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Review

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Phytohormones as integrators of environmental signals in the regulation of mycorrhizal symbioses

María J. Pozo, Juan A. López-Ráez, Concepción Azcón-Aguilar and José M. García-Garrido

Department of Soil Microbiology and Symbiotic Systems, Estación Experimental del Zaidín (CSIC), Granada, Spain

Author for correspondence:
María J. Pozo
Tel: +34 958 181600 ext. 233
Email: mjpozo@eez.csic.es

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Summary

For survival, plants have to efficiently adjust their phenotype to environmental challenges, finely coordinating their responses to balance growth and defence. Such phenotypic plasticity can be modulated by their associated microbiota. The widespread mycorrhizal symbioses modify plant responses to external stimuli, generally improving the resilience of the symbiotic system to environmental stresses. Phytohormones, central regulators of plant development and immunity, are instrumental in orchestrating plant responses to the fluctuating environment, but also in the regulation of mycorrhizal symbioses. Exciting advances in the molecular regulation of phytohormone signalling are providing mechanistic insights into how plants coordinate their responses to environmental cues and mycorrhizal functioning. Here, we summarize how these mechanisms permit the fine-tuning of the symbiosis according to the ever-changing environment.

I. Introduction

Plants are dynamic systems able to continuously adapt to changing environmental conditions, showing a remarkable phenotypic plasticity. This is particularly advantageous in heterogeneous environments where precise allocation of limited resources between growth and defence is critical for survival (Goh *et al.*, 2013). In the 'omics' era, functional approaches have provided evidence of the convergence of signalling pathways regulating plant responses to developmental cues and abiotic and biotic stress factors. They have highlighted the role of phytohormones and redox signalling, and identified key regulatory elements – *molecular hubs* – where multiple signalling cascades converge (Fig. 1). The integration of multiple signals through these hubs allows the plant to fine-tune its response to particular conditions (Sparks *et al.*, 2013).

Beneficial microbes can enhance plant fitness by alleviating the effect of stress factors. They can directly remove or diminish the stress, for example by increasing nutrient availability or antagonizing pathogens, but they can also affect plant phenotypic plasticity in

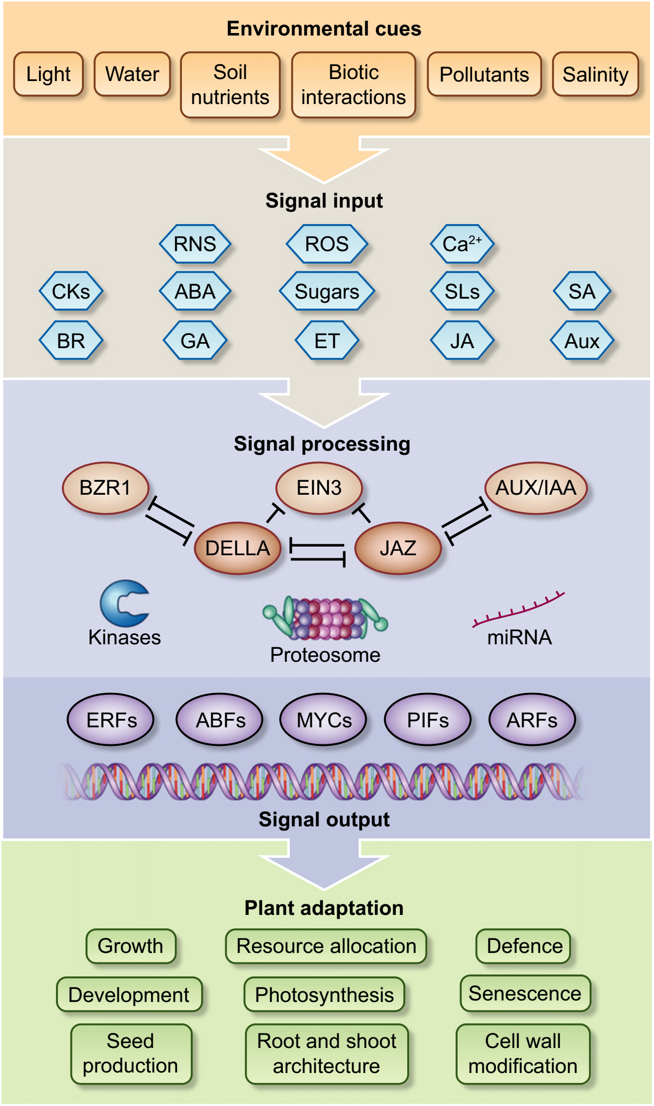

Fig. 1 Integrative model describing how plants perceive and respond to environmental cues. Perception of environmental cues alters the concentrations of several phytohormones and other signalling compounds (signal input). They trigger signalling cascades regulating activators/repressors and transcription factors that can interact with each other, thus processing and integrating the multiple signals (signal processing). Typically, the binding of the hormones to their receptors regulates master regulators (e.g. repressor proteins DELLA, JASMONATE ZIM DOMAIN (JAZ) and AUX/IAA, ETHYLENE INSENSITIVE 3 (EIN3) protein and BRASSINAZOLE RESISTANT 1 (BZR1) protein, for gibberellin, jasmonate, auxin and brassinosteroid signalling, respectively) through post-transcriptional modifications and/or proteasome-mediated degradation. This enables specific families of transcription factors (e.g. ETHYLENE RESPONSE FACTORS (ERFs), ABA RESPONSIVE ELEMENT BINDING FACTORS (ABFs), JA-related, MYC-type basic helix-loop-helix transcription factors (MYCs), PHYTOCHROME INTERACTING FACTORS (PIFs) and AUXIN RESPONSE FACTORS (ARFs)) to activate transcriptional responses. Interactions among the regulators mediate pathway crosstalk, so they act as molecular hubs integrating multiple signalling cascades to shape the final response. This signal processing enables plants to flexibly respond and adapt their phenotype to their context (signal output). The lists are not exhaustive as only major regulators and transcription factor families are included for clarity. Blunt-ended bars indicate negative interactions. RNS, reactive nitrogen species; ROS, reactive oxigen species; CKs, citokinins; ABA, abscisic acid; SLs, strigolactones; SA, salycilic acid; BR, brassinosteroids; GA, gibberellins; ET, ethylene; JA, jasmonates; Aux, Auxin.

a broad range of traits towards improved resistance or tolerance to stress situations (Goh *et al.*, 2013). Interestingly, plants can often regulate their interaction with microbes according to external conditions, promoting some over others, and even modulating microbial behaviour (Laksmanan *et al.*, 2014).

Among the most widespread beneficial microbe–plant associations are the arbuscular mycorrhizas (AMs), mutualistic symbioses established between soil fungi from the phylum Glomeromycota and most plants. An extensive network of fungal hyphae increases the plant's exploratory capacity for water and mineral nutrients, while specialized fungal structures called arbuscules develop within root cells to facilitate nutrient exchange between the partners (Gutjahr & Parniske, 2013). In addition to improving plant nutrition, the symbiosis can induce significant changes in multiple host traits, such as root architecture, growth, flowering and stress tolerance, processes that are all regulated by phytohormones (Ruiz-Lozano *et al.*, 2012; Selosse *et al.*, 2014). AM establishment is finely regulated, and the final outcome of the interaction is highly context dependent (Hoeksema *et al.*, 2010; Pineda *et al.*, 2013). Remarkably, nearly all phytohormones studied to date appear to play a role in AM formation and/or functioning, although there are still big gaps in our understanding of how they act to integrate environmental cues and regulate mycorrhizal interactions accordingly. This review presents an integrative overview of the latest research on phytohormone-mediated regulation of AM symbiosis in the context of ever-changing environments, building on a wealth of earlier research on phytohormone signalling (Pieterse *et al.*, 2012; Vanstraelen & Benková, 2012 and references therein).

II. Hormonal balance regulates plant growth and defence

Phytohormones are small molecules that act at low concentrations as versatile regulators in almost every developmental and defence process in plants. They enable the transduction of environmental cues into plastic responses, for instance, regulating changes in root system architecture in response to phosphorous (P) starvation, balancing plant growth and defence according to light quality, or shaping the appropriate immune response to particular attackers while modulating beneficial interactions (Fig. 1) (reviewed in Pieterse *et al.*, 2012; Vanstraelen & Benková, 2012).

Far from acting independently, phytohormones interact either synergistically or antagonistically, depending on the cellular context. This *hormone crosstalk* regulates a plethora of functions, challenging the traditional distinction between developmental – auxins, gibberellins, brassinosteroids, cytokinins and strigolactones – and stress hormones – salicylates, jasmonates, ethylene, and abscisic acid (ABA). For example, jasmonates are crucial in the coordination of defence responses to attackers through interactions with the salicylate, ethylene and ABA pathways, but they also regulate growth and development, interacting with auxins and gibberellins (Wasternack & Hause, 2013). Similarly, strigolactones regulate above- and below-ground plant architecture in interaction with auxins (Ruyter-Spira *et al.*, 2013), but they also modulate stress responses through interactions with ABA or jasmonate signalling (Ha *et al.*, 2014; Torres-Vera *et al.*, 2014).

Perception of environmental stimuli results in differential accumulation of these phytohormones and other signal molecules, such as small RNAs and reactive oxygen and nitrogen species. Then, binding of the hormones to their receptors initiates signalling cascades that involve multiple molecular regulators, including a variety of protein activators and repressors and transcription factors (Fig. 1). Protein–protein interactions are instrumental for pathway interactions, and the stability of the protein regulators, controlled by targeted degradation through the proteasome, is a keystone in hormone signalling (Shabek & Zheng, 2014). For example, DELLA and JAZ proteins, key repressors of gibberellins and jasmonate signalling, respectively, interact to integrate both pathways to balance growth and defence. Their stability mediates the promotion of plant defences under nonshady conditions, but also stem and petiole elongation and reduced disease resistance under shady conditions (Ballaré, 2014). They also mediate the interactions with other pathways, such as ethylene and brassinosteroid signalling. The dose-dependent regulation of DELLA stability by gibberellins, but also by auxins, ethylene, light and other external signals, makes these proteins master regulators of plant responses (Xu *et al.*, 2014). Downstream, several families of transcription factors are also crucial for mediating the pathway interactions shaping the final responses (Fig. 1) (Buscaill & Rivas, 2014). Sugars also play a role in fine-tuning growth and defence by integrating, together with hormones, local molecular events with systemic responses (Ruan, 2014). Indeed, the regulation of the signal distribution across tissues/organs is essential to achieve efficiently coordinated systemic plant responses (Sparks *et al.*, 2013).

III. Phytohormones control the arbuscular mycorrhizal symbiosis

Phytohormones also interact to regulate the establishment and functioning of the AM symbiosis (Foo *et al.*, 2013; Bucher *et al.*, 2014; Gutjahr, 2014). Most evidence derives from pharmacological or genetic approaches through the analysis of plants with altered hormone biosynthesis or signalling (Supporting Information Table S1). Some hormones control the early steps of the interaction mediating pre-symbiotic signalling, while others regulate root morphological adaptations to accommodate the fungus, control the extension of fungal colonization or control symbiosis functionality (Fig. 2).

Fungal and plant exudates are important in the first colonization steps. The concentrations and structural features of the strigolactones secreted by the plant are important for AM fungal development (Ruyter-Spira *et al.*, 2013), and fungal chitin oligomers, stimulated by strigolactones, trigger the symbiotic programme in the root (Gutjahr, 2014). Salicylates, ethylene and cytokinins have negative effects at the fungal penetration or root colonization steps (Fig. 2) (Foo *et al.*, 2013). At later stages, phytohormones also regulate arbuscule development and lifespan (Fig. 2) (Gutjahr & Parniske, 2013). Biologically active gibberellins suppress arbuscule development and, accordingly, the DELLA repressors are essential for their formation (Floss *et al.*, 2013; Foo *et al.*, 2013; Martín-Rodríguez *et al.*, 2014). By contrast, ABA and auxins positively regulate arbuscule development and functionality (Martín-Rodríguez *et al.*, 2011; Etemadi *et al.*, 2014), and positive and negative effects have been described for jasmonates (Wasternack & Hause, 2013).

As in other plant processes, the impact of hormones on mycorrhizas depends on pathway crosstalk. The mainly antagonic interactions of ABA–ethylene and ABA–gibberellins regulate AM development and arbuscule formation, respectively

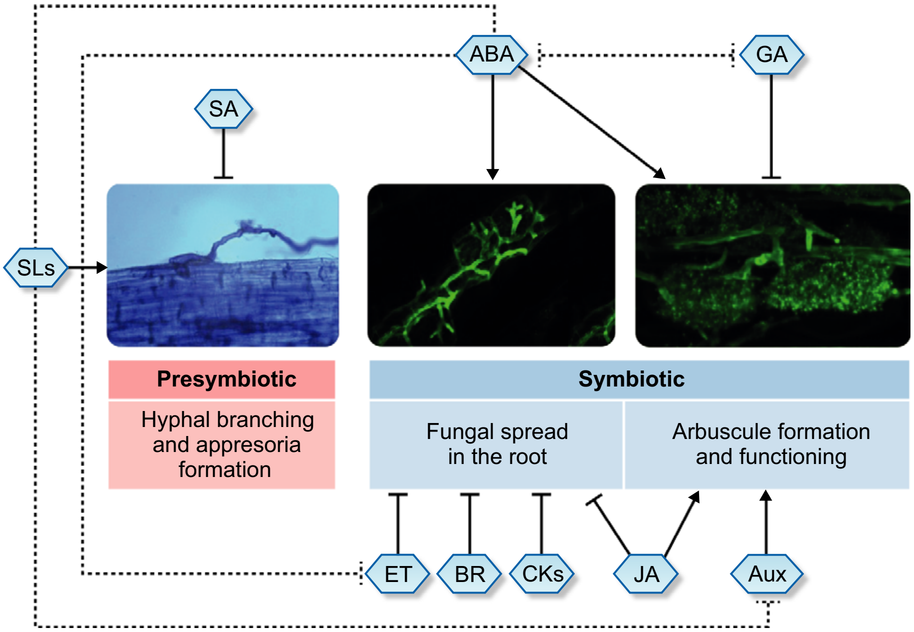

Fig. 2 Phytohormone regulation of arbuscular mycorrhiza (AM) formation and functioning. The scheme summarizes the role of plant hormones in different stages of mycorrhiza development (presymbiotic, fungal hypha branching and appresoria formation; symbiotic, fungal colonization of the root cortex and arbuscule formation and functioning). Positive and negative effects are illustrated by arrows and blunt-ended bars, respectively, and dashed lines indicate interactions suggested to play a role in AM regulation. Multiple functions can be envisaged for a particular hormonal group and, conversely, multiple hormones interact to fine-tune particular functions. ABA, abscisic acid; Aux, auxins; BR, brassinosteroids; CKs, cytokinins; ET, ethylene; GA, gibberellins; JA, jasmonates; SA, salicylic acid; SLs, strigolactones.

(Martín-Rodríguez *et al.*, 2011; Gutjahr, 2014). Elements of sugar signalling also interact with jasmonates and brassinosteroids to finely modulate mycorrhizas (Bitterlich *et al.*, 2014). Thus, it is likely that the molecular hubs in hormone crosstalk integrate external and developmental cues with symbiotic programmes during mycorrhiza formation (Gutjahr, 2014). Accordingly, the gibberellin–DELLA complex may play a pivotal role in the control of the symbiosis according to the physiological status of the plant under particular environmental conditions.

As in plant–pathogen interactions, mycorrhizal fungi have evolved strategies to manipulate host signalling to promote colonization through the secretion of protein effectors. Remarkably, the only functional secreted effectors characterized to date in mycorrhizal fungi target phytohormone signalling hubs. SP7 (Secreted Protein 7), secreted by the AM fungus *Rhizophagus irregularis,* interacts with an ETHYLENE RESPONSE FACTOR (ERP) to suppress ethylene signalling (Kloppholz *et al.*, 2011) and MiSSP7 (Mycorrhiza induced small secreted protein 7) from the ectomycorrhizal fungus *Laccaria bicolor* stabilizes a JAZ repressor of jasmonate signalling (Plett *et al.*, 2014). As a larger repertoire of fungal effectors has been predicted, it is likely that different effectors may target different host signalling processes at specific stages of mycorrhizal interactions.

IV. Environmental conditions have an impact on the partner's interactions

The plant–AM fungus relationship varies with multiple factors including the partners' genotypes and their biotic context, successional stages, light intensity and nutrient availability (Hoeksema *et al.*, 2010). The effects of nutrient availability and plant nutritional status on the symbiosis are the best studied, and the involvement of phytohormones is well established. P deficiency promotes the symbiosis by increasing strigolactone biosynthesis and reducing shoot cytokinin signalling to the root, thereby favouring mycorrhiza formation (Cosme & Wurst, 2013; Fusconi, 2014). By contrast, poor development of arbuscules is observed under high-P conditions, probably associated with the destabilization of DELLAs (Floss *et al.*, 2013). A stimulatory effect of nitrogen (N) deficiency on AM symbiosis has also been reported, although its effect seems to be generally weaker than that of P deficiency (Nouri *et al.*, 2014). As for P, promotion of strigolactones by N deprivation has been reported (Ruyter-Spira *et al.*, 2013). Conversely, strigolactone biosynthesis is reduced in well-established mycorrhizas, maybe as a consequence of a better nutritional status or autoregulation mechanisms of the host aiming to prevent over-colonization (López-Ráez *et al.*, 2015). The concentrations of other essential mineral nutrients such as iron, potassium and calcium do not appear to affect mycorrhiza formation (Nouri *et al.*, 2014).

Water-related stresses such as drought and salinity also affect AM symbiosis. Experimental data do not support a general increase in AM colonization under such conditions, but mycorrhizal plants perform better (Ruiz-Lozano *et al.*, 2012; Aroca *et al.*, 2013). ABA regulation in response to these stresses is altered in mycorrhizal roots and an increase in strigolactone production under salinity has been reported in the presence of AM fungi (Aroca *et al.*, 2013). Thus, stress-induced ABA and strigolactones may actively promote AM function.

The biotic context also influences mycorrhizas. Multiple direct interactions occur in the rhizosphere, but plant-mediated effects of above-ground communities on AM have also been described. Phloem-feeding aphids and early season herbivory reduce AM fungal colonization, although reports of increases also exist (Barto &

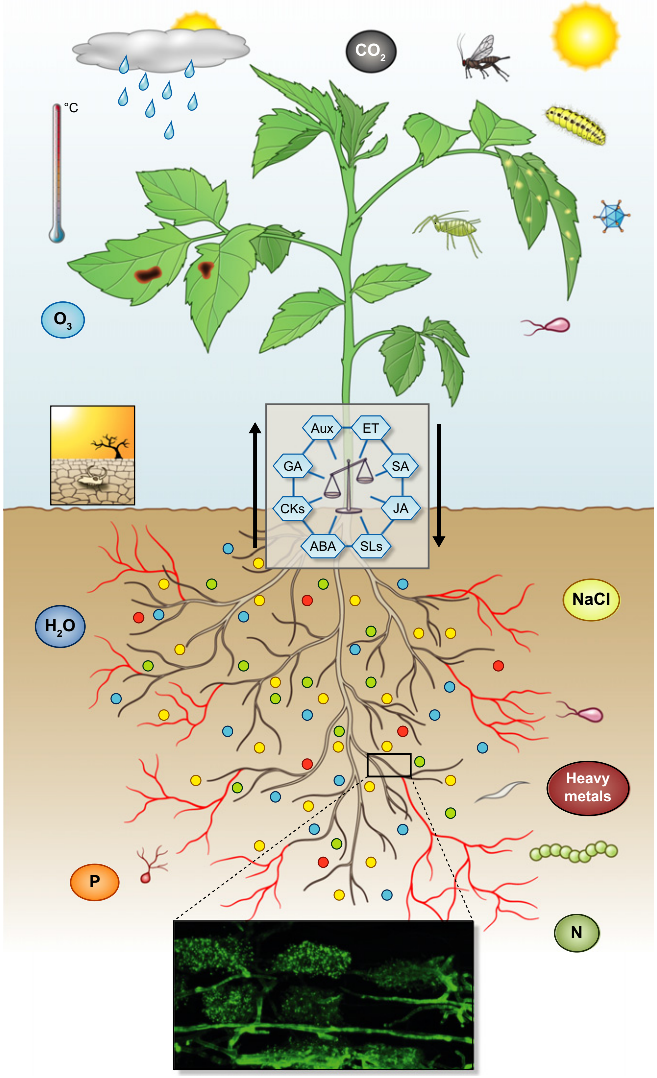

Fig. 3 Phytohormones as mediators of the context dependence of mycorrhiza establishment and function. Plants adjust their phenotype according to nutrient availability, light, and other abiotic and biotic factors through precise spatio-temporal signalling regulation. Phytohormone networks integrate plant responses to the different cues and mycorrhiza formation and function. Hormone homeostasis has an impact on, and is impacted by, the mycorrhizal symbiosis. Thus, the phytohormone signalling hubs may allow the plant to orchestrate the symbiosis according to its physiological needs under particular environmental conditions, and mediate the fine-tuning of the plant response by mycorrhizas. Holistic approaches are required to understand the contribution of phytohormone signalling to the context dependence of mycorrhizal interactions and the effects of the symbiosis on plant adaptation to the ever-changing environments. ABA, abscisic acid; Aux, auxins; BR, brassinosteroids; CKs, cytokinins; ET, ethylene; GA, gibberellins; JA, jasmonates; SA, salicylic acid; SLs, strigolactones.

Rillig, 2010; Babikova *et al.*, 2014). The plant, and the type and frequency of herbivory seem to be determinants of the final outcome. Although host carbon (C) limitation or reallocation may explain some of the patterns, meta-analyses challenge the C limitation hypothesis, suggesting the contribution of other mechanisms (Barto & Rillig, 2010). As shoot herbivory alters root-hormone profiles (Fragoso *et al.*, 2014), these changes may contribute to the effects on AM. Evidence of systemic signalling in mycorrhizas exists, such as wounding of *Medicago* leaves resulting in jasmonate-mediated promotion of AM colonization (Landgraf *et al.*, 2012).

V. Mycorrhizal symbiosis alters hormone homeostasis in the host and its response to environmental challenges

Phytohormone homeostasis is altered in mycorrhizal plants, and this alteration has been associated with their enhanced tolerance to stresses (Fernández *et al.*, 2014; Selosse *et al.*, 2014). Arbuscular mycorrhizal formation changes root architecture which is important for anchoring, water and nutrient uptake, plant associations and stress tolerance. Root architecture is regulated by the concerted action of cytokinins, auxins and strigolactones, whose concentrations are altered in mycorrhizas (Fusconi, 2014). The symbiosis can also alter root hydraulic properties, regulated by ABA, increasing plant water uptake under unfavourable conditions (Ruiz-Lozano *et al.*, 2012). Although under nonstress conditions ABA concentrations may be unaltered or even lower in mycorrhizal plants, under osmotic stress the increase in ABA content is higher in these plants, and is likely to lead to primed stress responses (Aroca *et al.*, 2013). In plants with ectomycorrhizas both ABA and salicylate pathways are primed, increasing host tolerance to abiotic stresses (Luo *et al.*, 2009). In addition, AMs can alter the outcome of interactions between plants and other organisms. They can promote resistance against a wide range of soil- and air-borne deleterious organisms, including herbivorous insects and pathogens, and they can even affect other trophic levels, such as the natural enemies of herbivores (Jung *et al.*, 2012). Among the underlying mechanisms, improved plant nutrition, changes in root architecture and priming of plant immunity are all regulated by phytohormones to some extent (Jung *et al.*, 2012). Here, priming of jasmonate-dependent defences is crucial, not only within individual plants, but even between plants connected through common mycorrhiza mycelial networks (Song *et al.*, 2014)

VI. Conclusions and outlook

We are just beginning to understand the complexity of phytohormone regulation in plant physiology. Studies of individual stimuli in model systems have been instrumental to understand the precise regulation of particular plant responses. However, plants are simultaneously exposed to multiple cues and stress factors, and they need to prioritize responses for efficient resource management. The latest research is now uncovering the multiple molecular connections that coordinately mediate phytohormone crosstalk for signal integration, and how their spatial and temporal regulation permits the fine-tuning of the response (Xu *et al.*, 2014).

Box 1 Outstanding research questions

- How is hormone crosstalk orchestrated at local and whole-plant levels?
- How is the suppression of the local immunity (to allow AM fungal colonization) combined with enhanced stress tolerance and systemic priming of plant defences at the molecular level?
- What are the host targets of the diverse mycorrhizal fungi effectors?
- Are fungal effectors regulated by host signals and environmental conditions?
- Are specific AM interactions promoted/tailored under stressful conditions to improve stress tolerance?

Phytohormone homeostasis also regulates, and is regulated by, AM symbiosis. Changes in host hormone profiles in response to environmental cues (nutrient availability, abiotic stresses and biotic interactions) may translate into changes in the colonization process or efficiency. Conversely, AM symbiosis can alleviate plant stress under unfavourable conditions, at least in part, by altering host hormonal homeostasis (Fig. 3). Thus, recent discoveries regarding the precise regulation of phytohormone signalling provide new clues to the molecular basis of the contribution of mycorrhizas to plant resilience to environmental challenges, and to the context dependence of mycorrhizal effects in ecological or agricultural settings. Many questions remain unanswered (Box 1), but future research should allow us to understand the precise molecular regulation of the symbiosis under natural conditions. Models that integrate multiple responses, tissues and scales must be used in order to understand the roles of phytohormones in mycorrhizal regulation and their contribution to the functioning of ecosystems (Fig. 3).

Deciphering how phytohormones act and interact and characterizing new players in signalling networks are crucial to understand how plants, in close interaction with their symbionts, thrive and survive in changing environments. This knowledge should also contribute to improving strategies to optimize plant symbioses and their adaptation to adversity.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Mutant and transgenic plants altered in hormone signalling pathways and their impact on mycorrhizal development