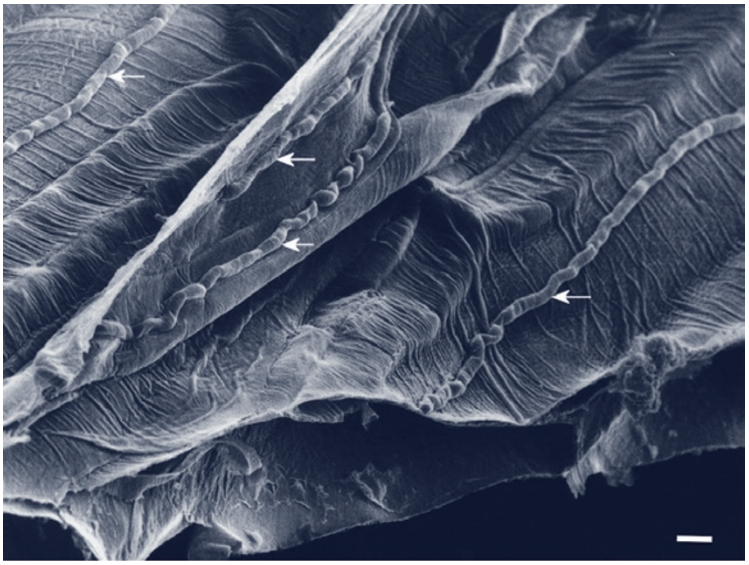
FUNGAL BIOLOGY

Breaking the mould?

A paper in a recent issue of *Fungal Genetics and Biology* could overturn the long-held belief that filamentous fungi grow only through extension at the hyphal tip.

All plants examined to date have been shown to harbour at least one endophytic fungal species. Endophytes from the genera *Neotyphodium* and *Epichloë* form stable symbioses with grasses and are transmitted in grass seeds. The paradigmatic view of fungal growth is that vegetative hyphae grow only through division and expansion at the hyphal tip. However, this model cannot adequately explain how endophytes within the shoot apical meristem are able to invade actively growing leaves.

Michael Christensen and colleagues began investigating this conundrum by closely examining the hyphal growth of *Epichloë festucae* in rye grass. The growth measurements demonstrated that, over time, there was an increase in the intercalary hyphal length (that is, growth occurred along the entire length of the hypha) in growing but not mature leaves. This increase matched the increase in leaf length during the same time period. The authors were able to rule out the possibility that this growth occurred through the expansion of short pre-formed hyphal compartments, and so they suspected that they were observing a new phenomenon — intercalary hyphal growth.



Freeze-fracture scanning electron micrograph showing four hyphae (arrows) of the fungal endophyte *Neotyphodium lolii* attached to cell walls of the host, perennial ryegrass (*Lolium perenne*). The scale bar represents 5 μm. Image kindly provided by Hironori Koga, Ishikawa Prefectural University, Japan.

What could be driving this phenomenon? Using transmission and scanning electron microscopy to examine grasses infected with *Epichloë* and *Neotyphodium* species, Christensen *et al.* found that the hyphae of these endophytes appeared to be attached to the plant cell wall. The authors propose that this attachment leads to hyphal stretching, and intercalary growth is therefore necessary to relieve this physical stress. The attachment would also explain why the hyphae of these endophytes are always orientated along the longitudinal axis of the leaf in the direction of leaf growth and why hyphal growth can keep pace with leaf growth. The intercalary-growth hypothesis was further supported by detailed ultrastructural analysis of *Epichloë* and *Neotyphodium* species. This showed that in actively growing areas of a grass leaf, the hyphal structure is simple, but it becomes increasingly more complex as the leaves mature. This would be expected for intercalary growth, as if the hyphae are growing by intercalary extension, and therefore growing at the same rate as the host, then within a particular developmental zone of a leaf all the hyphae should be at the same stage of development. The authors conclude with a detailed model for endophyte colonization and growth within grasses.

This work challenges the long-held assumption that filamentous fungi grow exclusively at hyphal tips and, as the authors suggest, has "profound implications for the way in which we view hyphal growth processes in fungi."

Sheilagh Molloy

ORIGINAL RESEARCH PAPER Christensen, M. J. *et al. Epichloë* endophytes grow by intercalary hyphal extension in elongating grass leaves. *Fungal Genet. Biol.* **45**, 84–93 (2008)