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REVIEW

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Phylogenetic distribution and evolution of mycorrhizas in land plants

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Abstract A survey of 659 papers mostly published since 1987 was conducted to compile a checklist of mycorrhizal occurrence among 3,617 species (263 families) of land plants. A plant phylogeny was then used to map the mycorrhizal information to examine evolutionary patterns. Several findings from this survey enhance our understanding of the roles of mycorrhizas in the origin and subsequent diversification of land plants. First, 80 and 92% of surveyed land plant species and families are mycorrhizal. Second, arbuscular mycorrhiza (AM) is the predominant and ancestral type of mycorrhiza in land plants. Its occurrence in a vast majority of land plants and early-diverging lineages of liverworts suggests that the origin of AM probably coincided with the origin of land plants. Third, ectomycorrhiza (ECM) and its derived types independently evolved from AM many times through parallel evolution. Coevolution between plant and fungal partners in ECM and its derived types has probably contributed to diversification of both plant hosts and fungal symbionts. Fourth, mycoheterotrophy and loss of the mycorrhizal condition also evolved many times independently in land plants through parallel evolution.

Keywords Mycorrhizas · Land plants · Fungi · Parallel evolution

Introduction

Mycorrhizas, dual organs of absorption formed when symbiotic fungi inhabit healthy tissues of most terrestrial plants (Trappe 1996), have widespread occurrence among land plants and are increasingly believed to have played an important role in the successful colonization of the land by plants (Pirozynski and Malloch 1975; Malloch et al. 1980; Harley and Harley 1987; Trappe 1987; Selosse and Le Tacon 1998; Read et al. 2000; Brundrett 2002). Since Nägeli first described them in 1842 (see Koide and Mosse 2004), only a few major surveys have been conducted on their phylogenetic distribution in various groups of land plants either by retrieving information from literature or through direct observation (Trappe 1987; Harley and Harley 1987; Newman and Reddell 1987). Trappe (1987) gathered information on the presence and absence of mycorrhizas in 6,507 species of angiosperms investigated in previous studies and mapped the phylogenetic distribution of mycorrhizas using the classification system by Cronquist (1981). He found that 82% of the species were mycorrhizal. From the occurrence of various types of mycorrhizas in different subclasses and orders of angiosperms, he further inferred that the ancestral type was glomeromycetous (the original word "zygomycotous" is not used because fungi forming this type of mycorrhiza are now placed in the new phylum Glomeromycota, see Schussler et al. 2001) mycorrhiza, and ascomycetous and basidiomycetous mycorrhizas belong to the derived types, and that evolution of mycorrhizas in plants had progressed from obligate to facultative mycorrhizas and ultimately to nonmycorrhizas. In the same year, Harley and Harley (1987) published a checklist of the mycorrhizal status of 144 families of vascular plants in the British flora, documenting various types of mycorrhizas in an entire flora for the first time. More recently, Gemma et al. (1992) and Zhao (2000) investigated the mycorrhizal status of 89 and 256 species of pteridophytes in Hawaii and Yunnan, China, respectively. They found that the percentages of mycorrhizal species in pteridophytes (74 and 33%, respectively) were lower than in angiosperms as reported by Trappe (1987). Whether bryophytes have mycorrhizas or not is still a debatable issue, but many liverworts and hornworts have fungal associations (Read et al. 2000). In two surveys of British liverworts, Pocock and Duckett (1985) and Duckett et al. (1991) reported that among the 206 and 284 examined species, respectively, 16% contained fungal endophytes in their rhizoids or thalli.

Mycorrhizal research has advanced at an astonishing pace over the last two decades due to a recent surge of interest in

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