
Vesicular-arbuscular mycorrhiza—an evolutionary approach

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Vesicular-arbuscular mycorrhizal (VAM) fungi forming mutualistic symbiosis with roots of higher plants are present in soil throughout the world. This suggests that VAM fungi disseminated intercontinentally prior to continental drift of the supercontinent Gondwana. The first mycorrhizal symbiosis appears to have occurred early in geological time, as evidenced by their presence in fossil soil and roots. Evidences available to date suggest that VAM fungi co-evolved with land plants. The ability of host and fungus to maintain the association depended on favourable gene combinations in both partners. Differences in morphology and development of spores of different VAM fungi reflect independent evolution from a number of distinct points of origin. The centre of evolution of VAM fungi appears to be the tropics.

Key-words—Evolution, *Glomus*, Vesicular-arbuscular Mycorrhiza, Zygomycotina.

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सारांश

पुटिकामय-कूर्चकी कवकमूल - वैश्वसिक दृष्टिकोण

डी० जे० बाग्यराज एवं टी० पद्मावती रवीन्द्र

पुटिकामय-कूर्चकी कवकमूल, जो समुन्नत पौधों की जड़ों में सहजीवन यापन करते हैं, समस्त विश्व में पाये जाते हैं। इससे यह प्रस्तावित होता है कि इन कवकों का विकीरण गोंडवाना महाद्वीप के महाद्वीपीय-विस्थापन के पहले ही विस्तृत रूप से हो चुका था। कवकमूल सहजीविता के प्रमाण अशिमत भिद्री एवं जड़ों से प्राप्त हुए हैं। उपलब्ध प्रमाणों से व्यक्त होता है कि ये कवकमूल स्थली पौधों के ही साथ-साथ सहविकसित हुए हैं। कवक एवं पौषी का साहचर्य दोनों के अनुकूल जीनों के संयोजन पर निर्भर करता है। विभिन्न कवकमूलों के बीजाणुओं की आकारिकी एवं विकास में विभिन्नता से व्यक्त होता है कि इनकी उत्पत्ति विभिन्न पूर्वजों से हुई है। परन्तु इन कवकमूलों के विकास का केन्द्र उष्णकटिबन्धीय क्षेत्र ही रहे हैं।

BOTANIST Albert Bernard Frank (1885) introduced the Greek word mycorrhiza into scientific terminology which literally means "fungus root". Mycorrhizae result from a mutualistic symbiosis between roots of higher plants and certain fungi. Though the word was introduced in 1885, mycorrhizae are millions of years older, for fossil mycorrhizae have been found in carbonaceous deposits (Berch *et al.*, 1985). In natural ecosystems it is exceptional for a plant not to possess a mycorrhizal root system. So it could be said that mycorrhizal association is a very common or almost universal phenomenon in the Plant Kingdom. There are different types of mycorrhizae. The most common type is the vesicular-arbuscular mycorrhizae (VAM) occurring in the majority of

agricultural crops, most shrubs, most tropical tree species and some temperate tree species.

VAM—ITS OCCURRENCE AND EFFECT ON PLANT GROWTH

According to Gerdemann (1975) it is easier to list plant families that do not form VAM than to list those that do. Families not forming VAM include Pinaceae, Betulaceae, Orchidaceae, Fumariaceae, Commelinaceae, Urticaceae and Ericaceae. Families that rarely form VAM include the Brassicaceae, Chenopodiaceae, Polygonaceae and the Cyperaceae.

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In addition to the widespread occurrence of VAM, the association is geographically ubiquitous and occurs in plants growing in arctic, temperate, and tropical regions. VAM occur over a broad ecological range from aquatic to desert environments (Mosse *et al.*, 1981; Bagyaraj, 1990).

VAM are formed by non-septate zygomycetous fungi belonging to the genera *Glomus*, *Gigaspora*, *Acaulospora*, *Entrophospora*, *Scutellospora* and *Sclerocystis*, in the family Endogonaceae. These fungi are obligate symbionts and have not been cultured on nutrient media. VA endophytes are not host specific although evidence is growing that certain endophytes may form preferential association with certain host plants (Mosse, 1977; Bagyaraj, 1992). The VAM fungi form the largest fungal resting spores known. These are often several hundred micrometers in diameter and can survive adverse soil conditions and germinate when conditions are favourable. A root system colonized by VAM fungi does not show any morphological modifications from the normal root system and hence cannot be distinguished visually.

Pot experiments conducted earlier in sterilized soil showed that VAM inoculation can drastically improve plant growth. Later investigations indicated that even in unsterile soil, plants do respond to inoculation with efficient strains of VAM fungi (Powell, 1984; Gianinazzi *et al.*, 1989; Bagyaraj, 1992). The increased growth of mycorrhizal plants is favoured in soil with low to moderate fertility. Greater soil exploration by mycorrhizal roots resulting in the increased uptake of P, Zn, Cu, S, etc., is well established. The other beneficial effects are their role in the biological control of root pathogens, biological nitrogen fixation, hormone production and greater ability to withstand water stress. A large economic impact on agriculture would result if the beneficial effects of VAM fungi observed under pot culture studies could be obtained under field conditions (Jeffries, 1987).

DISTRIBUTION OF VAM FUNGI

VAM fungi are present in soil throughout the world. In fact, many VAM species are represented on most continents. As an explanation for their remarkably widespread distribution, Trappe (1977), proposed that VAM fungi were disseminated intercontinentally prior to continental drift. The supercontinent Gondwana is thought to have begun to break apart and some sections drifting north about 125 million years ago (Raven *et al.*, 1976). Fossil plants containing VAM-like structures (Kidston & Lang, 1921), have been suggested from about 370

million years ago (Chaloner, 1970), so that the distribution of VAM fungi could have occurred as Trappe suggested. Alternatively, the widespread distribution of VAM fungi may simply reflect the millions of years over which dispersal of these fungi has occurred.

EVOLUTION OF VAM FUNGI

The first mycorrhizal symbiosis appears to have occurred early in geological time. Subterranean organs of early land plants have been found to contain hyphae and vesicles that closely resemble those of modern *Glomus* mycorrhizae (Kidston & Lang, 1921), although there has been some debate over whether these fungi were mycorrhizal or saprophytic in nature (Taylor, 1981). Colonization pattern and vesicle morphology of modern *Acaulospora* and *Entrophospora* mycorrhizae may distinguish them from *Glomus* and *Sclerocystis* mycorrhizae. In *Gigaspora* intracortical vesicles are few and borne on spiralled hyphae. Vesicles of "fine endophytes" are much smaller than those of other taxa. Hypha diameter and pattern of branching and colonization also differentiate fine endophytes from other VAM fungi. Assuming that mycorrhizal morphology was stable and that no major extinction of VAM fungi has occurred, it may be possible to identify genera of fossil fungi based only upon their VAM and thereby establish when the various VAM fungi appeared. Similarly, generic identity of fungi forming VAM of modern plants may be determined if mycorrhizal morphologies are examined more closely.

Fossilized *Glomus* and *Sclerocystis* spores are common in fossil soil and roots, though they have seldom been recognized as such and therefore have received a number of different names. *Microcodium elegans* Gluck is a name that has been applied to fossils variously interpreted as green algae (Gluck, 1912), Coral (Capeder, 1904), and ectomycorrhizae (Klappa, 1978). When Wood and Basson (1972) reported finding them in Palaeozoic shales of Missouri, they were actually describing and illustrating remarkably well preserved sporocarps of a *Sclerocystis* species, probably *S. rubiformis*. *Rhizophagites* Rosendahl was recognized by Gerdemann and Trappe (1974) as fossilized spores of *Glomus* species. Wagner and Taylor (1981) reported *Glomus*-like spores from tissues of Pennsylvanian-aged fossil plants. Apparently, no other modern VAM genera have been reported, possibly because they are not represented in the fossil record, but probably because they have not been recognized. The real potential existence of

such a fossil record means that in this group of fungi, classical evolutionary study may be possible.

If one accepts, for the moment, the hypothesis that VAM fungi co-evolved with land plants (Pirozynski & Malloch, 1975) it is necessary to imagine the environment that these fungi would have encountered in order to understand their early development. Beginning with the Late Precambrian, soils were organically modified by algae, bacteria and viruses adapted to surviving periodic drying. It is possible that saprophytic or lichenized fungi were also present by this time (Taylor, 1981). Land plants began to develop either in the Late Ordovician (Gray & Boucot, 1977) or Late Silurian (Edwards *et al.*, 1979) and by the Lower Devonian there is good evidence that fungi resembling modern VAM already colonized their rhizomes and roots (Retallack, 1981).

Morton (1990) also proposed a model of evolution in VAM fungi taking *Glomus* as an example. This model may answer the questions of origin, speciation, phenotypic divergence among lineages and differential increase in the number of species in supraspecific taxa. According to this model:

1. The progenitor of *Glomus* was an asexual saprobic, zygomycete fungus.
2. The most ancient terrestrial plants became established on land either independent of fungal symbiosis or with an association that was neutral or weakly mutualistic.
3. The symbiosis arose from contact between host and fungus that was not maladaptive to either. Clonal reproduction in both partners insured faithful replication and fixation of favourable gene combinations. Evolution of mutualism was gradual rather than saltational.
4. New fungal species arose during co-evolution of the mutualistic symbiosis. Speciation stopped or it was greatly diminished after the fungus became obligately biotrophic and most plant lineages possessed genes ameliorating compatible interactions.
5. Descendent arbuscular species originated from one or more clones of ancestral species in response to adaptations favouring fecundity, survival and localized dissemination. Thus geographic distribution of the new species might not correlate with that of ancestral species.
6. Species have persisted from about Cretaceous to modern times relatively unchanged in those spore phenotypes which delimit a species. Trends in morphological change emerged from patterns of speciation rather than from

differential extinction.

7. Clonal populations of species are fundamental units of contemporary evolutionary processes. Genetic change in clonal genotypes are directed by selection pressures optimizing fitness of both partners and this is expressed in mycorrhizal phenotypes.

The following statements support the proposed model. This model is a hypothesis based on a small amount of data, in part because so little emphasis has been placed on the biology of the organisms in the mycorrhizal association. It is believed that terrestrial plants began to develop either in the Ordovician or the Silurian, and by the Devonian VAM fungi colonized their root (Gray & Boucot, 1977; Edwards *et al.*, 1979). Pirozynski and Malloch (1975) and Pirozynski (1981) suggested that the mycorrhizal association arose from an early saltational events that lead to a partnership between an Oomycete fungus and an algal progenitor of land plants. But *Glomus* was not oomycetous in origin. Chitinaceous cell wall (Weijman & Meuzelaar, 1979) and multiperforate septa (Gibson *et al.*, 1986) place *Glomus* as a member of the Zygomycetes.

The emergence of plants into terrestrial habitat required an obligate mutualistic association and this association was necessary for the adaptive radiation in plant groups (Pirozynski, 1981). The first interaction between a plant and its fungal invader cannot be ascertained. The only possibility is that the host genes responsible for causing physical or physiological barriers against "foreign" biotic and/or abiotic agents were circumvented by the genes in fungus which produced "host recognizable" components. The ability of host and fungus to maintain the association depended on favourable gene combinations in both partners. The advantages to both partners are (i) faithful replication of the advantageous genotype in progeny, (ii) numerical superiority to maximize the spread to new habitats, (iii) lower reproductive cost due to transfer of the genetic complement, and (iv) long term persistence of the favourable genotypes (Silander, 1985). Thus transformation of this association into one that was mutualistic was more likely to have been gradual in the absence of prolific sexual recombination.

In VAM fungi, generic differences in morphology and development of spores and mycorrhizae reflect independent evolution of shared nutritional habit from a number of distinct points of origin (Berch *et al.*, 1985). This suggests possible evolution in the following way:

1. *Glomus*—*Sclerocystis*
2. *Acaulospora*—*Entrophospora*

3. *Gigaspora—Scutellospora*
4. Fine endopyte.

EVOLUTION OF MYCORRHIZAL ASSOCIATION IN PLANTS

VAM species are "historical entities" (Wiley, 1980) and their role in mycorrhizal interactions must be defined by their clonal populations. Modern plant species and fungal clones are well co-adapted. The continuous dependence of plant on the endomycorrhizal association results in obligate to facultative to non-mycotrophic systems (Newman & Reddell, 1987; Tester & Smith, 1987; Trappe, 1987). These patterns of mycotrophy indicate that symbiosis is being selected against in some groups of plants, and that non-mycotrophic plants are being selected for (Trappe, 1987; Pirozynski, 1981). Regarding the evolution of mycotrophy and autotrophy Pirozynski and Malloch (1975) proposed a hypothesis that mycotrophy is the primary nutritional habit of most terrestrial plant systems. The fossil record is scanty but the classic studies of Kidston and Lang (1921) showed zygomycetous-like fungal colonization of lycopsid and rhyniophyte rhizomes. Baylis (1975) proposed that the magnolioid root, with its minimal development of root hairs and strong development of zygomycetous mycorrhizae, represents the primitive condition of vascular plants. The test of this hypothesis by St. John (1980) with tropical trees supports this proposal. According to the hypothesis (i) asco- and basidio-mycetous mycorrhizae are a more advanced symbiosis than the zygomycetous type. Baylis's proposal is supported by fossil record which records a relatively greater number of asco- and basidio-mycetous types on more advanced host taxa and the general understanding that the fungi involved are more advanced than the Zygomycotina (Berch *et al.*, 1985; Pirozynski, 1981; Malloch *et al.*, 1980); (ii) the facultatively mycotrophic and autotrophic capabilities as represented in the graminoid type of root (Baylis, 1975) with its well developed root hairs and frequent absence of fungal colonization are the most advanced characters of all; (iii) vascular and terrestrial plants evolved through a trophic association with primitive fungi and are progressing in their evolution through other, more advanced types of fungal associations to an ultimate independence from fungi (Trappe, 1987).

CENTRE OF EVOLUTION OF VAM FUNGI AND VAM

VAM is the most common type of mycorrhizal

association both in areas of tropical and temperate vegetation, but in the boreal forest there is a switch to predominantly ectomycorrhizae. This suggests that the centre of evolution and distribution of VAM fungi has been the tropics, but it is not determined that specific taxa are found primarily in particular climatic zone, this remains an untested hypothesis. If VAM fungi co-evolved with early land plants, it is reasonable to suggest that their early environment was tropical.

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