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A.B. Frank and mycorrhizae: the challenge to evolutionary and ecologic theory

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Abstract A. B. Frank's observations and hypotheses about mycorrhizae in 1885 flew in the face of conventional thinking of the time. He reported that what we now term ectomycorrhizae were widespread on root systems of many woody plant species in a great diversity of habitats and soils. He hypothesized that mycorrhizae represent a pervasive mutualistic symbiosis in which fungus and host nutritionally rely on each other; that the fungus extracts nutrients from both mineral soil and humus and translocates them to the tree host; and that the tree, in turn, nourishes the fungus. Initially opposed by much of the scientific community, nearly all of Frank's major hypotheses have since been unequivocally demonstrated, although many decades were required to achieve conclusive evidence. Nonetheless, the revolution in thinking about plant and fungal evolution, ecology and physiology generated by Frank is still in the process of acceptance by much of the scientific community, 120 years and tens of thousands of scientific papers since he coined the term "mycorrhiza". The reasons for this extraordinary lag time in themselves present an intriguing research subject.

Keywords Symbiosis · Mutualism · Heterotrophy · Ectomycorrhizae · Nutrient uptake

Introduction

It began as an exploration of the possibility of growing truffles in Prussia. It quickly evolved into a revolutionary theory of tree nutrition via symbiosis between fungi and tree roots in a single organ newly termed "mycorrhiza." Professor Albert Bernhard Frank (Fig. 1) combined careful morphological studies of feeder rootlets of various trees with broad ecological observations to formulate hypotheses that stood conventional botanical wisdom on its head (Frank 1885a). These discoveries elicited vigorous controversy for 40 years, but experimental and observational evidence gradually overcame even the most adamant opponents. Now the pervasiveness of the mycorrhiza phenomenon, together with the fossil record, evidence that plants and plant communities have evolved in mycorrhizal relationships throughout the world. The massive experiment of evolution has arrived at the same answers independently in all the continents, Gondwanan and Laurasian alike. Even Antarctica, now depauperate of mycorrhizal plants, bears a fossil record of mycorrhizal communities in past eras of more tractable climate (Stubblefield et al. 1987a,b). The conceptual revolution continues to this day, as the implications of mycorrhizal associations to evolutionary theory and plant ecology find their way slowly but inexorably into scientific thinking.

Frank had achieved eminence as a botanist well before his work on mycorrhizae, as detailed by Wittmack (1900). Born in Dresden in 1839, he studied at the University of Leipzig, where he was appointed curator at the age of 26, lecturer at 28, and professor at 39. During this period he published studies on plant identification, anatomy and photo- and geotropism. Prior to 1885 he produced a textbook on plant physiology but became best known for his massive book on *Plant Pathology*, first published in 1880 but later reissued as a 3-volume 2nd edition in 1895–1896. In 1881 he was appointed Professor of Plant Pathology at the Royal College of Agriculture in Berlin.

Frank was neither alone nor the first to observe mycorrhizae, or more specifically what later became designated as "ectomycorrhizae" (Peyronel et al. 1969). What set him apart was the care he exercised in his research and the depth and perceptiveness of his interpretations. He let the facts lead him to logical conclusions, even though they flew in the face of conventional thinking. Fifty years passed before some of his hypotheses were convincingly tested and confirmed. Frank elaborated on his original hypotheses in ensuing papers (Frank 1885b,c, 1887b, 1888, 1889, 1891, 1892, 1894). He studied an array of symbiotic phenomena: lichens and root nodules of legumes and alders

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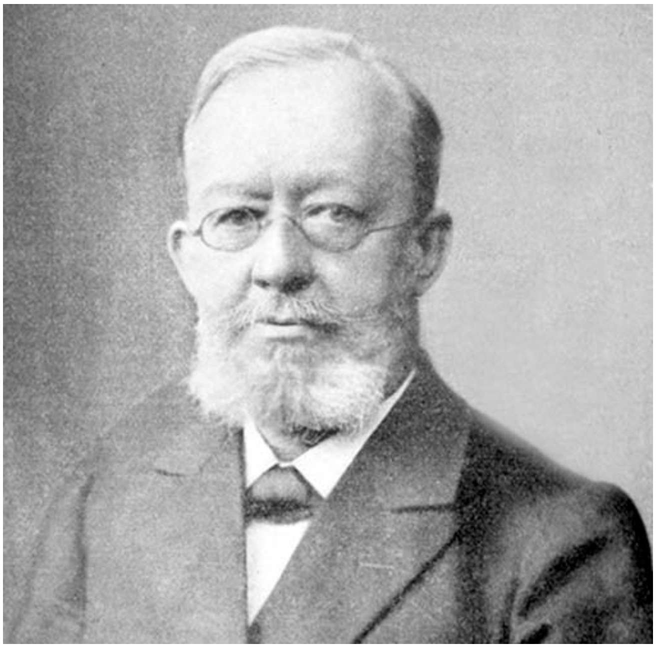

Fig. 1 Albert Bernhard Frank, 1839–1900

(Frank 1879, 1887a) in addition to mycorrhizae. But even before his landmark paper of 1885, Frank (1877) had espoused Schwendener's (1869) idea of an association of fungi with algae in lichens and coined the term "symbiotism" for that. The concept was later taken up as "symbiosis" by de Bary (1879), who is often credited as its originator.

In this paper I briefly review Frank's observations and hypotheses in a historical context and highlight how they stood up to testing over the years. This is not an exhaustive review; that has been done in many books and papers over the years. Rather, my intent is to remind us that our present research and concepts about mycorrhizae and their importance are based on a rich heritage of research, natural history and experimentation combined to produce an understanding that no single approach alone could achieve.

Developmental morphology of ectomycorrhizae

Though not the first to describe ectomycorrhizae, Frank was the first to correctly interpret their meaning. Theodor Hartig (1840) described and illustrated both the fungal mantle and intercellular hyphal network of pine mycorrhizae, thereby gaining his immortality by way of the term "Hartig net." However, he failed to recognize the fungal origin of these structures, interpreting them as "a persistent periderm" of the root and "a peculiar wall structure" of the root cells. His illustrations are diagrammatic and not particularly elegant, his descriptions brief and incomplete, and his conclusions wrong. Nonetheless, he was the first to report these phenomena, an accomplishment overlooked until his son Robert Hartig, also a respected botanist, resurrected it in 1886. Bruchmann (1874) was the first to determine that the mantle and Hartig net were fungal. Boudier (1876), Reess (1880) and Gibelli (1883) all described and illustrated what Frank later termed a mycorrhiza, but regarded the fungus as a pathogen. Kamienski (1882) reported his studies on *Monotropa* roots, also recognizing the fungal nature of the mantle and network but, for lack of evidence, equivocating about the nature of the association. Gibelli (1883) and Frank (1885a) surpassed their predecessors in descriptive detail and accuracy accompanied by illustrations unsurpassed to this day.

Frank (1885a) was the first to detail the developmental stages of ectomycorrhizae, from initial contact of hypha with root to full development. Now we recognize more variations in developmental morphology than Frank encountered, but he laid the groundwork. As had Gibelli (1883) before him, Frank described and beautifully illustrated the stimulation of branching, hypertrophy of outer cortical cells, and suppression of root hair formation that accompanied colonization by ectomycorrhizal fungi. He speculated that the physical pressure of the mantle on the surface of the rootlet suppressed root hairs. In this he was uncharacteristically wrong, but not until Slankis (1948, 1949) reported suppression of root hair formation by fungal exudates and auxins did biochemical interactions between fungus and host became recognized as causal agents. These interactions are extremely complex and not likely to be explained by single physiological phenomena (Bonfante-Fasolo and Scannerini 1992). Finally, Frank (1885a) was the first to describe the occasional conversion of the usually short-lived mycorrhizae into perennial long roots, as has since been reported many times.

Distribution and ecology of ectomycorrhizae

Gibelli (1883) had recorded multiple tree species as having fungus-mantled rootlets over a wide area in Italy, and so did Frank (1885a) in Germany. Frank particularly noted the pervasiveness of mycorrhizae on Fagaceae and some Betulaceae, and on a great diversity of soils and topographies. Initially, he regarded a large number of woody and herbaceous plant species as lacking mycorrhizae, evidently taking the presence of the mantle as the distinguishing characteristic of a mycorrhiza. Soon, however, he discovered other mycorrhiza types that lacked a mantle, so he coined the terms "ectotrophic" for those with a mantle, "endotrophic" for those without (Frank 1887b). He then commissioned his student, Albert Schlicht, to conduct a broad survey of plants in Germany in a great diversity of habitats. Schlicht (1888, 1889) produced extensive lists of plants that had ecto- or endomycorrhizae. The conclusion from these activities was that mycorrhiza formation was pervasive in the plant world at all elevations in virtually all soils and habitats examined.

Frank (1885a) explored the relationship of mycorrhiza frequency to depth in soil. He concluded that the most prolific formation was in the upper soil layers and decreased with increases in soil depth. He compared seedlings with older trees, reporting that mycorrhizae were formed as soon as a seedling produced feeder rootlets and new mycorrhizae continued to form throughout the life of the tree. He reported the phenomenon of mycorrhiza turnover, that in some situations mycorrhizae were short-lived, in others long-lived, and in healthy trees new mycorrhizae replaced those that had died off. These conclusions have since been reconfirmed by many researchers.

The ectomycorrhizal fungi

The hypogeous stag truffle, *Elaphomyces granulatus* and closely related species, was the first fungal species reported to mantle and induce morphological changes in tree roots (Tulasne and Tulasne 1841; Vittadini 1842; Boudier 1876; Reess 1880). These fungi have slowly developing fruiting bodies from which hyphae grow profusely to form mycorrhizae with nearby rootlets. The affected rootlets are stimulated to proliferate around the fruiting bodies, enclosing them in a husk of mycorrhizae and mycelium. Boudier (1876) observed not only *Elaphomyces* spp. but also *Cenococcum geophilum* as mantling rootlets, and Reess (1880) reported that diverse fungi could do this. Frank (1885a) was a bit vague on the fungi involved, in some places referring to "the fungus," in others to "the fungi." He was inclined to attribute mycorrhiza formation to hypogeous fungi, but he is not clear about whether he means all or just some species. In any event, he recognized that multiple fungi were involved.

The function of mycorrhizae

Although Frank's studies of the developmental morphology, distribution and ecology of mycorrhizae were essential background for inferring mycorrhizal function, other workers as noted above had studied similar material without understanding what it meant. Accordingly, Frank is mostly renowned for perceiving the meaning of the mycorrhizal association. Most importantly, he understood from what he saw that a mutualistic symbiosis between fungus and plant had to be involved. This was the only logical conclusion, considering that both fungus and host flourished. Yet few others before had made this intellectual leap, because fungi were so firmly entrenched in human thinking as causes of disease and decay. To be sure, Vittadini (1842) had concluded from careful observations more than 40 years before Frank that "...it is our decided opinion that beyond all doubt the higher plants absorb nutrients from the fungus by their feeder rootlets." He did not, however, venture the next step, that the fungus is nourished from the roots. Pfeffer (1877) briefly suggested a mutualism in reference to the root-fungus association of orchids. Kamienski's (1882) studies of *Monotropa* mycorrhizae led him to conclude that the rootlets functioned primarily as a physical base for the fungus, which in turn substitutes for root hairs by providing nutrients to the host. He hypothesized that the same fungi parasitize the nearby rootlets of associated trees and somewhat ambiguously implied epiparasitism by the *Monotropa* on the trees via the shared mycelium. He does not suggest mutualism between the fungus and the tree roots.

It befell Frank, then, to state the conclusion that escaped others, and he did so without ambiguity: "...certain tree species...do not nourish themselves independently in the soil but regularly establish a symbiosis with fungal mycelium over their entire root system. This mycelium performs a 'wet nurse' function and performs the entire nourishment of the tree from the soil...The intimate, reciprocal dependence that follows the growth of both partners and the tight interrelationships of physiological functions that must exist between the two appear to be a new example of symbiosis in the plant kingdom...the basic nutritional needs of the fungus are primarily the carbon compounds procured from the photosynthesizing tree. In contrast, the fungus is evidently independent in regard to uptake of soil minerals, in that it alone contacts the soil by its peripheral position on the mycorrhiza and the innumerable hyphae it extends into the soil to grow around soil particles like root hairs....the root fungus, at least in the mycelial state, can inflict absolutely no disadvantage to the tree...the root fungus is the sole organ for uptake of water and soil nutrients by oaks, beech, etc." (Frank 1885a). He then coined the term "heterotrophy" to designate this mode of nutrition.

Experimental evidence over the years supported Frank's hypothesis, for example the work of Hatch (1937). Direct confirmation of the uptake of minerals by ectomycorrhizal fungi and their translocation to tree hosts did not appear until a series of papers initiated by Melin and Nilsson in 1950, 65 years after Frank ennunciated his hypothesis. As reviewed by Melin (1962), Melin and Nilsson demonstrated, by elegantly simple isotope tracer experiments, the direct transfer of nitrogen and minerals from an external source to tree seedlings via ectomycorrhizal hyphae. They also demonstrated translocation of ^{14}C photosynthesized by the tree to the fungus (Melin and Nilsson 1957), the first direct confirmation of this phenomenon more than 70 years after Frank so hypothesized.

Frank (1885c, 1888) pointed out that ectomycorrhizal fungi proliferate in humus in forest soils and proposed that the fungi extract nutrients from organic matter for use by the host plant. He elaborated on this in 1894, hypothesizing that the fungi particularly aided in releasing nitrogen from the humus. A primary source of organically bound nitrogen in humus would likely be proteins (Frank 1894). Ninety-three years after Frank presented his organic nitrogen hypothesis, Read (1987) demonstrated that mycorrhizal fungi can assimilate protein nitrogen and make it available to host plants, which cannot access it without the fungi. Durall et al. (1994) then demonstrated with ^{14}C-labeled substrates that several mycorrhizal fungi in symbiosis with host seedlings readily decompose hemicellulose and cellulose, an activity important for accessing proteins in humus, and that some species decompose humic polymers, an additional source of nitrogen in humus. This further confirmation of Frank's hypothesis emerged a century after his paper of 1894.

Discussion

Frank was a careful and systematic scientist, not only in observing his research subjects meticulously but also in designing and conducting the logical steps needed to answer questions. His particular genius was not that alone, however; many scientists of the time were equally adept. Rather, it was his intuitive ability to interpret the meaning of what he discovered in light of the evidence and draw the logical conclusions, disregarding conventional thinking. Moreover, once convinced he was on the right track, he was bold enough to put his reputation on the line by announcing it to his peers. His hypotheses aroused considerable opposition, especially by R. Hartig (1886, 1888). Hartig (1888) emphasized his thoughts by titling a critique of Frank's ideas "On root parasites." As the years passed, however, Frank's hypotheses became so widely evidenced that they could be raised to the more exalted status of theories. Still, the direct evidence for much of what Frank proposed emerged only after decades or even a century. In nearly all aspects, Frank was proved correct.

The implications of Frank's discoveries and interpretations to evolutionary theory and plant and fungal physiology and ecology are truly revolutionary. They challenge the neo-Darwinian concept that evolution proceeds strictly by competitive struggle (Margulis and Fester 1991; Sapp 1994; Speidel 2000; Ryan 2002; Bronstein 2003). As Ryan (2002) phrases it in reference to Frank's accomplishment, "The intimate cooperation between wholly different life forms—plants and fungi—is not only an amazing biological phenomenon but also a vitally important factor in the diversity of plant life on earth. It should have been of enormous interest to evolutionary theorists, but few scientists were paying attention. In those formative years at the end of the nineteenth century, as the fundamental principles of biology were being hammered into place in laboratories around the world, Darwinian evolution took center stage. And as Darwinism, with its emphasis on competitive struggle, thrived, symbiosis, its cooperative alter ego, languished in the shadows, derided or dismissed as a novelty."

Frank's theories profoundly altered our understanding of how ecosystems operate. The change in thinking has been slow: 120 years, after all, have passed since he coined the term "mycorrhiza." By 1991, some 12,000 publications on mycorrhizae had appeared (Trappe and Castellano 1991; Klironomos and Kendrick 1993). At the rate of publication as of 1991 (Klironomos and Kendrick 1993), that number by now would total more than 21,000, a conservative estimate that includes many dozens of books focusing on mycorrhizae. However, a tally of page-indexed references to mycorrhizae in the 35 volumes of the *Annual Review of Ecology and Systematics*, published from 1970 through 2003, totals 23, and most of these just mention mycorrhizae in passing. This out of the 18,665 pages of articles in those volumes! Many mycorrhiza researchers have published insightful papers on the importance of mycorrhizae to ecological phenomena such as succession and competition, but evidently the preaching has been heeded mostly by the already converted, i.e., other mycorrhiza researchers. The reluctance of many evolutionists, ecologists, agronomists and foresters to consider the importance of the belowground ecosystem is fading: what is seen above the root collar is a function of what happens below it, a fact that cannot be rationally ignored. The glacial pace at which Frank's accomplishment has become recognized is in itself a phenomenon deserving historical, psychological and sociological study.

Epilogue

Frank's initial charge (1885a) was to study the occurrence and biology of truffles. His discoveries about mycorrhizae soon consumed his attention, however, and his occupation with truffles per se receded. His publications on mycorrhizae ended in 1894, and we hear no more on the topic from his student Schlicht or other researchers at his institution in Berlin. Frank continued to publish on topics in botany and plant pathology, including a 2-volume textbook of botany in 1892 and one on plant science for agricultural schools in 1894. His special interest in plant pathology was manifested in a co-authored handbook on plant protection and, in 1899, his acclaimed "Kampfbuch" ("battle book") on plant pest control. His last book, co-authored with his assistant Friedrich Krüger and published the year of his death, was on scale insects of fruit trees.

For many years Frank served as editor of the journal of the German Botanical Society. In 1895 he had been appointed Rector of the Royal Agricultural College and in 1899 he founded and was appointed Director of the Biological Division for Agriculture and Forestry of the Royal Board of Health. He was greatly esteemed by his students and colleagues. Wittmack (1900) began his memorial article on Frank, "A man whose name is honored in all parts of the world..." and noted that despite Frank's high administrative appointments "...he kept up his lecturing on plant pathology at the Royal Agricultural College, so that we did not entirely lose our beloved colleague." Frank had been honored by the Emperor with award of the Order of the Red Eagle Class 4 and the Centenary Medal at the opening of the monument to Emperor Wilhelm the Great.

Albert Bernhard Frank died after a brief illness at the peak of his career in 1900, age 61. He was buried at Darmstadt, where his widow decided to move to be with their daughter and son-in-law, a government economist and administrator in the Grand Duchy of Hesse (Wittmack 1900). Were he here today, he would see that his discoveries and theories on symbiosis have profoundly influenced thinking in a wide range of scientific endeavors. He might be amazed to learn that his ideas are even among the progenitors of recent, innovative concepts of sociopolitical interactions in human societies (Van Loon 2000).

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References

Bary A de (1879) Die Erscheinung der Symbiose. Tübner, Strassbourg

Bonfante-Fasolo P, Scannerini S (1992) The cellular basis of plant-fungus interchanges in mycorrhizal associations. In: Allen MF (ed) Mycorrhizal functioning—an integrative plant-fungal process. Chapman & Hall, New York, pp 65–101

Boudier E (1876) Du parasitisme probable de quelques espèces du genre *Elaphomyces* et de la recherché de ces Tubéracées. Bull Soc Bot Fr 23:115–119

Bronstein JL (2003) The scope for exploitation within mutualistic interactions. In: Hammerstein P (ed) Genetic and cultural evolution of cooperation. MIT Press, Cambridge, Mass., pp 185–202

Bruchmann H (1874) Wachstum der Wurzeln von *Lycopodium* und *Isoetes*. Z Naturwiss 8:522–580

Durall DM, Todd AW, Trappe JM (1994) Decomposition of ^{14}C-labelled substrates by ectomycorrhizal fungi in association with Douglas-fir. New Phytol 127:725–729

Frank AB (1877) Über die biologischen Verhältnisse des Thallus einiger Krustflechten. Cohn Beitr Biol Pflanz 2:123–200

Frank AB (1879) Ueber den Parasiten in den Wurzelanschwellungen der Papilionaceen. Bot Ztg 37:377–388

Frank AB (1885a) Ueber die auf Wurzelsymbiose beruhende Ernährung gewisser Bäume durch unterirdische Pilze. Ber Dtsch Bot Ges 3:128–145 [In English translation (2005), Mycorrhiza 15:in press]

Frank AB (1885b) Ueber den gegenwärtigen Stand der Trüffelfrage und die damit zusammenhängende Ernährung gewisser Bäume durch Wurzelpilze. Gart Ztg 4:423–426

Frank AB (1885c) Neue Mittheilungen über die Mycorhiza der Bäume und der *Monotropa hypopitys*. Ber Dtsch Bot Ges 3: XXVII–XXXIII

Frank AB (1887a) Sind die Wurzelanschwellungen der Erlen und Eläagnaceen Pilzgallen? Ber Dtsch Bot Ges 5:50–58

Frank AB (1887b) Ueber neue Mykorrhiza-Formen. Ber Dstch Bot Ges 5:395–409

Frank AB (1888) Ueber die physiologische Bedeutung der Mykorhiza. Ber Dtsch Bot Ges 6:248–269

Frank AB (1889) Was nützen den Waldbäumen die Wurzelpilze? Forstl Blätt Ser 3 13:1–7

Frank AB (1891) Ueber die auf Verdauung von Pilzen abzielende Symbiose der mit endotrophen Mykorhizen begabten Pflanzen, sowie der Leguminosen und Erlen. Ber Dtsch Bot Ges 9:244–253

Frank AB (1892) Sur l'importance des mycorhizes dans la nutrition des plantes humicoles. Ann Sci Agron France Étrang 9:351–361

Frank AB (1894) Die Bedeutung der Mykorhiza für die gemeine Kiefer. Forstwiss Centralbl 38:185–190

Gibelli G (1883) Nuovi studii sulla malattia del castagno detta dell'inchiostro. Mem Accad Sci Ist Bologna 4:287–314

Hartig R (1886) Über die symbiotischen Erscheinungen in Pflanzenleben. Bot Centralbl 25:350–352

Hartig R (1888) Die Pflanzen Wurzelparasiten. Allg Forst Jagd Ztg 64:118–123

Hartig T (1840) Vollständige Naturgeschichte der forstlichen Culturpflanzen Deutschlands. Förstner'sche Verlagsbuchhandlung, Berlin

Hatch AB (1937) The physical basis of mycotrophy in the genus *Pinus*. Black Rock For Bull 6:1–168.

Kamienski FM (1882) Les organs végétatifs du *Monotropa hypopitys* L. Mem Soc Nat Sci Nat Math Cherbourg 24:5–40

Klironomos JN, Kendrick WB (1993) Research on mycorrhizas: trends in the past 40 years as expressed in the 'Mycolit' database. New Phytol 125:595–600

Margulis L, Fester R (eds) (1991) Symbiosis as a source of evolutionary innovation: speciation and morphogenesis. MIT Press, Cambridge, Mass.

Melin E (1962) Physiological aspects of mycorrhizae of forest trees. In: Kozlowski TT (ed) Ronald Press, New York, pp 247–263

Melin E, Nilsson H (1950) Transfer of radioactive phosphorus to pine seedlings by means of mycorrhizal hyphae. Physiol Plant 3:88–92

Melin E, Nilsson H (1957) Transport of C^{14} labeled photosynthate to the fungal associate of pine mycorrhiza. Svensk Bot Tidskr 51:166–186

Peyronel B, Fassi B, Fontana A, Trappe JM (1969) Terminology of mycorrhizae. Mycologia 61:410–411

Pfeffer W (1877) Ueber fleischfressende Pflanzen und über die Ernährung durch Aufnahme organischer Stoffe überhaupt. Landwirtschaftl Jahrb 6:969–998

Read DJ (1987) In support of Frank's organic nitrogen theory. Angew Bot 61:25–37

Reess M (1880) Ueber den Parasitismus von *Elaphomyces granulatus*. Bot Ztg 38:729–733

Ryan F (2002) Darwin's blind spot: evolution beyond natural selection. Houghton Mifflin, Boston

Sapp J (1994) Evolution by association: a history of symbiosis. Oxford University Press, Oxford

Schlicht A (1888) Ueber neue Fälle von Symbiose der Pflanzenwurzeln mit Pilzen. Ber Dtsch Bot Ges 6:269–279

Schlicht A (1889) Beitrag zur Kenntniss der Verbreitung und der Bedeutung der Mykorhizen. Landwirts Jahrb 18:477–505

Schwendener S (1869) Die Flechten als Parasiten der Algen. Verh Schweiz Naturforsch Ges Basel 5:527–550

Slankis V (1948) Einfluss von exudaten von *Boletus variegatus* auf die dichotomische Verzweigung isolierter Kiefernwurzeln. Physiol Plant 1:390–400

Slankis V (1949) Wirkung von β-Indolylessigsäure auf die dichotomische Verzweigung isolierter Wurzeln von *Pinus sylvestris* L. Svensk Bot Tidsk 43:603–607

Speidel M (2000) The parasitic host: symbiosis contra neo-Darwinism. Pli 9:119–138

Stubblefield SP, Taylor TN, Trappe JM (1987a) Fossil mycorrhizae: a case for symbiosis. Science 237:59–60

Stubblefield SP, Taylor TN, Trappe JM (1987b) Fossil vesicular-arbuscular mycorrhizae from the Triassic of Antarctica. Am J Bot 74:1904–1911

Trappe JM, Castellano MA (1991) MYCOLIT: a mycorrhiza bibliography, 1758–1991. Mycologue, Waterloo, Ontario

Tulasne L-R, Tulasne C (1841) Observations sur le genre *Elaphomyces*, et description de quelques espèces nouvelles. Ann Sci Nat Part Bot 16:5–9

Van Loon J (2000) Parasite-politics: on the significance of symbiosis and assemblage in theorizing community-formations. In: Pierson C, Tormey S (eds) Politics at the edge. MacMillan, London pp 241–253

Vittadini C (1842) Monographia Lycoperdineorum. Augustae Taurinorum, Torino

Wittmack L (1900) Albert Bernhard Frank. Gartenflora 1900:542–545