Review

Symbiotic options for the conquest of land

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The domination of the landmasses of Earth by plants starting during the Ordovician Period drastically altered the development of the biosphere and the composition of the atmosphere, with far-reaching consequences for all life ever since. It is widely thought that symbiotic soil fungi facilitated the colonization of the terrestrial environment by plants. However, recent discoveries in molecular ecology, physiology, cytology, and paleontology have brought into question the hitherto-assumed identity and biology of the fungi engaged in symbiosis with the earliest-diverging lineages of extant land plants. Here, we reconsider the existing paradigm and show that the symbiotic options available to the first plants emerging onto the land were more varied than previously thought.

The current paradigm

The colonization of the terrestrial environment by plants was a major turning point in the evolutionary history of the Earth. In conquering the land, plants have sculpted the biosphere and geosphere through their influence on global carbon, nutrient, and water cycles [1], leading to the development of climates and habitats that are essential for supporting the diverse array of life that now exists in terrestrial environments [2,3]. It is estimated that more than 80% of living plant species form symbioses (see Glossary) with horizontally transmitted filamentous fungi, representing 92% of plant families worldwide [4] (Figure 1). These intimate associations are known as 'mycorrhizas', or 'mycorrhiza-like' when referring to plants lacking true roots, such as nonvascular plants. Through mycorrhizas and mycorrhiza-like associations, plants assimilate fungus-acquired mineral nutrients far beyond the soil depletion zones of their roots and from soil pores too narrow for their root hairs. In return, plants supply their fungal symbionts with carbohydrates fixed from atmospheric CO_2 through photosynthesis [5].

Plant life diversified on land some 70 million years (My) after the diversification of most major animal lineages in the seas during the Cambrian explosion (Figure 1) [6]. Classic paleoclimate modeling shows that land plants diversified against a backdrop of falling atmospheric CO_2 [7] (Figure 2), likely driven by growing demand and evolving capacity for carbon assimilation of the burgeoning Earth

Glossary

Arbuscular mycorrhizal (AM) fungi: members of the phylum Glomeromycota that form cell-to-cell nutritional associations with plant roots and extend filaments into soil to forage for minerals, colonize other roots, and form spores. They often produce characteristic highly branched tree-like structures, known as arbuscules, within colonized plant cells.
Biotroph: an organism nutritionally dependent on another living organism.
Coenocytic: refers to a multinucleate mass of cytoplasm, characteristic of nonseptate filamentous fungi.
Depletion zone: the volume of soil surrounding a root that becomes depleted of nutrients.
Embryophyte: plant in which the embryo is retained within maternal tissues, includes all clades of living land plants.
Endophyte: typically cryptic and asymptomatic microbe living within a plant, or any microbe within or between intact fossilized plant cells.
Gametophyte: haploid stage in the alternation of generations during the life cycle of plants, it is dominant in nonvascular plants.
Glomeromycota: a fungal phylum comprising biotrophs, including all known AM fungi and a mutualistic fungus of photosynthetic bacteria (i.e., *Geosiphon*). It includes the orders Archaeosporales, Paraglomerales, Diversisporales, and Glomerales.
Hypha: a fungal filament comprising tubular cells.
Mucoromycotina: a fungal subphylum of early-diverging fungal lineages comprising saprotrophs, parasites, and mutualists. It includes the orders Endogonales (pea truffles) and Mucorales (pin molds).
Mutualism: a symbiosis that increases the fitness of all partners.
Mycorrhiza: 'fungus root', a typically mutualistic symbiosis between plant roots and fungi. 'Mycorrhiza-like' is used to refer to mutualistic fungal symbiosis in plants without true roots.
Nonvascular plants: land plants without true (i.e., lignin-containing) vascular tissue, also known as bryophytes. They include three phyla: Marchantiophyta (liverworts), Anthocerotophyta (hornworts), and Bryophyta (mosses).
Rhizoid: unicellular tubular extension of an epidermal plant cell into the substrate functioning in attachment and resource uptake.
Saprotroph: an organism that fulfills its nutritional needs from dead organic matter, a decomposer.
Sporophyte: diploid stage in the alternation of generations during the life cycle of plants. It is dominant in vascular plants.
Symbiosis: the living together of unlike organisms, sometimes restricted to persistent mutualisms.
Thallus: body of some plants and fungi that is not differentiated into organs.
Vascular plants: land plants with lignified vascular tissue (i.e., xylem), also known as tracheophytes. They include the phyla Lycopodiophyta (lycopods or club mosses), Pteridophyta (ferns and allies), Pinophyta (conifers), Cycadophyta (cycads), Ginkgophyta (*Ginkgo*), Gnetophyta (*Gnetum*, *Welwitschia*, and *Ephedra*), and Magnoliophyta (flowering plants or angiosperms).

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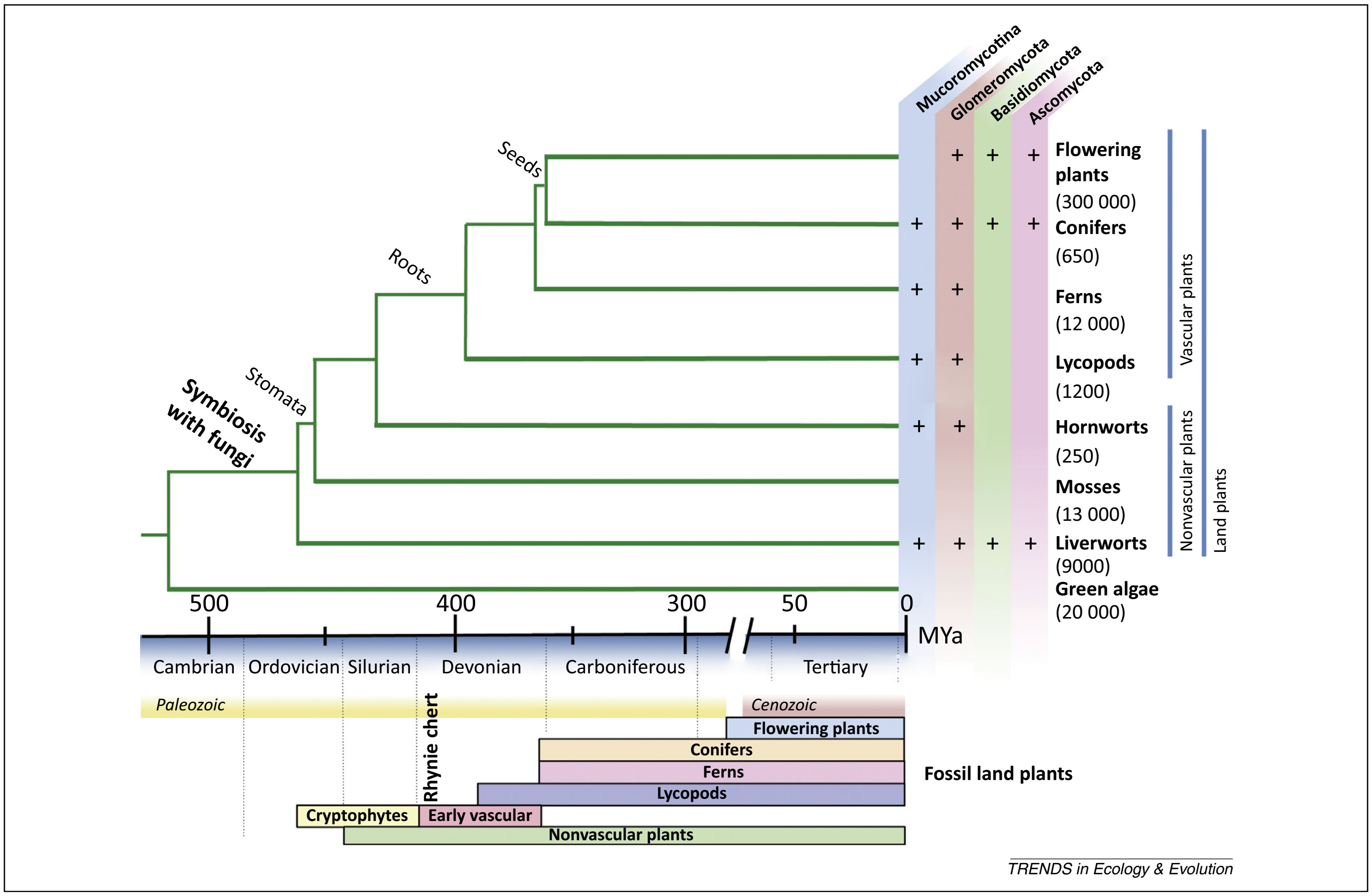

Figure 1. Land plant phylogeny showing estimated dates of divergence, symbiotic fungi, and key features of major land plant clades. A + indicates the presence of a fungal group within extant members of a plant clade. The numbers of living species in each plant group are shown between parentheses and fossilized plant groups are shown at the bottom with approximate dates of fossilization. Liverworts are the earliest-diverging group of extant plants and are shown to associate with Mucoromycotina, Glomeromycota, Basidiomycota, and Ascomycota fungi. The only other clade known to associate with all mycorrhizal fungal groups are the conifers. Mosses are asymbiotic, while hornworts, lycopods, and ferns are only known to associate with Mucoromycotina and Glomeromycota fungi. The Rhynie chert fossils provide the only detailed snapshot of early vascular plants and their associated fungi, some of which bear resemblance to extant examples of plant–Glomeromycota and/or plant–Mucoromycotina partnerships.

flora [8,9]. However, long before land plants emerged, the terrestrial environment had been colonized by fungi [10,11]. Among the early-branching fungal lineages were those that today form mutualistic associations with most plants (Figure 1). The macrofossil record of nonvascular plants is even more fragmentary than that of vascular plants, although the study of microfossils is now providing key new data [12,13], and molecular studies that date land plant origins and the divergence of the nonvascular groups (i.e., liverworts, mosses, and hornworts [14]) remain imprecise compared with those on flowering plant evolution [15]. This has resulted in some doubt over the precise evolutionary relations both among nonvascular plants themselves and between nonvascular and vascular plants [16,17]. Despite these lacunae, it has been proposed by plant and fungal biologists [18,19] that initial plant colonization of the terrestrial environment was facilitated through interactions with symbiotic fungi. Such hypothesis is supported by data spanning five decades of research and three scientific disciplines. First, the incredibly well-preserved early-Devonian Rhynie chert macrofossils show individual vascular plant cells harboring fungal structures that are strikingly similar to those formed by arbuscular mycorrhizal (AM) fungi of the phylum Glomeromycota within living cells of modern vascular plants [20,21] (Box 1). Second, molecular evidence indicates that genes and biochemical signaling pathways initiating and regulating the AM symbiosis are ubiquitous across all living land plant lineages [22–25]. Third, physiological data demonstrate nutritional mutualisms between Glomeromycota fungi and living members of the earliest-branching lineages of land plants [24,25].

The resulting paradigm is that the earliest, rootless, terrestrial plants coevolved with Glomeromycota fungi [4,26–30] that, in exchange for plant photosynthates, enhanced access to soil mineral nutrients (Box 2). This hypothesis was elaborated in classic papers by T.H. Nicolson [18], and K.A. Pirozynski and D.W. Malloch [19]. All other mycorrhizal symbioses (i.e., ectomycorrhizal, ericoid, and orchid) are thought to have evolved through later switches to other fungal lineages [31]. Even symbioses between flowering plants and nitrogen-fixing bacteria, such as *Rhizobium*, must have evolved from the ancient AM symbiosis [23]. These diverse plant–microbe partnerships continue to drive the establishment and development of terrestrial ecosystems [31,32]. Recent discoveries showing that the earliest-diverging groups of land plants form mutualistic associations with fungi other than Glomeromycota mean that it is now timely to challenge the existing paradigm for plant and fungal colonization of land. In this review, we