

Something old, something new

Auxin and strigolactone interact in the ancient mycorrhizal symbiosis

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Arbuscular mycorrhizal symbiosis, formed between more than 80% of land plants and fungi from the phylum Glomeromycota, is an ancient association that is believed to have evolved as plants moved onto land more than 400 mya.^{1,2} Similarly ancient, the plant hormones auxin and strigolactone are thought to have been present in the plant lineage since before the divergence of the bryophytes in the case of auxin and before the colonisation of land in the case of strigolactones.^{3,4} The discovery of auxin in the 1930s predates the discovery of strigolactones as a plant hormone in 2008 by over 70 y.⁵⁻⁷ Recent studies in pea suggest that these two signals may interact to regulate mycorrhizal symbiosis.⁸ Furthermore, the first quantitative studies are presented that show that low auxin content of the root is correlated with low strigolactone production,⁸ an interaction that has implications for how these plant hormones regulate several developmental programs including shoot branching, secondary growth and root development.⁹⁻¹² With recent advances in our understanding of auxin and strigolactone biosynthesis,^{13,14} together with the discovery of the fungal signals that activate the plant host,¹⁵ the stage is set for real breakthroughs in our understanding of the interactions between plant and fungal signals in mycorrhizal symbiosis.

In 2000, a review of the roles of auxin and cytokinin in mycorrhizal symbiosis predicted great advances in our understanding of the roles of these two important hormones, with the availability of new

molecular and genetic tools.¹⁶ Up to that point, hormone application and somewhat limited hormone measurement studies indicated auxin may play a role in mycorrhizal symbiosis, but the most powerful approach to addressing this question, namely the use of plant auxin mutants, was not available in a mycorrhizal species. The predictions of this review are only now beginning to be realized with two studies in the last two years examining the mycorrhizal phenotype of plant mutants with altered auxin content, transport or response indicating that auxin plays an important role during early events in mycorrhizal colonisation.^{8,17}

Mycorrhizal studies were conducted with the pea *bushy* (*bsh*) mutant, one of the few mutants available in a mycorrhizal species with low levels of the active auxin, indole-3-acetic acid (IAA).^{18,19} The *bsh* mutant was found to have reduced mycorrhizal colonisation rates (Fig. 1), but the internal hyphae and arbuscules that did form appeared to be normal, suggesting that auxin may regulate early rather than later events in the symbioses.⁸ Indeed, *bsh* mutant roots were found to exude low levels of at least two strigolactones, the plant signals that activate the fungal partner in the soil by inducing spore germination and hyphal branching.²⁰⁻²² Consistent with this, *bsh* mutant plants have reduced expression of the strigolactone biosynthesis gene *PsCCD8*. This low strigolactone exudation may be at least part of the reason why *bsh* mutants are poorly colonised as application of the synthetic strigolactone GR24 could partially rescue the mycorrhizal phenotype of *bsh* mutants (Fig. 1).⁸ This role for auxin in regulating

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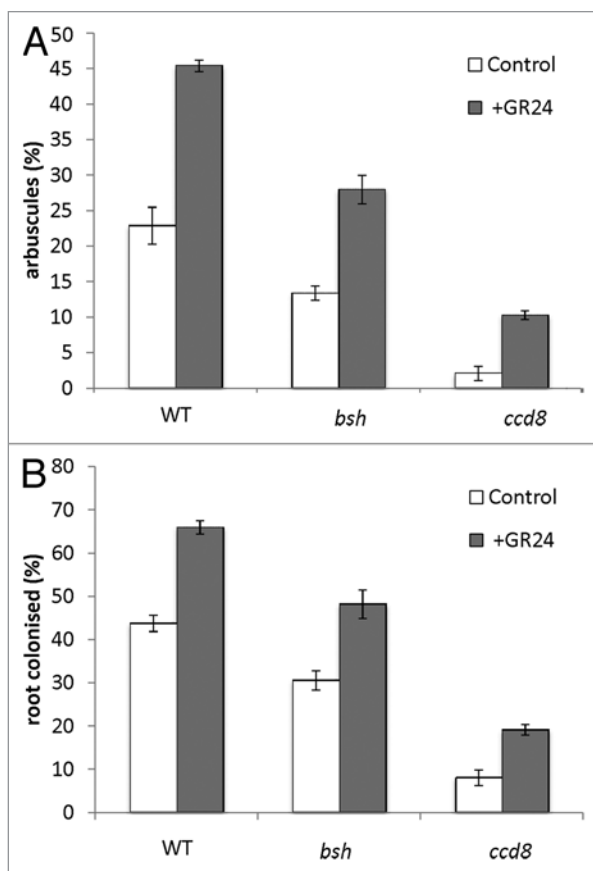


Figure 1. Mycorrhizal colonization of roots of wild type, *ccd8* (strigolactone-deficient) and *bsh* (low auxin) mutants in response to the synthetic strigolactone GR24. (A) Percentage of the root containing arbuscules and (B) percentage of the root colonized by mycorrhizae. Plants were grown for 6 weeks in pot culture with *Glomus intraradices* under low phosphate (0.05 mM NaH_2PO_4) and treated 3 times a week with water (control) or 2×10^{-8} M GR24. Values are mean \pm s.e., n = 4–6. Data from reference 8.

early events in mycorrhizal symbiosis is consistent with recent studies with auxin mutants in tomato that found that early stages of colonisation were disrupted in both the *dgt* and *pct* mutants grown in soil.¹⁷ These mutants display an auxin resistant and auxin hyper-transporting phenotype respectively. The authors speculated that a reduction in strigolactones may contribute to the failure of *dgt* mutant roots to attract mycorrhizal fungal hyphae rather than disrupting later events, as like the pea *bsh* mutant, once inside the root of *dgt* mutants the mycorrhizal fungus was able to form fully mature arbuscules.¹⁷ The disruption of mycorrhizal colonisation in intact auxin hyper-transporting *pct* mutant indicates that supra-optimal levels of auxin inputs from the shoot may also suppress mycorrhizal development.

In addition to providing evidence for a role for auxin in mycorrhizal colonisation of pea and revealing this may be in part through altered strigolactone exudation, the studies by Foo⁸ provide the first quantitative studies to link auxin content of the root with strigolactone exudation. Studies in several developmental systems and across several species have indicated auxin may interact with strigolactones.^{9–12} This has been based on auxin and strigolactone response assays, expression of strigolactone biosynthesis genes and the use of auxin and strigolactone mutants. However, due to the relatively recent ability to measure endogenous plant strigolactones there has been a lack of direct evidence to investigate if auxin regulates strigolactone production. Foo⁸ demonstrated that lowering auxin content of the root, either due to the *bsh* mutation or by shoot decapitation or

stem girdling of wild type pea plants, was correlated with a reduction in strigolactone exudation of the roots (Fig. 2). In the case of shoot decapitation, strigolactone exudation could be restored by replacing the shoot apex with exogenous auxin. This direct correlation between auxin and strigolactone production in two independent experimental systems provides the first evidence based on strigolactone quantification for this potentially crucial hormone interaction.

In the last decade the use of hormone biosynthesis mutants²³ has been instrumental in providing novel evidence for roles of several hormones in mycorrhizal symbiosis, including strigolactones, jasmonic acid, abscisic acid and gibberellins.²⁴ However, the severe shortage of auxin mutants in mycorrhizal species has restricted progress. This may now be changing, with reverse genetics approaches such as TILLING (Targeting Induced Local Lesions IN Genomes) yielding new auxin mutants, that due to lethality or gene families, may never have been selected through conventional mutagenesis. Such an approach to targeting genes that may act in the auxin biosynthesis pathway(s) in species such as pea is crucial not only for defining auxin biosynthesis,²⁵ a work in progress for more than 70 y, but also to provide new tools for research into the biological roles of auxin, such as in the ecologically widespread mycorrhizal symbiosis.

Exciting avenues for future research include the intriguing finding that strigolactones may not act only to activate the fungal partner but might also play a role as an endogenous plant signal during mycorrhizal symbiosis. Plant mutants in pea and rice with lesions in RMS4/D3 F-box protein, which mediates strigolactone response, also disrupts mycorrhizal symbiosis^{26–28} and one possibility is that plants themselves must perceive strigolactones to enhance mycorrhizal colonisation. It will be interesting to explore if such an interaction between auxin and strigolactones affects events in the rhizosphere as well those inside the root during early stages of colonisation (Fig. 2). In addition, in the related symbiosis between rhizobial bacteria and leguminous plants the perception of the bacteria-derived Nod factors leads

to changes in auxin transport that ultimately contributes to nodule organogenesis in some species.²⁹ With the very recent identification of the fungal-derived Myc factors as signals that activate early plant responses¹⁵ it will be interesting to determine whether an analogous interaction occurs with auxin production or distribution to facilitate mycorrhizal colonisation.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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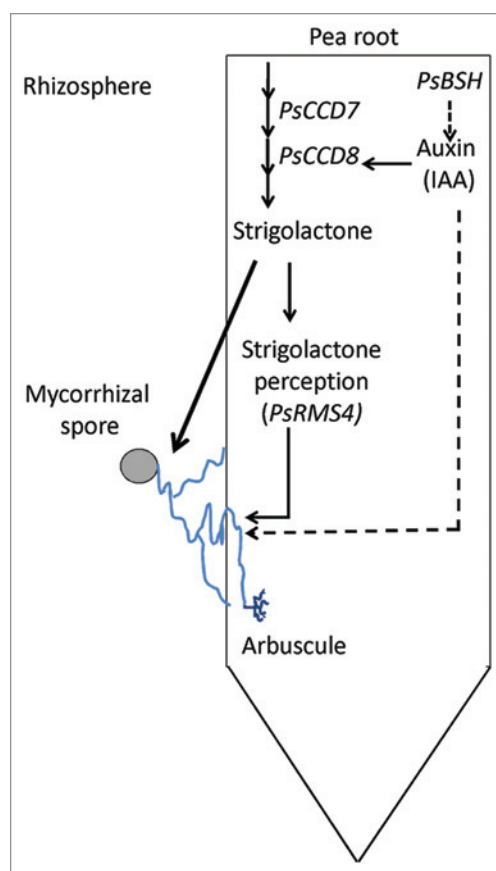


Figure 2. Proposed interaction between of strigolactone and auxin in mycorrhizal development of pea roots. *PsBSH* gene positively influences auxin (indole-3-acetic acid, IAA) levels, although dashed arrow indicates molecular mechanism is unknown. IAA positively regulates expression of strigolactone biosynthesis gene (*PsCCD8*) and strigolactone exudation, in turn promoting mycorrhizal colonization. IAA may also influence early mycorrhizal development independently of strigolactones, although dashed arrow indicates mechanism is unknown. A role for strigolactone perception (*PsRMS4*) in mycorrhizal development has also been suggested.

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