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REVIEW

Strigolactones as mediators between fungi and plants

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Abstract
A constantly changing environment is challenging for all organisms on Earth, especially for terrestrial plants, which face several environmental stresses despite their static way of life. In attempts to understand the mechanisms responsible for plant growth and development, scientists have recently focused on a small group of carotenoid derivatives called "strigolactones" (SLs), which are synthesized mostly in the roots in response to a variety of external factors. Strigolactones are compounds that define plant plasticity towards many environmental factors, including the establishment of mycorrhizal symbiosis under nutrient-deficient conditions. As exogenous signals, they can stimulate the branching of arbuscular mycorrhizal fungal (AMF) hyphae and as endogenous signals they adjust a plant architecture, including changes within the roots, allowing host plant and fungi to meet. SLs can also function as signaling molecules that allow colonization and establishment of the later stages of mutualistic symbioses between organisms such as AMF. SLs act on AMF metabolism by stimulating its mitochondrial respiration. Genes encoding enzymes crucial for SL biosynthesis – *CCD7* and *CCD8* – are also found in gymnosperm genomes, which encourages speculation that strigolactones may also be part of a host-plant and ectomycorrhizal fungi signaling pathway during the establishment of symbiosis. Nevertheless, SLs impact on ectomycorrhiza formation remain unknown. The broad spectrum of SL bioactivity has made these compounds valuable from an industrial perspective. In the future, SLs may be commercialized in plant protection products, biostimulants, or as substances used in genetic engineering to allow the creation of crops capable of growing under disadvantageous conditions.

Keywords
plant–microbial interactions; symbiosis; arbuscular mycorrhizal fungal (AMF); ectomycorrhizal fungi (ECM); pathogenic fungi

Strigolactones (SLs): a new class of plant hormones

Strigolactones (SLs) are evolutionarily old signaling molecules that affect plant growth and development. Strigolactones belong to a group of naturally synthesized secondary metabolites with a butenolide ring in their structure (called the D-ring) connected by an ether enol bridge to a second moiety [1,2]. The first indications of the presence of SLs were found while studying the interactions between parasitic plants and their hosts. It was suggested that there may exist a factor that has the ability to stimulate the germination of parasitic plants from the genus *Striga*. Strigol was isolated for the first time in 1966 from cotton root exudates (*Gossypium hirsutum* L.) [3]. Strigolactones participate in the modification of root and shoot architecture and also in the establishment of the symbiosis between plants and microorganisms, e.g., arbuscular mycorrhizal fungi (AMF). This is the basis for the inclusion of SLs in the phytohormone family. SLs have

recently been shown to be active in the following processes: (***i***) photomorphogenesis, secondary growth, (***ii***) leaf senescence, (***iii***) and plant response to stress factors, such as a lack of nutrients or water [4–6]. The wide range of plant–SL interactions, both systemic and environmental, is the reason for the growing scientific and commercial interest. In the future, SLs may be used in plant protection products, e.g., herbicides, or as biostimulators that can boost the efficiency of nutrient intake [7].

The role of strigolactones in symbiotic interactions between arbuscular fungi (AMF) and plants

Mycorrhiza is a widespread phenomenon in the plant kingdom, which relates to more than 90% of terrestrial plant species. The formation of symbiotic radical associations is extremely significant for the physiology of both symbionts and ecosystem stability, which depends on the functionality of the symbiosis [8]. Establishment of arbuscular and ectomycorrhizal symbiosis in plant roots may involve the same factors regulating the recognition of symbionts and further symbiotic actions. Such factors may undoubtedly include strigolactones because the genes responsible for their biosynthesis have been shown to be present in almost all plants that exist in mutualistic relationships with fungi. Currently, research on the secretion of strigolactones is far more advanced in the case of arbuscular mycorrhiza. The main reason for this is the numerous similarities between the early stages of arbuscular mycorrhiza development and the symbiosis between *Rhizobium* bacteria and legumes. The following subsections will present the current knowledge on arbuscular and ectomycorrhizal systems and their SL synthesis activity.

The branching of AMF hyphae towards the roots of its host is considered to be the most important stage in the entire formation of arbuscular mycorrhizae. How does it happen and what kind of role do strigolactones play when released into the rhizosphere? AMF spores can germinate in the soil even when no potential host is nearby, but germinated spores die in the absence of root exudates. This leads to the conclusion that there must be some kind of presymbiotic communication among the symbionts, as is the case in the *Rhizobium*–legume symbiosis, where flavonoids released by the plants are the signal for the transcription of genes vital for the production of bacterial Nod factors. Legume plants are also hosts for AMF, and Becard et al. [9] conducted an experiment in 1995 in which they studied maize mutants that were unable to produce flavonoids. The authors used exudates from transformed carrot roots (because the carrot was the model plant used in the fungal interaction studies) that induced branching in both mutated and wild-type maize at the same level [9]. Before SLs earned their name, they were called branching factors (BFs). In 2005, Akiyama et al. [10] identified a compound called 5-deoxystrigol in *Lotus japonicus* exudates, which is similar to other natural SLs (sorgolactone, strigol, or synthetic SL GR24) caused intensive hyphal branching of *Gigaspora margarita*, a fungus belonging to the AMF family. Furthermore, the characteristics of 5-deoxystrigol conformed with the criteria of the Nagahashi and Douds [11] biotest for chemical analysis and identification of SLs. In 2003, Tamasloukht et al. [12] used partially purified fractions of carrot exudates to show that SLs could induce the expression of mitochondrial fungal genes, along with an intense stimulation of mitochondrial respiration and effects on mitochondrial reorganization prior to the onset of branching. Three years later, Besserer et al. [13] applied the synthetic analogue of SL – GR24 – and noticed an intense and sudden increase in cell proliferation and changes in the shape and amount of mitochondria. Subsequently, Besserer et al. [14] and Besserer and Roux [15] demonstrated that these effects were accompanied by a rapid increase in cell respiration in mitochondria, increased NADH concentration, and an increase in ATP levels in the fungal cells. This kind of mitochondrial activation could lead to the oxygenation of lipids, which are the carbon source found in the AMF spore reserve materials. Thus, SLs may be the key components in root exudates that are capable of triggering lipid catabolism in the presymbiotic stage of plant–fungi interactions. The data discussed above support the hypothesis that SLs participate in specific mechanisms of recognition and signal transduction between the host plant and AMF [16].

Strigolactones play a crucial role in AMF root colonization processes. They are involved in the recognition stage, thus increasing the probability of encountering a root zone that is well adapted to colonization [17]. Inoculation of pea mutants that were unable to produce SLs with AMF spores exhibited significantly lower levels of root colonization compared to that of wild-type plants. GR24 application partially reversed the observed effect [18]. These studies provide the first direct evidence of the essential role that SLs play in the process of hyphae branching, as well as host root colonization. Nevertheless, as García-Garrido et al. [19] rightly pointed out, in the case of mutated plants, that mycorrhization should not occur at all. However, if it takes place, it may indicate that the mutants have a reduced level of SL synthesis, or that these compounds have the ability to stimulate AMF branching and root colonization and the plant can produce other substances that control the mechanisms allowing interaction between the symbionts. In addition, AMF spores can germinate independently, and therefore symbiosis may form in the vicinity of the roots. The effect of GR24 is enigmatic and it is difficult to determine whether it is the result of induction of spore germination or stimulation of hyphae branching. Mutated plants inoculated with GR24 should display a profuse branched fungi phenotype, regardless of the distance between the hyphae and the roots [19]. Hence, an explanation for the mechanisms involved in the interaction of SLs with AMF in the presymbiotic and colonization stage is necessary to answer these emerging questions.

An interesting issue of the previously mentioned study area was the discovery of the diffusible factor from AMF, called Myc factor (or Myc-LCO). Myc factors are lipochitooligosaccharides that are able to activate the early plant response to the following mycorrhization (Fig. 1) through the induction of gene expression related to the transduction pathway and biogenesis of the plant's prepenetration apparatus (PPA) allowing fungi to grow inside the host cells [20]. Despite the suggestions emerging from various studies, the Myc factor transduction is independent of Nod factor transduction. Kosuta et al. [21] conducted a study in which they separated *Gigaspora rosea* spores and transformed *Medicago truncatula* roots (a plant that has the ability to establish symbiosis with both mycorrhizal fungi and rhizobia) with a cellophane membrane that allowed their growth in proximity and signal exchange. The fungal mycelium of *M. truncatula* secreted substances smaller than 3.5 kDa that activated expression of the *MtENOD11* gene. The expression was also synchronized with the induction of hyphae branching. This result could not be observed in the dead spores of AMF or mycelium of pathogenic strains. Another factor confirming this pathway's independence was that *M. truncatula* mutants, unable to form a mycorrhizal or nodule symbiosis, begin the wild-type *MtENOD11* activation when exposed to the AMF [22]. The main challenge of contemporary research is to identify the Myc factors, recognize their signaling pathways, and distinguish plant responses.

The existence of Myc factors is not the only indicator of AMF and rhizobia interactions with plants. In 2000, Vierheilig et al. [23] demonstrated the existence of a plant regulatory mechanism called autoregulation of mycorrhization, which inhibits mycorrhization after a certain level is reached, which was similar to the autoregulation of nodulation (AON) that prevents nodule overgrowth in roots. Autoregulation of mycorrhization is not related to phosphorus availability [24] or to carbon-access competition [25]. The data collected thus far indicate that SL levels in mycorrhizal plants vary over time. According to the Lendzemo and Kuyper [26] research, plants such as sorgo and maize show a high tolerance to plant–parasite infections compared to nonmycorrhizal control plants, which may be associated with the aforementioned autoregulation. It also may be related to the reduced stimulation of parasitic plant germination as a result of reduced SL secretion into the rhizosphere. Thus, mycorrhization can negatively regulate SL production, affecting the branching processes and general progress of AMF colonization. Although only the SLs effect on autoregulation of mycorrhization has been documented, it may not be the only plant mechanism to prevent AMF colonization outgrowth that could cause the mutualistic relation to turn parasitic [19].

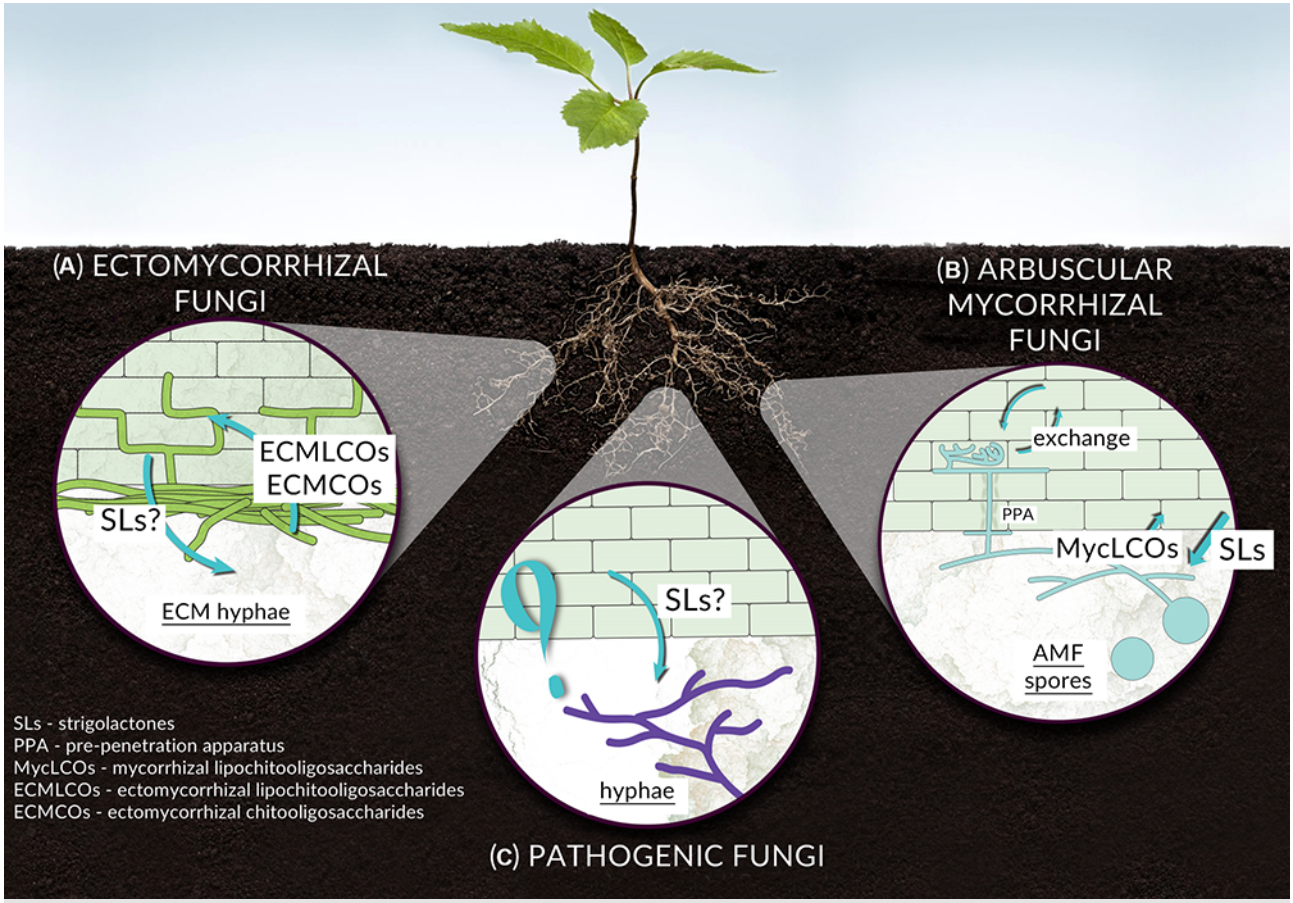

Fig. 1 Schematic summary of the possible root–fungi interactions involving SLs. (**A**) Ectomycorrhiza. The initial stage of ECM symbiosis establishment is the signal exchange between the host and the fungi. Plants secrete a variety of substances with the flavonoids responsible for the stimulation of spore germination [29] and fungi release of the still poorly studied lipochitooligosaccharides (LCO), chitooligosaccharides (CO), and small secreted proteins (SSP). The current lack of research conducted on the SL–ECF relationship makes it impossible to assume with certainty that SLs are not involved in the signaling mechanisms, as they can act on pathways other than recognition symbiosis pathways or interact with fungal effectors [31]. (**B**) Arbuscular mycorrhiza. SLs are proven to act in the presymbiotic stage as triggering spore-germination signals when released into the soil in the proximity of AMF spores. Secreted SLs along with other plant exudates induce the expression of fungal mitochondrial genes followed by an intense stimulation of mitochondrial respiration with increased NADH and ATP concentration in the fungal cells [12,14,15]. This is the proposed way in which lipid catabolism allowing spores to germinate is activated through host–fungi signaling. After germination, SLs allow fungal hyphae to branch towards the roots prior to the proper recognition of symbionts, leading to the activation of the fungal signaling pathway and the release of Myc lipochitooligosaccharides (MycLCOs). Subsequently, MycLCOs induce the expression of *NOD* genes that is correlated with the induction of hyphae branching [22]. (**C**) Pathogenic fungi interactions. In the preliminary data, SLs were not found to induce hyphal branching or respiration processes of the examined plant pathogens [30,34]. Even though there is no clear evidence that SLs are or are not a part of a host–pathogen signaling relation, it is an area that is interesting and undoubtedly tempting to explore, with some indications that SLs may be engaged in this process as signals preventing infection by promoting AM symbiosis.

Strigolactones and ectomycorrhizal fungi (ECM)

Although there are seven types of mycorrhizal [27] associations, it is the previously mentioned arbuscular mycorrhiza (endomycorrhiza) and ectomycorrhiza that are considered the most ecologically and economically important. However, the arbuscular mycorrhiza is the most widely studied type and consequently, the mechanisms associated with arbuscular mycorrhiza establishment in host plants and fungi are far better understood than those of ECM symbiosis. The initial stage of ectomycorrhiza formation includes a signal exchange between the two symbionts. Plants secrete primary and secondary metabolites, along with sugars, hormones, and enzymes that can affect the root microbiome. In 1987, Fries et al. [28] showed that abietic acid present in *Pinus sylvestris* root exudates stimulated *Suillus* spp. spore germination. The molecules responsible were flavonoids – rutin secreted by *Eucalyptus globulus* spp. bisocata stimulated the growth of *Pisolithus* spp. hyphae [29]. When data confirming the positive activity of SLs towards AMF was published [10], researchers realized a new possibility regarding the

possible roles of SLs with respect to both types of mycorrhiza. Steinkellner et al. [30] conducted a study that included the ectomycorrhizal fungi *Paxillus involutus*, *Laccaria bicolor*, *Amanita muscaria*, and *Cenococcum geophilum*. None of these expressed any changes in branching patterns after the application of exogenous GR24. Nevertheless, this preliminary data should be confirmed. Furthermore, SLs may activate symbiosis pathways or positively affect the production of effectors or fungal chitin signals (Fig. 1) [31]. There are still many questions regarding whether fungal compounds, such as lipochitooligosaccharides (LCO), chitooligosaccharides (COs), small secreted protein (SSP), and plant hormones, affect the early stages of ECM symbiosis formation [32]. SLs are found in almost all terrestrial plants, they are synthesized at lower concentrations even in nonhost plants, and CCD7 and CCD8 enzymes were found to play a key role in SL biosynthesis in genomes and transcriptomes of gymnosperms. Consequently, research on the relationship between ECM symbiosis and strigolactone should be continued.

Strigolactones and pathogenic fungi

In the section focused on AMF it was stated that the stimulating effect of SLs on AMF spore germination has been documented, but do SLs work in a similar way for plant pathogens? In research by Steinkellner et al. [30], the authors sought to establish whether the SL synthetic analogue GR24 could stimulate the microconidia germination of *Fusarium oxysporum* f. sp. *lycopersici*. The results were negative, suggesting that SLs may act as specific signals for AMF. GR24 effects on hyphal branching patterns were also examined for soil-borne pathogens (*Rhizoctonia solani*, *Fusarium oxysporum*, *Verticillum dahlia*) and aerial plant-part pathogens (*Botrytis cinerea*, *Cladosporium* sp.) with the same result, indicating no effects on their growth [30]. Another study conducted in 2001 by Martinez et al. [33] showed that fractions of maize root exudates could induce the transition of yeast to a hyphal form. In later research, Sabbagh [34] analyzed the transcriptome expression of a haploid strain of *S. reilianum* using different concentrations of GR24, and most of the expressed sequence tag (EST) after SL application was related to genes taking part in cell respiration processes. Exogenous GR24 effects on *Ustilago maydis*, a fungus causing smut on maize, induced genes involved in cell respiration at 1 h, increased the process at 5 h, and stopped it at 8 h postsupplementation; further analysis of cells induced at 8 h showed the lack of any candidate gene transcripts [34]. Even if strigolactones do not affect the pathogenicity pathway of other fungi, they can still be used as compounds to prevent host plants from being infected through the promotion of arbuscular mycorrhiza formation.

Possible uses of strigolactones in industry

SLs are characterized by high activity and effectiveness in biological systems. Thus, research into their potential use is being intensified. SLs may be used as biofertilizers thereby indirectly promoting the initiation and establishment of AMF symbiosis or Rhizobium–legume symbiosis because microorganism associations are the primary way plants cope with a lack of nutrition [7]. However, there are numerous problems standing in the way of commercialized products based on SL bioactivity. High SL production costs exist primarily because the method of their laboratory synthesis has not yet been optimized. The high lability of SLs hampers the processes to isolate and purify them. The isolation is exceptionally hard to perform because the natural synthesis of SL is very limited. For example, cotton synthesizing two naturally occurring strigolactones – strigol and strigol acetate – can secrete 15 and 2 pg/plant/day, respectively [35]. Consequently, their mass production would require appropriate laboratory equipment and a specially developed methodology. Attempts to accumulate SLs in a culture medium failed because of their rapid degradation. Strigol and its analogues are highly susceptible to hydrolysis in alkaline media because of the high reactivity of their enol ether bridge. In the most recent studies, a mixture of a synthetic SL analogue – GR24 – can last up to 10 days in a

neutral pH, whereas 5-deoxystrigol only lasts 1.5 days. The stability of SLs in the soil is one of the most important aspects of their future use because of the DDT effect, which is known to this day. On the other hand, their chemical structure needs to be refined, so it could prevent their rapid hydrolysis. Therefore, plant cultures are not the most efficient method for SL acquisition and organic synthesis is complicated because of the lack of knowledge regarding some of the natural biosynthesis stages of SLs [7]. There are still many unknowns that need to be identified before we will be able to synthesize SL products for the market.

Summary

Plants exhibit a high degree of plasticity towards environmental conditions. SLs may be molecules that play a key role in plant reactions because they act as (***i***) exogenous signals perceived by microorganisms in their vicinity and (***ii***) endogenous compounds regulating the shoot and root architecture according to plant needs. In both cases, the SL signaling pathways are a response to environmental factors, such as nutrient availability, temperature, light, or biotic stress. Interactions occurring with SLs and other phytohormones that allow plants to respond correctly have yet to be investigated at the cellular and molecular level. One very interesting yet poorly understood issue is that of SL interactions with microorganisms other than AMF. The predicted ubiquity of SLs in a variety of land plants and numerous questions related to their activity indicate the enormous need for further research in this area. New technologies, growing interest and investments from agrobiotechnological companies, combined with an increase in data, may have a positive effect in the future on the final legislation of SL products, allowing them to be introduced on the market.

References

1. Al-Babili S, Bouwmeester HJ. Strigolactones, a novel carotenoid-derived plant hormone. Annu Rev Plant Biol. 2015;66(1):161–186. https://doi.org/10.1146/annurev-arplant-043014-114759
2. Lopez-Obando M, Ligerot Y, Bonhomme S, Boyer FD, Rameau C. Strigolactone biosynthesis and signaling in plant development. Development. 2015;142(21):3615–3619. https://doi.org/10.1242/dev.120006
3. Cook CE, Whichard LP, Turner B, Wall ME, Egley GH. Germination of witchweed (*Striga lutea* Lour.): isolation and properties of a potent stimulant. Science. 1966;154(3753):1189–1190. https://doi.org/10.1126/science.154.3753.1189
4. Shen H, Zhu L, Bu QY, Huq E. MAX2 affects multiple hormones to promote photomorphogenesis. Mol Plant. 2012;5(3):750–762. https://doi.org/10.1093/mp/sss029
5. Agusti J, Herold S, Schwarz M, Sanchez P, Ljung K, Dun EA, et al. Strigolactone signaling is required for auxin-dependent stimulation of secondary growth in plants. Proc Natl Acad Sci USA. 2011;108(50):20242–20247. https://doi.org/10.1073/pnas.1111902108
6. Bu Q, Lv T, Shen H, Luong P, Wang J, Wang Z, et al. Regulation of drought tolerance by the F-box protein MAX2 in *Arabidopsis*. Plant Physiol. 2014;164(1):424–439. https://doi.org/10.1104/pp.113.226837
7. Vurro M, Prandi C, Baroccio F. Strigolactones: how far is their commercial use for agricultural purposes? Pest Manag Sci. 2016;72(11):2026–2034. https://doi.org/10.1002/ps.4254
8. Raudaskoski M, Kothe E. Novel findings on the role of signal exchange in arbuscular and ectomycorrhizal symbioses. Mycorrhiza. 2015;25(4):243–252. https://doi.org/10.1007/s00572-014-0607-2
9. Becard G, Taylor LP, Douds DD, Pfeffer PE, Doner LW. Flavonoids are not necessary plant signal compounds in arbuscular mycorrhizal symbioses. Mol Plant Microbe Interact. 1995;8:252. https://doi.org/10.1094/MPMI-8-0252

10. Akiyama K, Matsuzaki KI, Hayashi H. Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. Nature. 2005;435(7043):824–827. https://doi.org/10.1038/nature03608

11. Nagahashi G, Douds DD. Rapid and sensitive bioassay to study signals between root exudates and arbuscular mycorrhizal fungi. Biotechnology Techniques. 1999;13(12):893–897. https://doi.org/10.1023/A:1008938527757

12. Tamasloukht M, Séjalon-Delmas N, Kluever A, Jauneau A, Roux C, Bécard G, et al. Root factors induce mitochondrial-related gene expression and fungal respiration during the developmental switch from asymbiosis to presymbiosis in the arbuscular mycorrhizal fungus *Gigaspora rosea*. Plant Physiol. 2003;131(3):1468–1478. https://doi.org/10.1104/pp.012898

13. Besserer A, Puech-Pagès V, Kiefer P, Gomez-Roldan V, Jauneau A, Roy S, et al. Strigolactones stimulate arbuscular mycorrhizal fungi by activating mitochondria. PLoS Biol. 2006;4(7):1239–1247. https://doi.org/10.1371/journal.pbio.0040226

14. Besserer A, Becard G, Jauneau A, Roux C, Sejalon-Delmas N. GR24, a synthetic analog of strigolactones, stimulates the mitosis and growth of the arbuscular mycorrhizal fungus *Gigaspora rosea* by boosting its energy metabolism. Plant Physiol. 2008;148(1):402–413. https://doi.org/10.1104/pp.108.121400

15. Besserer A, Roux C. Role of mitochondria in the response of arbuscular mycorrhizal fungi to strigolactones. Plant Signal Behav. 2009;1(4):75–77. https://doi.org/10.4161/psb.4.1.7419

16. Bouwmeester HJ, Roux C, Lopez-Raez JA, Bécard G. Rhizosphere communication of plants, parasitic plants and AM fungi. Trends Plant Sci. 2007;12:224–230. https://doi.org/10.1016/j.tplants.2007.03.009

17. Nagahashi G, Douds DD. Partial separation of root exudate components and their effects upon the growth of germinated spores of AM fungi. Mycol Res. 2000;104(12):1453–1464. https://doi.org/10.1017/S0953756200002860

18. Gomez-Roldan V, Fermas S, Brewer PB, Puech-Pagès V, Dun EA, Pillot JP, et al. Strigolactone inhibition of shoot branching. Nature. 2008;455(7210):189–194. https://doi.org/10.1038/nature07271

19. García-Garrido JM, Lendzemo V, Castellanos-Morales V, Steinkellner S, Vierheilig H. Strigolactones, signals for parasitic plants and arbuscular mycorrhizal fungi. Mycorrhiza. 2009;19(7):449–459. https://doi.org/10.1007/s00572-009-0265-y

20. Harrison MJ. Cellular programs for arbuscular mycorrhizal symbiosis. Curr Opin Plant Biol. 2012;15:691–698. https://doi.org/10.1016/j.pbi.2012.08.010

21. Kosuta S, Chabaud M, Lougnon G. A diffusible factor from arbuscular mycorrhizal fungi induces symbiosis-specific *MtENOD11* expression in roots of *Medicago truncatula*. Plant Physiol. 2003;131(3):952–962. https://doi.org/10.1104/pp.011882

22. Catoira R. Four Genes of *Medicago truncatula* controlling components of a Nod factor transduction pathway. Plant Cell. 2000;12(9):1647–1666. https://doi.org/10.1105/tpc.12.9.1647

23. Vierheilig H, Garcia-Garrido JM, Wyss U, Piché Y. Systemic suppression of mycorrhizal colonization of barley roots already colonized by AM fungi. Soil Biol Biochem. 2000;32(5):589–595. https://doi.org/10.1016/S0038-0717(99)00155-8

24. Vierheilig H, Maier W, Wyss U, Samson J, Strack D, Piche Y. Cyclohexenone derivative- and phosphate-levels in split-root systems and their role in the systemic suppression of mycorrhization in precolonized barley plants. J Plant Physiol. 2000;157(6):593–599. https://doi.org/10.1016/S0176-1617(00)80001-2

25. Lerat S, Lapointe L, Gutjahr S, Piché Y, Vierheilig H. Carbon partitioning in a split-root system of arbuscular mycorrhizal plants is fungal and plant species dependent. New Phytol. 2003;157(3):589–595. https://doi.org/10.1046/j.1469-8137.2003.00691.x

26. Lendzemo VW, Kuyper TW. Effects of arbuscular mycorrhizal fungi on damage by *Striga hermonthica* on two contrasting cultivars of sorghum, *Sorghum bicolor*. Agric Ecosyst Environ. 2001;87(1):29–35. https://doi.org/10.1016/S0167-8809(00)00293-0

27. Harley JL, Smith SE. Mycorrhizal symbiosis. London: Academic Press Inc.; 1983.

28. Fries N, Serck-Hanssen K, Dimberg LH, Theander O. Abietic acid, and activator of basidiospore germination in ectomycorrhizal species of the genus *Suillus* (Boletaceae). Exp Mycol. 1987;11(4):360–363. https://doi.org/10.1016/0147-5975(87)90024-7

29. Lagrange H, Jay-Allgmand C, Lapeyrie F. Rutin, the phenolglycoside from eucalyptus

root exudates, stimulates *Pisolithus* hyphal growth at picomolar concentrations. New Phytol. 2001;149(2):349–355. https://doi.org/10.1046/j.1469-8137.2001.00027.x

30. Steinkellner S, Lendzemo V, Langer I, Schweiger P, Khaosaad T, Toussaint JP, et al. Flavonoids and strigolactones in root exudates as signals in symbiotic and pathogenic plant–fungus interactions. Molecules. 2007;12(7):1290–1306. https://doi.org/10.3390/12071290
31. Genre A, Chabaud M, Balzergue C, Puech-Pagès V, Novero M, Rey T, et al. Short-chain chitin oligomers from arbuscular mycorrhizal fungi trigger nuclear Ca^{2+} spiking in *Medicago truncatula* roots and their production is enhanced by strigolactone. New Phytol. 2013;198(1):190–202. https://doi.org/10.1111/nph.12146
32. Garcia K, Delaux PM, Cope KR, Ané JM. Molecular signals required for the establishment and maintenance of ectomycorrhizal symbioses. New Phytol. 2015;208:79–87. https://doi.org/10.1111/nph.13423
33. Martinez C, Buée M, Jauneau A, Bécard G, Dargent R, Roux C. Effects of a fraction from maize root exudates on haploid strains of *Sporisorium reilianum* f. sp. *zeae*. Plant Soil. 2001;236(2):145–153. https://doi.org/10.1023/A:1012776919384
34. Sabbagh SK. Effect of GR24, a synthetic analogue of strigolactones, on gene expression of solopathogenic strain of *Sporisorium reilianum*. Afr J Biotechnol. 2011;10(70):15739–15743. https://doi.org/10.5897/AJB11.393
35. Sato D, Awad AA, Takeuchi Y, Yoneyama K. Confirmation and quantification of strigolactones, germination stimulants for root parasitic plants *Striga* and *Orobanche*, produced by cotton. Biosci Biotechnol Biochem. 2005;69(1):98–102. https://doi.org/10.1271/bbb.69.98