have been studied, consisting of one plant in relation to one microbe. These studies should be strengthened but should go hand-in-hand with microbial community analysis by the application of various “omics” approaches that allow in-depth insights into the microbial diversity of the rhizosphere (Dessaux et al. 2016). With the different strigolactone mutants at hand, precise surveys can be made of the effects of strigolactone exudation on the microbial life in the rhizosphere. From these studies, key interactions influenced by strigolactones will be identified that should be further investigated with dedicated studies to tell us how broadly strigolactones impact on the microbial life in the rhizosphere.

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