



A mycorrhizal revolution

Grace A Hoysted¹, Jill Kowal², Alison Jacob³,
William R Rimington^{2,3,4}, Jeffrey G Duckett²,
Silvia Pressel², Suzanne Orchard⁵, Megan H Ryan⁵,
Katie J Field¹ and Martin I Bidartondo^{3,4}

It has long been postulated that symbiotic fungi facilitated plant migrations onto land through enhancing the scavenging of mineral nutrients and exchanging these for photosynthetically fixed organic carbon. Today, land plant–fungal symbioses are both widespread and diverse. Recent discoveries show that a variety of potential fungal associates were likely available to the earliest land plants, and that these early partnerships were probably affected by changing atmospheric CO₂ concentrations. Here, we evaluate current hypotheses and knowledge gaps regarding early plant–fungal partnerships in the context of newly discovered fungal mutualists of early and more recently evolved land plants and the rapidly changing views on the roles of plant–fungal symbioses in the evolution and ecology of the terrestrial biosphere.

Addresses

¹ Centre for Plant Sciences, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK

² Department of Life Sciences, National History Museum, London SW7 5BD, UK

³ Comparative Plant & Fungal Biology, Royal Botanic Gardens, Kew, Richmond TW9 3DS, UK

⁴ Department of Life Sciences, Imperial College London, London SW7 2AZ, UK

⁵ UWA School of Agriculture and Environment, and Institute of Agriculture, The University of Western Australia, 35 Stirling Hwy, Crawley (Perth), WA 6009, Australia

Corresponding author: Hoysted, Grace A (g.a.hoysted@leeds.ac.uk)

Current Opinion in Plant Biology 2018, 44:1–6

This review comes from a themed issue on **Biotic interactions**

Edited by **Sebastian Schornack** and **Caroline Gutjahr**

<https://doi.org/10.1016/j.pbi.2017.12.004>

1369-5266/© 2017 Published by Elsevier Ltd.

Introduction

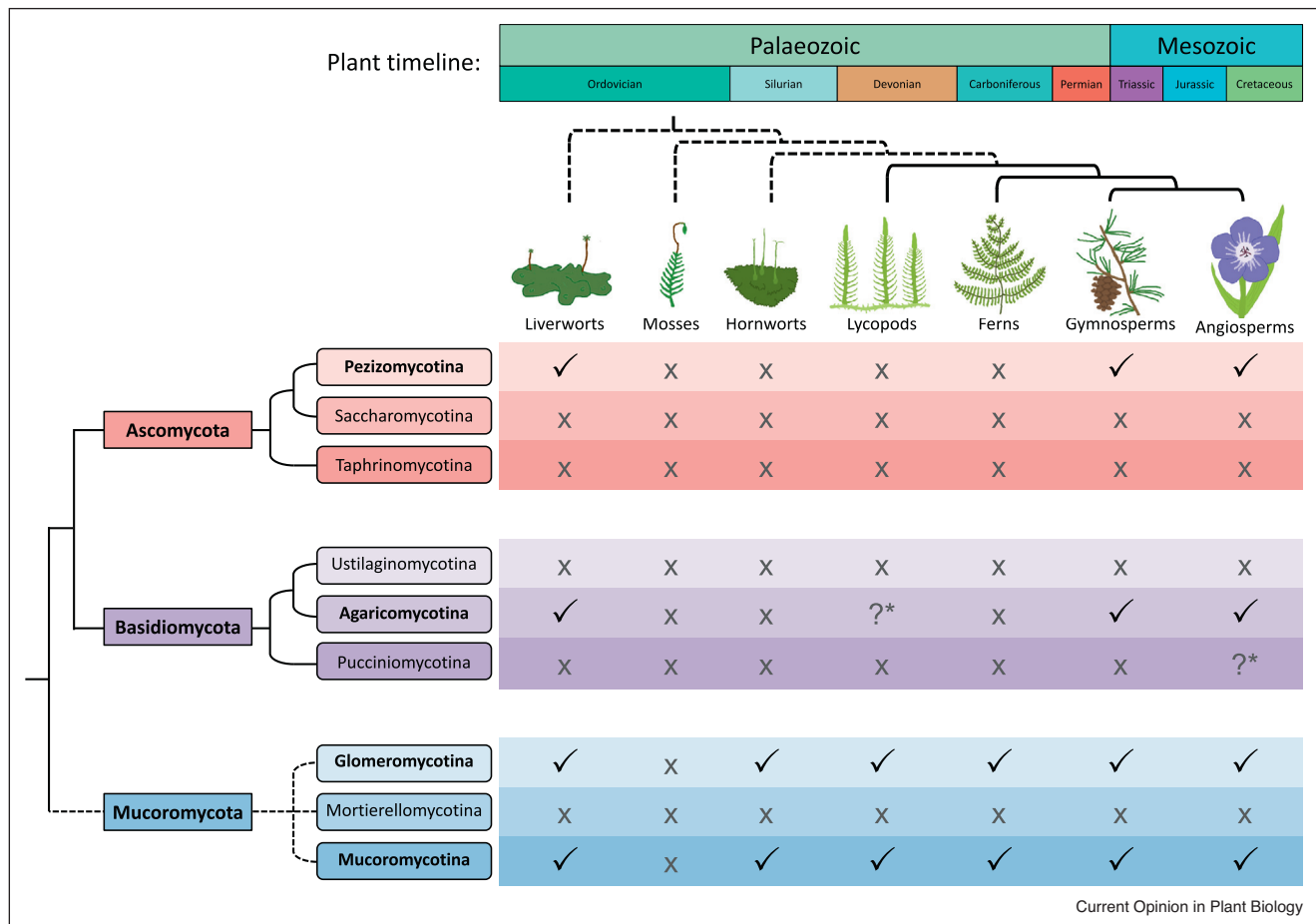
Amongst the most important symbioses in nature after mitochondria and plastids are those between plants and soil-dwelling filamentous fungi. The vast majority of extant land plants, including most crops, form intimate symbioses with fungi in the phyla Mucoromycota,

Ascomycota and Basidiomycota (Figure 1 [1*,2*]); these mutually beneficial partnerships are thought to have played a key role in plant terrestrialisation and diversification [3,4]. Such associations are termed ‘mycorrhizas’ (fungus–roots) in vascular plants, or ‘mycorrhiza-like’ in rootless non-vascular plants with intracellular fungal structures such as coils and/or arbuscules that are similar to those formed in rooted species [5]. In exchange for up to 20% of photosynthetically-fixed, organic carbon-based compounds (C) [6,7], mycorrhizal fungi may provide their plant partners with up to 80% of the nitrogen (N) and 100% of the phosphorus (P) required for plant growth and proliferation [8–12].

The first plants to colonise Earth’s land surfaces in the Ordovician period (~475 Ma) were thought to have formed associations with arbuscular mycorrhizal Glomeromycotina fungi thereby gaining access to fungal-acquired mineral nutrients in return for plant carbohydrates [13] and/or lipids [14,15] in a manner similar to modern arbuscular mycorrhizal associations [7]. Thus, the first fungal symbionts may well have co-evolved with, and facilitated the transition of, rootless plants from water onto land [16,17] and subsequent terrestrial diversification [3,4]. This hypothesis has been strongly supported by cytological [18], molecular [19,20] and physiological evidence [4] alongside fossilised examples of early plants containing fungal structures bearing strong morphological similarity to modern mycorrhizas [21]. However, recent findings are now challenging the long-standing assumption that the symbionts of early land plants were solely Glomeromycotina fungi; instead they suggest that Mucoromycotina fungi have also played a major role [2*,22*].

Despite advances in our knowledge of non-vascular plant–fungal partnerships in liverworts and hornworts, there remains a significant gap regarding the occurrence, frequency, identity, appearance and function of Mucoromycotina associations in later-derived vascular plant lineages, including modern angiosperms, that have been of key significance in the development of Earth’s terrestrial atmosphere and biota to the present day. More recently, an ascomycete fungus facilitating the growth of a non-mycorrhizal flowering plant under P-limited conditions was reported [23]; the study uncovers a previously unappreciated role of root fungal microbiota in nutrient cycling and highlights the diversity in plant–

Figure 1



The mycorrhizal status of the main land plant groups in relation to fungal phylogenetic diversity. Dashed lines indicate currently unresolved phylogenetic positions and asterisks signify uncertain mycorrhizal status with only one report of mycorrhizal formation in each case [57,38].

fungal nutritional interactions. Here we provide an overview of the recent leaps in understanding of the interactions between early land plants and symbiotic fungi in both the Glomeromycotina and Mucoromycotina [2*,24], with emphasis on the role, evolution and distribution of Mucoromycotina symbionts across the land plant tree of life.

Changing views on non-vascular plant symbioses with fungi

The symbioses between non-vascular plants and Mucoromycotina fungi have, in the last few years, received increasing attention. Unlike the strictly biotrophic and, to our current knowledge, asexual Glomeromycotina, e.g. the model mycorrhizal fungus *Rhizophagus irregularis*, Mucoromycotina encompasses saprotrophic, biotrophic, and putatively sexual lineages of fungi, including only poorly studied genera like *Endogone* and *Sphaerocreas* [25]. Until recently, the biology of the Endogonales was largely unknown [26*,27*]. In addition to endomycorrhizal associations, some members of *Endogone* can form ectomycorrhizal associations with trees [28,29], characterised by a

root-covering mantle and intercellular penetration where hyphae form a network between cortical cells known as a Hartig net [7,30]. The remarkable versatility of these ancient and diverse fungi may be attributed to life history traits of the Endogonales, for example, facultative saprotrophy. However, more traits remain to be uncovered to understand further the evolutionary and ecological significance of these fungi.

The potential significance of Mucoromycotina fungi in land plant evolution was first recognised when *Endogone*-like fungi were found to associate with the likely earliest-diverging extant land plant lineage, Haplomitriopsida liverworts ([26*] Figure 1). This discovery generated the alternative hypothesis that a relict association with Mucoromycotina, apparently lost through land plant evolution, might have played a significant part in ancestral mycorrhizal-like symbioses [26*,31*]. This hypothesis was further supported by fossil evidence following re-examination of the Early Devonian Rhynie Chert plant *Horneophyton lignieri* [32]. In addition to

Glomeromycotina-like fungal structures in the aerial axes of *H. lignieri*, structures indicative of Mucoromycotina colonisation also appeared to be present within the plant's distinctive corm [32]. These fungal structures also showed similarities to symbiotic features in fossilised *Glomites rhyniensis* colonising *Nothia aphylla* [33]. These findings place Mucoromycotina as potential key players in the initial colonisation of Earth's landmasses [32]. However, structure does not always translate into function, particularly in fossils. A new cytological study showing intracellular colonisation of non-vascular plants with the broad-host range oomycete *Phytophthora palmivora* [34] suggests that branched haustoria-like structures and prolific intracellular hyphal growth could be interpreted as mycorrhizal-like if fossilised. Nonetheless, it is clear that fungal associations in early land plants were much more varied than previously assumed and likely included diverse mutualists and pathogens. Recent works show that in addition to the Halomitriopsida liverworts, many extant non-vascular plants such as complex and simple thalloid liverworts [35^{*}], hornworts [31^{*}], and early-diverging vascular plants [27^{*}], harbour both Mucoromycotina and Glomeromycotina, sometimes simultaneously in the same host plant.

The earliest divergent lineage of liverworts, the Haplomitriopsida, form apparently exclusive partnerships with Endogonales [26^{*}]. The first study on the cytology and functioning of liverworts with Mucoromycotina demonstrated a nutritional mutualism between partners, with plant-fixed carbon detected in the fungus and fungus-acquired nutrients (¹⁵N and ³³P) in the plant [22^{*}]. These findings clearly demonstrate that the nutritional role played by Mucoromycotina in Haplomitriopsida is analogous to that of Glomeromycotina in complex thalloid liverworts [18]. Additional experiments tested the carbon-for-nutrient exchange responses of liverwort-fungal associations against a simulated Palaeozoic decline in atmospheric CO₂ concentration, representative of the conditions experienced by early land plants [36]. In liverwort-Mucoromycotina symbioses, the amount of ³³P gained from the fungus by the plant, per unit of carbon delivered by the plant to the fungus, was either unaffected or even increased in response to declining CO₂, similarly to vascular plant-Glomeromycotina symbioses [4], but in direct contrast to observations in liverwort-Glomeromycotina associations [4]. Differences in CO₂ responsiveness between Mucoromycotina-plant and Glomeromycotina-plant symbioses, and between vascular-plant and non-vascular plant symbioses, likely provided physiological niches ensuring the persistence of both symbioses to the present [2^{*}]. The subsequent discovery that some early diverging thalloid liverworts form simultaneous (dual) symbioses with nutritionally mutualistic Glomeromycotina and Mucoromycotina [26^{*}] lent weight to this view, with the intriguing possibility that early plant-fungal symbioses were not only

taxonomically and functionally diverse, but also potentially transient in nature, with plant and fungal partners shifting according to environmental conditions [2^{*}].

Hornworts are an ancient plant phylum (300–400 Mya) that in some phylogenies are the sister group of the earliest vascular plants [37–39]. Molecular evidence of fungi in hornworts was limited [26^{*}] until the extensive study by Desirò *et al.* [31^{*}] revealed that these plants also have various symbiotic options. Hornworts were shown to form both single and dual associations with Glomeromycotina and/or Mucoromycotina, or to 'opt out' of symbioses altogether, suggesting the same may be true for other early-diverging plant lineages such as the liverworts and indeed, the first land colonists [26^{*},31^{*},40]. However, functional studies testing for nutritional mutualism between fungi and hornworts have yet to be performed.

Changing views on vascular plant symbioses with fungi

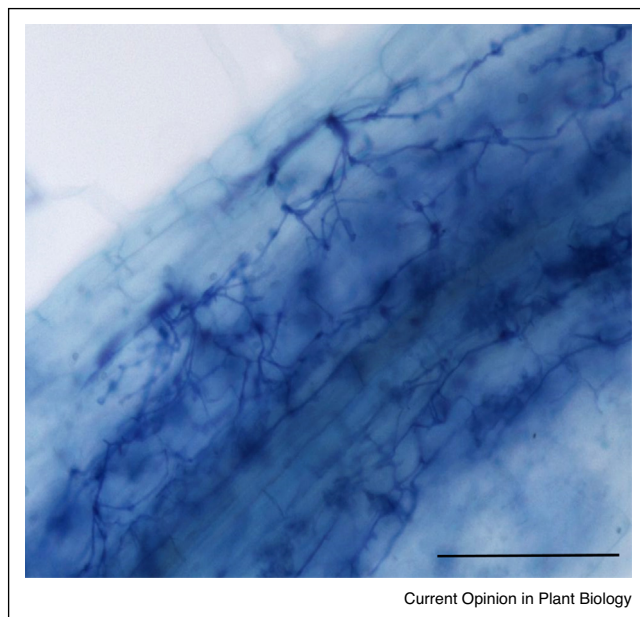
Research into early diverging vascular plant-Mucoromycotina symbiosis is in its infancy. Fungi have long been recognised to be present within lycopods [41,42], however, until recently their identity had been unclear [32,40,43]. Molecular analyses have now shown that Mucoromycotina associations, both single and in combination with Glomeromycotina, occur in this earliest diverging clade of extant vascular plants [27^{*}], but, as with hornworts, there is still no functional evidence of mutualism in lycopod-fungal symbioses. In ferns, the most diverse early-diverging vascular plants, molecular, microscopical and physiological data have documented arbuscular mycorrhizas [1^{*},4,44]. Recent analysis of fern-fungal symbioses showed that although many ferns associate with Glomeromycotina, at least one — *Anogramma leptophylla* — can be colonised by Mucoromycotina and Glomeromycotina [27^{*}]. So far, there is evidence of mutualistic nutrient exchange with Glomeromycotina for only two ferns, *Ophioglossum* and *Osmunda* [4,45].

The presence of Mucoromycotina in some early diverging vascular plants supports the idea that plants across the evolutionary tree are much more symbiotically versatile than hitherto assumed. However, with few exceptions, occurrence and knowledge of fungal associations across pteridophytes is based solely on light microscopy [44], a technique which may overlook Mucoromycotina co-colonisation [26^{*}]. Cytological, molecular and physiological approaches are urgently needed to further understand the nature and functioning of these fungal partnerships in lycopods and ferns.

Fine root endophytes

Fungi known as fine root endophytes (*Glomus tenue*) colonise bryophytes and ferns [46–49] as well as the roots of vascular plants [50^{*}]. Whilst their colonisation morphology is distinctive from that of the arbuscular

Figure 2



Colonisation by fine root endophytes within the roots of *Lotus subbiflorus* (Fabaceae). Bar 100 μm .

mycorrhizal fungi, the ability to produce arbuscules (Figure 2) led to their initial classification as *Glomus* within the arbuscular mycorrhizal fungi [50]. However, recent research by Orchard *et al.* [51] suggests that fine root endophytes are members of the Mucoromycotina, related to several Mucoromycotina identified from liverworts and lycopods by Field *et al.* [22,35] and Rimington *et al.* [27,40]. This makes fine root endophytes the only known fungi to produce arbuscules outside of Glomeromycotina. A meta-analysis by Orchard *et al.* [50] showed that fine root endophytes, which are likely a species group, are globally distributed across many ecosystems and colonise numerous vascular plant families [50]. In Australia and New Zealand they are prevalent within the roots of crop and pasture species, where colonisation levels may be high and match those of arbuscular mycorrhizal fungi [50]. Fine root endophytes have been associated both with disturbed or extreme environments and early successional plant establishment [46,50,52–56] and may provide growth benefits to the host plant [50,57], yet little is understood about the relationships between these fungi and plants. Even less is known of the evolutionary relationships between fine root endophytes and the arbuscular mycorrhizal fungi, for example, how they evolved to co-exist within plant species and even individual root segments [50]. Putative fine root endophytes were recently identified in fossilised (permineralised) Permian specimens of root mantle from the tree fern *Psaronius* [58], raising questions about the evolutionary relationship between fine root endophytes and the arbuscular mycorrhizal fungi, and when arbuscules first evolved.

Box 1 Outstanding questions

- How widespread are Glomeromycotina and Mucoromycotina in plant fossils?
- How is the colonisation and function of Mucoromycotina-plant symbioses controlled — by genetics, environment, or both?
- To what extent do fine root endophytes (FRE), other Mucoromycotina associations and Glomeromycotina associations overlap in nature?
- Why are FRE rarely observed without the presence of arbuscular mycorrhizal Glomeromycotina?
- Are Mucoromycotina associations with hornworts, lycopods, ferns and angiosperms mutualistic, both when present alone and when in dual symbiosis with Glomeromycotina?
- Do arbuscular mycorrhizal signals and colonisation pathways overlap with Mucoromycotina symbioses?

Developing methods to target and study fine root endophytes in a comparative context is imperative.

Future directions

The presence of symbioses with Glomeromycotina and Mucoromycotina in non-vascular and early vascular plants, in conjunction with evidence for Mucoromycotina nutritional mutualisms in early-diverging liverworts [26,31], strengthens the hypothesis that Mucoromycotina aided pioneering land plants. Genetic studies of plant–fungal symbioses [2,24] are revealing extensive molecular and chemical crosstalk between the partners. To date, strigolactones from roots and lipochitoooligosaccharides from fungi have been implicated in the establishment of arbuscular mycorrhizas [59,60]. However, the molecular basis for the functioning of Mucoromycotina fungal partnerships, including those of fine root endophytes, in non-vascular and vascular plants, has yet to be investigated (Box 1). Given that many model plants are not symbiotic (e.g. *Arabidopsis*, *Marchantia polymorpha*, *Physcomitrella*), molecular and functional analysis of targeted symbiotic liverworts, lycopods, ferns and angiosperms will go a long way toward elucidating the nature and dynamics of ancient and widespread Mucoromycotina symbioses, informing the interpretation of fossils [61], and our understanding of how lineages of fungi and plants co-evolved on land and transformed their environments.

Acknowledgements

This work was supported by a Natural Environment Research Council standard grant to KJF, SP (NE/N00941X/1) and MIB (NE/N009665/1). MHR is funded by ARC Future Fellowship FT140100103. KJF is funded by a BBSRC Translational Fellowship (BB/M026825/1).

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
 - of outstanding interest
1. Wang B, Qiu YL: **Phylogenetic distribution and evolution of mycorrhizas in land plants.** *Mycorrhiza* 2006, **16**:299–363.

Most extensive survey to date of mycorrhizal types in plants (i.e. arbuscular, ectomycorrhizal, ericoid, orchid, etc.).

2. Field KJ, Pressel S, Duckett JG, Rimington WR, Bidartondo MI: **Symbiotic options for the conquest of land.** *Trends Ecol Evol* 2015, **30**:477-486.
- Comprehensive critical review of fungal endosymbioses in non-vascular plants.
3. Selosse MA, Le Tacon F: **The land flora: a phototroph–fungus partnership?** *Trends Ecol Evol* 1998, **13**:15-20.
4. Field KJ, Cameron DD, Leake JR, Tille S, Bidartondo MI, Beerling DJ: **Contrasting arbuscular mycorrhizal responses of vascular and non-vascular plants to a simulated Palaeozoic CO₂ decline.** *Nat Commun* 2012, **3**:835.
5. Read DJ, Duckett JG, Francis R, Ligrone R, Russell A: **Symbiotic fungal associations in 'lower' land plants.** *Philos Trans R Soc* 2000, **355**:815-830.
6. Jakobsen I, Rosendahl L: **Carbon flow into soil and external hyphae from roots of mycorrhizal cucumber plants.** *New Phytol* 1990, **115**:77-83.
7. Smith SE, Read DJ: *Mycorrhizal Symbiosis*. edn 3. Academic Press; 2010.
8. Jakobsen I, Abbott LK, Robso AD: **External hyphae of vesicular-arbuscular mycorrhizal fungi associated with *Trifolium subterraneum* L. 1. Spread of hyphae and phosphorus inflow into roots.** *New Phytol* 1992, **120**:371-380.
9. Leake JR, Johnson D, Donnelly DP, Muckle GE, Boddy L, Read DJ: **Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning.** *Can J Bot* 2004, **82**:1016-1045.
10. Smith SE, Smith FA: **Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystem scales.** *Annu Rev Plant Biol* 2011, **62**:227-250.
11. Hodge A, Storer K: **Arbuscular mycorrhiza and nitrogen: implications for individual plants through to ecosystems.** *Plant Soil* 2015, **386**:1-19.
12. Luginbuehl LH, Menard GN, Kurup S, Van Erp H, Radhakrishnam GV, Breakspear A, Oldroyd GE, Eastmond PJ: **Fatty acids in arbuscular mycorrhizal fungi are synthesised by the host plant.** *Science* 2017. eaan0081.
13. Lewis DH, Harley JL: **Carbohydrate physiology of mycorrhizal roots of beech.** *New Phytol* 1965, **64**:224-237.
14. Jiang Y, Wang W, Xie Q, Liu N, Liu L, Wang D, Zhang X, Yang C, Chen X, Tang D *et al.*: **Plants transfer lipids to sustain colonization by mutualistic mycorrhizal and parasitic fungi.** *Science* 2017, **356**:1172-1175.
15. Keymer A, Pimprikar P, Wewer V, Huber C, Brands M, Bucerius S, Delaux PM, Klingl V, von Roepenack-Lahaye E, Wang TL *et al.*: **Lipid transfer from plants to arbuscular mycorrhizal fungi.** *BioRxiv* 2017:143883.
16. Pirozynski KA, Malloch DW: **The origin of land plants: a matter of mycotrophism.** *Biosystems* 1975, **6**:153-164.
17. Redecker D, Kodner R, Graham LE: **Glomalean fungi from the Ordovician.** *Science* 2000, **289**:1920-1921.
18. Pressel S, Bidartondo MI, Ligrone R, Duckett JG: **Fungal symbioses in bryophytes: new insights in the Twenty First Century.** *Phytotaxa* 2014, **9**:238-253.
19. Wang B, Yeun LH, Xue JY, Liu Y, Ané JM, Qiu YL: **Presence of three mycorrhizal genes in the common ancestor of land plants suggests a key role of mycorrhizas in the colonisation of land by plants.** *New Phytol* 2010, **186**:514-525.
20. Delaux PM, Séjalon-Delmas N, Bécard G, Ané JM: **Evolution of the plant–microbe symbiotic 'toolkit'.** *Trends Plant Sci* 2013, **18**:298-304.
21. Krings M, Taylor TN, Dotzler N: **Fungal endophytes as a driving force in land plant evolution.** In *Biocomplexity of Plant–Fungal Interactions*. Edited by Southworth D. John Wiley & Sons; 2012:5-28.
22. Field KJ, Rimington WR, Bidartondo MI, Allison KE, Beerling DJ, Cameron DD, Duckett JG, Leake JR, Pressel S: **First evidence of mutualism between ancient plant lineages (Haplomitriopsida liverworts) and Mucoromycotina fungi and its response to simulated Paleozoic changes in atmospheric CO₂.** *New Phytol* 2015, **205**:743-756.
- Demonstration of nutritional exchange between Mucoromycotina and the earliest diverging non-vascular plants, and fulfilment of Koch's postulates.
23. Almario J, Jeena G, Wunder J, Langen G, Zuccaro A, Coupland G, Bucher M: **Root-associated fungal microbiota of nonmycorrhizal *Arabidopsis thaliana* and its contribution to plant phosphorus nutrition.** *Proc Natl Acad Sci* 2017, **114**:E9403-E9412.
24. van der Heijden MGA, Martin FM, Selosse MA, Sanders IR: **Mycorrhizal ecology and evolution: the past, the present, and the future.** *New Phytol* 2015, **205**:1406-1423.
25. Desirò A, Rimington WR, Jacob A, van de Pol N, Smith ME, Trappe JM, Bidartondo MI, Bonito GM: **Multigene phylogeny of Endogonales, an early diverging lineage of fungi associated with plants.** *IMA Fungus* 2017, **8**:245-257.
26. Bidartondo MI, Read DJ, Trappe JM, Merckx V, Ligrone R, Duckett JG: **The dawn of symbiosis between plants and fungi.** *Biol Lett* 2011, **7**:574-577.
- First identification of Mucoromycotina symbioses in plants (i.e. liverworts, hornworts, ferns) and diverse Glomeromycotina in non-vascular plants.
27. Rimington WR, Pressel S, Duckett JG, Bidartondo MI: **Fungal associations of basal vascular plants: reopening a closed book?** *New Phytol* 2015, **205**:1394-1398.
- Extensive and detailed analysis of the distribution of fungal endosymbioses in lycophytes and ferns showing Glomeromycotina fungi are dominant, but Mucoromycotina are also present.
28. Yamamoto K, Endo N, Degawa Y, Fukuda M, Yamada A: **First detection of *Endogone* ectomycorrhizas in natural oak forests.** *Mycorrhiza* 2017, **27**:295-301.
29. Walker C: ***Endogone lactiflua* forming ectomycorrhizas with *Pinus contorta*.** *Trans Br Mycol Soc* 1985, **84**:353-355.
30. Blasius D, Feil W, Kottke I, Oberwinkler F: **Hartig net structure and formation in fully ensheathed ectomycorrhizas.** *Nord J Bot* 1986, **6**:837-842.
31. Desiro A, Duckett JG, Pressel S, Villarreal JC, Bidartondo MI: **Fungal symbioses in hornworts: a chequered history.** *Proc Royal Soc B* 2013, **280**:20130207.
- Comprehensive analysis of Mucoromycotina and Glomeromycotina distribution and evolution in hornworts, showing single, dual and absent symbioses.
32. Strullu-Derrien C, Kenrick P, Pressel S, Duckett JG, Rioult JP, Strullu DG: **Fungal associations in *Horneophyton ligneri* from the Rhynie Chert (c. 407 million year old) closely resemble those in extant lower land plants: novel insights into ancestral plant–fungal symbioses.** *New Phytol* 2014, **203**:964-979.
33. Krings M, Taylor TN, Hass H, Kerp H, Dotzler N, Hermsen EJ: **An alternative mode of early land plant colonisation by putative endomycorrhizal fungi.** *Plant Signal Behav* 2007, **2**:125-126.
34. Carella P, Gogleva A, Tomaselli M, Alfs C, Schornack S: ***Phytophthora palmivora* establishes tissue-specific intracellular infection structures in the earliest divergent land plant lineage.** *bioRxiv* 2017 <http://dx.doi.org/10.1101/188912>.
35. Field KJ, Rimington WR, Bidartondo MI, Allison KE, Beerling DJ, Cameron DD, Duckett JG, Leake JR, Pressel S: **Functional analysis of liverworts in dual symbiosis with Glomeromycotina and Mucoromycotina fungi under a simulated Paleozoic CO₂ decline.** *ISME J* 2016, **10**:1514-1526.
- First direct functional comparison of Glomeromycotina and Mucoromycotina symbioses in plants showing significant differences between Glomeromycotina, Mucoromycotina and dual associations.
36. Berner RA: **GEOCARBSULF: a combined model for Phanerozoic atmospheric O₂ and CO₂.** *Geochim Cosmochim Acta* 2006, **70**:5653-5664.
37. Qiu YL, Li L, Wang B, Chen Z, Knoop V, Groth-Malonek M, Dombrowska O, Lee J, Kent L, Rest J *et al.*: **The deepest**

6 Biotic interactions

- divergences in land plants inferred from phylogenomic evidence.** *Proc Natl Acad Sci USA* 2006, **103**:15511-15516.
38. Renzaglia KS, Villarreal JC, Duff RJ: **New insights into morphology, anatomy, and systematics of hornworts.** In *Bryophyte Biology*. Edited by Goffinet B, Shaw AJ. Cambridge University Press; 2009:139-172.
 39. Villarreal JC, Renner SS: **Hornwort pyrenoids: carbon-concentrating mechanisms evolved and were lost at least five times during the last 100 million years.** *Proc Natl Acad Sci USA* 2009, **109**:18873-18878.
 40. Rimington WR, Pressel S, Field KJ, Strullu-Derrien C, Duckett JG, Bidartondo MI: **Reappraising the origin of mycorrhizas.** In *Molecular Mycorrhizal Symbiosis*. Edited by Martin F. John Wiley and Sons; 2016:31-32.
 41. Duckett JG, Ligrone R: **A light and electron microscope study of the fungal endophytes in the sporophyte and gametophyte of *Lycopodium cernuum* with observations on the gametophyte-sporophyte junction.** *Can J Bot* 1992, **70**:58-72.
 42. Schmid E, Oberwinkler F: **Mycorrhiza-like interaction between the achlorophyllous gametophyte of *Lycopodium clavatum* L. and its fungal endophyte studied by light and electron microscopy.** *New Phytol* 1993, **124**:69-81.
 43. Horn K, Franke T, Unterseher M, Schnittler M, Beenken L: **Morphological and molecular analyses of fungal endophytes of achlorophyllous gametophytes of *Diphasiastrum alpinum* (Lycopodiaceae).** *Am J Bot* 2013, **100**:2158-2174.
 44. Pressel S, Bidartondo MI, Field KJ, Rimington WR, Duckett JG: **Pteridophyte fungal associations: current knowledge and future perspectives.** *J Syst Evol* 2016, **54**:666-678.
 45. Field KJ, Leake JR, Tille S, Allison KE, Rimington WR, Bidartondo MI, Beerling DJ, Cameron DD: **From mycoheterophy to mutualism: mycorrhizal specificity and functioning in *Ophioglossum vulgatum* sporophytes.** *New Phytol* 2015, **205**:1492-1502.
 46. Turnau K, Ronikier M, Unrug J: **Role of mycorrhizal links between plants in establishment of liverworts thalli in natural habitats.** *Acta Soc Bot Pol* 1999, **68**:63-68.
 47. Turnau K, Anielska T, Jurkiewicz A: **Mycorrhizal symbiosis of chlorophyllous gametophytes and sporophytes of a fern, *Pellaea viridis* (Forsk.) Prantl (Pellaeaceae, Pteridales).** *Mycorrhiza* 2005, **15**:121-128.
 48. Turnau K, Anielska T, Ryszka P, Gawroński S, Ostachowicz B, Jurkiewicz A: **Establishment of arbuscular mycorrhizal plants originating from xerothermic grasslands on heavy metal rich industrial wastes — new solution for waste revegetation.** *Plant Soil* 2008, **305**:267-280.
 49. Turnau K, Przybyłowicz WJ, Ryszka P, Orłowska E, Anielska T, Mesjasz-Przybyłowicz J: **Mycorrhizal fungi modify element distribution in gametophytes and sporophytes of the fern *Pellaea viridis* from metalliferous soils.** *Chemosphere* 2013, **92**:1267-1273.
 50. Orchard S, Standish RJ, Dickie IA, Renton M, Walker C, Moot D, Ryan MH: **Fine root endophytes under scrutiny: a review of the literature on arbuscule-producing fungi recently suggested to belong to the Mucoromycotina.** *Mycorrhiza* 2017, **27**:618-638. Comprehensive review and meta-analysis of fine root endophytes.
 51. Orchard S, Hilton S, Bending GD, Dickie IA, Standish RJ, Gleeson DB, Jeffery RP, Powell JR, Walker C, Bass D *et al.*: **Fine endophytes (*Glomus tenue*) are related to Mucoromycotina, not Glomeromycota.** *New Phytol* 2017, **213**:481-486. Fine root endophytes belong in the Mucoromycotina, thus first report of arbuscules outside of the Glomeromycotina.
 52. Daft MJ, Nicolson TH: **Arbuscular mycorrhizas in plants colonizing coal wastes in Scotland.** *New Phytol* 1974, **73**:1129-1138.
 53. Johnson PN: **Mycorrhizal Endogonaceae in a New Zealand forest.** *New Phytol* 1977, **78**:161-170.
 54. Sigüenza C, Corkidi L, Allen E: **Feedbacks of soil inoculum of mycorrhizal fungi altered by N deposition on the growth of a native shrub and an invasive annual grass.** *Plant Soil* 2006, **286**:153-165.
 55. Sigüenza C, Crowley DE, Allen EB: **Soil microorganisms of a native shrub and exotic grasses along a nitrogen deposition gradient in southern California.** *Appl Soil Ecol* 2006, **32**:13-26.
 56. Orchard S, Standish RJ, Nicol D, Gupta VVSR, Ryan MH: **The response of fine root endophyte (*Glomus tenue*) to waterlogging is dependent on host plant species and soil type.** *Plant Soil* 2016, **403**:305-315.
 57. Crush JR: **Significance of endomycorrhizas in tussock grassland in Otago, New Zealand.** *New Zeal J Bot* 1973, **11**:645-660.
 58. Krings M, Harper CJ, White JF, Barthel M, Heinrichs J, Taylor EL, Taylor TN: **Fungi in a *Psaronius* root mantle from the Rotliegend (Asselian, Lower Permian/Cisuralian) of Thuringia, Germany.** *Rev Palaeobot Palynol* 2017, **239**:14-30.
 59. Luginbuehl L, Oldroyd GED: **Calcium signalling and transcriptional regulation in arbuscular mycorrhizal symbiosis.** In *Molecular Mycorrhizal Symbiosis*. Edited by Martin F. John Wiley and Sons; 2016:125-140.
 60. Gough C, Bécard G: **Strigolactones and lipochitooligosaccharides as molecular communication signals in the arbuscular mycorrhizal symbiosis.** In *Molecular Mycorrhizal Symbiosis*. Edited by Martin F. John Wiley and Sons; 2016:107-124. Extensive review on the roles of strigolactones and lipochitooligosaccharides as early mycorrhizal signals in arbuscular mycorrhizal networks.
 61. Taylor TN, Remy W, Hass H, Kerp H: **Fossil arbuscular mycorrhizae from the early Devonian.** *Mycologia* 1995, **87**:560-573.