The ecological role of mycorrhizal symbiosis and the origin of the land plants

Ekologická úloha mykorhizni symbiózy a původ suchozemských rostlin

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Phosphorus plays essential role in regulation and physiology of recent endomycorrhizas indicating possible evolutionary mechanism, involved in origin of symbiosis, based on improved phosphorus supply of first land plants. An evolutionary scenario of the origin of the endomycorrhizal symbiosis (*Glomales, Zygomycetes*) is constructed. Phosphorus was available in coastal anoxious sediments of Devonian and Silurian water reservoirs. Then the plants radiating to land lacked an effective mechanism for phosphorus accumulation in the oxidative environment. The cooperation between plants and fungal microorganisms would have resolved this problem. Partners then developed regulatory mechanisms balancing the nutritional relationship between them and formed the integrating structures (arbuscules), responsible for mass and signals interchange.

Fosfor hraje důležitou úlohu v regulačnich vazbách a ve fyziologii recentnich mykorhiz, čimž je naznačena i možnost existence evolučniho mechanismu, zúčastněného při vzniku symbiózy, jenž byl založen na zlepšené výživě prvnich suchozemských rostlin fosforem. Byl proto formulován evolučni scénář vzniku endomykorhizni symbiózy (*Glomales, Zygomycetes*). V bezkyslikatých pobřežnich sedimentech devonských a silurských vod byl dostatek pro rostliny dostupného fosforu. Proto rostliny, které pronikaly na souš, postrádaly efektivni mechanismus, kterým by mohly akumulovat fosfor v oxidativnim prostředi. Tento problém mohl být řešen kooperaci rostlin s houbovými mikroorganismy. Partneři pak rozvinuli regulačni mechanismus, který vyvažoval jejich výživu a vytvořili integrujici struktury (arbuskuly), zabezpečujici výměnu hmoty a signálů mezi nimi.

I. Introduction

Arbuscular mycorrhizal symbiosis is formed in root tissues of many plant taxa. Known arbuscular mycorrhizal fungi are members of the heterogenic order, *Glomales* (Morton and Benny 1990). The immense phylogenetical age of this mysterious group and its occurrence in fossilized prehistorical plant root tissues (compiled by Pirozynski and Dalpé 1989) offer the explanation of the land plants origin as a result of symbiosis between plant and fungus (Pirozynski and Malloch 1975, Pirozynski 1981).

The vascularization of plant organism was probably one of the major adaptive factors enabling their radiation onto dry land. The first vascular plants appeared in the fossil record in late Silurian (Obrhel 1962). Pirozynski and Malloch (1975) interpret the phylogenetical age of the first vascular land plants to be approx. 400 millions years. They assumed that these plants were probably living in symbiosis with fungi. We could speculate about whether symbiosis was the most important factor enabling the development of the land plants or the origin was "fungus independent" and only facilitated by symbiosis. Another essential question is: what possible mechanism favoured the symbiotic coexistence of both organisms during their transformation to dry land inhabitants. This will be the topic of this article.

II. Scenario

Morton (1990) presumes: "VA mycorrhizal 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 favorable gene combinations. . . . Genetic change in clonal genotypes are directed by selection pressures optimizing fitness of both partners, and this is expressed in mycorrhizal phenotypes." I should like to deal with this idea from the ecological point of view. The origin of the endomycorrhizal symbiosis of plants with glomalean fungi should be explainable as an ecological adaptation of both organisms to the changes of environmental parameters during expansion to dry land.

In the latest Silurian, an oxidative atmosphere was the most universal environment. Iron, manganese and some other elements were converted into their "modern" oxidized forms (Fe^{3+}). The atmosphere contained high, slowly increasing concentration of oxygen utilizable by living organisms (Cloud and Gibor 1970). Relatively advanced plants lived in coastal waters of Silurian seas. They produced, like recent plants, organic litter, forming a stout layer of anoxious sediment.

The plants, becoming vascularized, radiated to the land. Progression on land was retarded by lack of adaptations to environment, e. g. by unsufficient ability to absorb some nutrients in the form of oxidized minerals. A typical example of such nutrient is phosphorus. The sediments, formed in oxidative aquatic ecosystems, act as phosphorus trap due to the sedimentation of particulate, dead organic matter which is mineralized in the sediment and to the precipitation of metallic phosphates. In anaerobic organic detritus-containing sediments, phosphates are reduced, releasing soluble orthophosphate (Fenchel and Blackburn 1979, Pierrou 1976), available to plants. Then plants, growing in anoxious swamp layer, did not need to develop (or lost ?) adaptations enabling absorption of poorly soluble phosphate what was a serious barrier to expansion to terrestrical areas.

That problem could have been resolved by cooperation of plants with aerobic organisms of upper, aerobic layer of water reservoirs. Phosphate was present there in very low concentration and then these organisms had to have effective absorption mechanism. These organisms were probably coenocytic, microscopical autotrophs. On becoming to symbiotic they had lost the photosynthetic apparatus and adapted their energy metabolism to utilize compounds produced by plants.

The hypothetical cooperation of the first land plants taxa with possible symbiotic microorganisms would have resulted in the state, in which phosphate was absorbed in sufficient amount by the microorganism and transported and distributed in the plants with vascular system.

Both partners then developed adaptations, supporting the total biomass production and plant rhizomes receptivity (biochemical adaptations to infection) including the life-cycle control mechanism of fungal symbiont ancestor (necessary for succsessful regulation of development of fungal partner in symbiosis). Such state of coexistence represented serious success in expansion ability of both partners, when compared with their initial features. These changes resulted, being conserved, into the development of modern endomycorrhizal symbiosis of arbuscular type.

III. The coincidence of the postulated assumptions with the recent knowledge

The coenocytic symbionts are widespread in vascular plants (Newmann and Reddell 1987). It supports the idea of endomycorrhizal symbiosis of arbuscular type as a common and ancient phenomena. Because fungi forming other kinds of endomycorrhizas and ectomycorrhizas (e. g. ascomycetes and basidiomycetes) appeared later than coenocytic endosymbionts currently classified in *Zygomycetes* (deduced from Cavalier-Smith 1986 and Pirozynski 1981), they will not be considered further.

The formulation of above mentioned scenario was inspirated by two relevant facts: (i) phosphate availability strongly depends on the absence of oxygen in the environment (Pierrou 1976, Stumm 1973), and (ii) phosphorus metabolism plays a key regulatory role in modern arbuscular mycorrhizas (Elias and Safir 1987, Gianinazzi-Pearson et al. 1989). The presumption of effective phosphate absorption, mediated by the presence of symbiotic microorganisms is supported by interactions observed in recent arbuscular mycorrhizal symbiosis. Mycorrhizal fungi enhance absorption of less soluble forms of phosphorus (Murdoch, Jackobs and Gerdemann 1967) and improve exploitation of available phosphorus in soil (Gianinazzi-Pearson et al. 1981).

The fungus ancestor is postulated to have been adapted to aerobic environment. Recent arbuscular mycorrhizal fungi also are aerobes, sensitive to decreased oxygen concentrations in soil (Saif 1981, 1983). Spore germination is strongly depressed at low oxygen concentration, or at elevated levels of carbon dioxide which is a common product of anaerobic biochemical processes (LeTacon, Skinner and Mosse 1983). In normally aerated soil, the anaerobiosis occurs only in very limited area of root tip and elongation zone (Fischer, Flessa and Schaller 1989). The anaerobiosis is presumed to occur particularly in flooded, unaerated soils. Under such conditions, the population of infective propagules of arbuscular fungi is generally depressed (Haq et. al. 1987). Analogous results were obtained by Lodge (1989), with ectendomycorrhizal plants. These observations support presumption of non-mycorrhizal status of water inhabiting plants, including land plant ancestors.

The mycorrhizal infection process in the root is non-destructive, culminating in the final elimination of fungal structures (arbuscules) from host plant cells (Toth and Miller 1984). It suggest that the plant can recognize the fungal partner and that it is able to regulate the process of infection (Koide and Li 1990). The fungal partner is strictly dependent on the host. Attempts to cultivate arbuscular mycorrhizal fungi axenically were generally unsuccessful even though the fungi probably possess active components of energetical metabolism (Macdonald and Lewis 1978, Beilby and Kidby 1982).

IV. Possible cell cycle regulatory mechanism in glomalean fungi

According to the scenario, the expanding communities of land plants utilized phosphate afforded by the co-expanding symbiotic microorganisms, ancestors of arbuscular fungi. We could presume three parallel processes evolving under selection pressure of newly colonized ecosystem: (i) both partners in symbiosis developed the anatomical integration structures (responsible for phosphate flux into plant organism). That fact probably enabled also (ii) the development of mechanism for efficient exchange of carbon- and energy-rich compounds between plant and fungus. The third process is the most important for the understanding of relationships between both symbionts: (iii) the evolution of regulatory mechanisms in symbiosis.

In vitro, the mycelium of recent VA mycorrhizal fungi in the presymbiotic state (= germ tubes without contact with living root) does not show nuclear division and DNA synthesis (Burggraaf and Beringer 1989). The inhibited cell cycle is probable explanation, organism "is waiting" for a plant signal. We can interpret it to be the result of the regulatory mechanism function, preventing the saprotrophic growth of the fungus in the absence of plant. The ecological and evolutionary importance of this is evident. Microorganism, regularly supplied with carbon and energy via specialized organs in host tissue, cannot successfully compete with saprotrophic microorganisms in the soil: the regulatory mechanism defect causes the immediate elimination of defective individual. We presume that such an important regulatory mechanism would be highly conserved.

V. Rust fungi - an analogy in cell cycle regulatory mechanism?

It follows that the saprotrophic growth of the glomalean fungus could be observed only when competition for energy and carbon is eliminated for sufficient time (to cumulate cell cycle regulatory mechanism defective individuals). In the case of mycorrhizal fungi of arbuscular type no information was accumulated in this field (Very rarely is reported the axenic cultivation of arbuscular mycorrhizal fungus - Barrett 1947, Janardhanan, Gupta and Husain 1990 - but such results are not reproducible). But there are very interesting reports about axenic cultures of other obligate biotrophs, the rust fungi (*Uredinales*). In general, it is not possible to maintain the mycelium of rust fungi in serial culture. But when massive inoculum of urediospores of *Puccinia graminis* was incubated on a proper medium, the growth of several fungal colonies was observed after a long period of incubation (Maclean 1982). The mycelium in these colonies was subculturable, uninuclear (in contrast to the normal, dicaryotic condition) and probably genetically distinct from the parent fungus. We could presume the existence of some defect in the mechanism of cell cycle regulation.

The mechanisms of cell cycle regulation in eucaryotes consist of periodical activation of expression of different regulatory genes responsible for DNA synthesis and other processes connected with cell proliferation (Johnston 1990). The mechanisms of activation of regulatory genes in mycorrhizal fungi of arbuscular type is not yet known. These fungi, although being phylogenetically older and probably better adapted to biotrophy than the rust fungi, could demonstrate in axenic conditions some similarity to saprotrophic form of rust fungi. There is the opportunity to destroy presumed cell cycle regulatory genes using mutagenesis in the environment lacking pressure of competition for the energy and carbon with any other partner. It would allow us not only to maintain arbuscular fungi in axenic culture, but also present a more complex view of symbiosis, involving regulatory mechanism of mycorrhizal symbiosis of arbuscular type.

VI. Conclusion

In this article a speculative scenario of the evolution of arbuscular mycorrhizal symbiosis was constructed on the basis of facts derived from studies of recent arbuscular mycorrhiza. It aims to explain the influence of invironmental factors in the origin and stability of symbiosis. The cooperation between plants, lacking sufficiently effective phosphate absorption mechanism (radiating from phosphorus rich anoxic water ecosystems to land) and microorganisms inhabiting oxidative environment may have solved the problem of limited plant phosphorus supply in new oxidative conditions. The regulatory mechanism, balancing the relationship between the two partners probably plays an essential role in the phytogenetical stability there. It may also explain the unculturability of arbuscular fungi under axenic conditions.

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