SYMBIOSIS

Establishing the roots of a relationship

Pathogens and symbionts both interact closely with their host, but with vastly different outcomes. For a fungus to establish a mycorrhiza, a symbiotic interaction with plants in which the fungus penetrates the root tissue, it must overcome the immune defences of the plant and induce remodelling of the roots. Two articles in a recent issue of *Current Biology* show that secreted fungal effectors can induce changes in the host cells to allow the establishment of mycorrhizae.

In the first article, Kloppholz *et al.* investigated the role of secreted fungal proteins in the interaction of the arbuscular mycorrhizal fungus *Glomus intraradices* with host plants. They identified a family of proteins that contain a signal sequence (indicating that the proteins are secreted) and a nuclear localization signal, as well as several repeat domains of unknown function. Expression of one member of this family, Sp7, in *Aspergillus nidulans* (which was used as a surrogate, as there is no genetic system for *G. intraradices*), in the leaves of *Nicotiana benthamiana* and in the roots of *Medicago truncatula* showed that the protein is transferred to the plant cell nucleus. Moreover, GFP fused to the Sp7 signal sequence was taken up by the plant cells, indicating that no additional fungal proteins are required for Sp7 entry into the cell.


STOCKBYTE

A yeast two-hybrid screen and *in vivo* bimolecular complementation revealed that Sp7 binds to host ethylene-responsive factor 19 (ERF19), a member of the class IV ERF transcription factors. Interestingly, these transcription factors mediate the plant response to pathogens by regulating the expression of several defence-related genes. Indeed, the application of fungal extracts of various fungi, including that of *G. intraradices*, to *M. truncatula* roots induced expression of *ERF19*. However, infection of *M. truncatula* with live *G. intraradices* produced only a short and transient increase in *ERF19* activity. Interestingly, the fungus produced more mycorrhizae in stably transformed roots that expressed Sp7 than in wild-type roots, and when these transformed roots were infected with *Colletotrichum trifolii*, a pathogenic fungus, the induction of *ERF19* was greatly decreased. Furthermore, infection of plants with an Sp7-expressing mutant form of the hemibiotrophic mycorrhizal fungus *Magnaporthe oryzae* caused much milder root defects than infection with wild-type *M. oryzae*.

In a related study, Plett *et al.* showed that the ectomycorrhizal fungus *Laccaria bicolor* produces mycorrhizal induced small secreted protein 7 (Missp7), a small protein that, like Sp7, is secreted by the fungus and taken up by plant cells, in which it also reaches the nucleus. *L. bicolor* with a reduced level of Missp7 produced fewer mycorrhizae, and in cases for which the fungus did establish a mycorrhiza, the morphology was different to that of a mycorrhiza involving wild-type fungus. When the authors measured the transcriptional response in the plant (*Populus trichocarpa*), they discovered that genes involved in altering root morphology, including auxin–idole-3-acetic acid (AUX–IAA) genes, were upregulated and genes that inhibit root development, including *CLAVATA 3/ESR-RELATED 5*, were downregulated.

Sp7 and Missp7 provide examples of the ways in which fungi affect the host cell to promote the establishment of a biotrophic interaction. As mycorrhizal interactions are complex and require multiple alterations in the host, it is likely that additional effectors will be discovered.

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ORIGINAL RESEARCH PAPERS Kloppholz, S., Kuhn, H. and Requena, N. A secreted fungal effector of *Globus intraradices* promotes symbiotic biotrophy. *Curr. Biol.* **21**, 1204–1209 (2011) | Plett, J. M. *et al.* A secreted effector protein of *Laccaria bicolor* is required for symbiosis development. *Curr. Biol.* **21**, 1197–1203 (2011)