The structure of mycelial cords and rhizomorphs of fungi: A mini-review

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Abstract

Fungi are ubiquitous – they are found in any conceivable environment, i.e., both aquatic and terrestrial habitats. They remain one of the most diverse groups of organisms on Earth. Because fungi are heterotrophic, they obtain their nutrients by colonizing their substrates with a vegetative mass of hyphae called mycelium. These hyphae secrete enzymes that digest nutrients locked in colonized substrates, after which the nutrients are then absorbed by the hyphae. Not only do hyphae constitute the mycelium of fungi, but they also form other structures – mycelial strand, mycelial cords, and rhizomorphs – through which fungi are able to spread in their environment in search of new substrates to colonize. The aim of this present paper is to explore the structure of mycelial cords and rhizomorphs. Rhizomorphs are among the most complex organs produced by fungi. They are root-like structures constituted by a series of differentiated tissues each with distinctive hyphal type, orientation, size, and function. Thus, rhizomorphs are produced as a result of a coordinated growth of millions of bundled hyphae. Rhizomorph-forming fungi thrive in nutrient-poor environment and are known to cause devastating destruction to homes and plantations. Because rhizomorphs serve as exploratory organs, and they enhance the survival of rhizomorph-forming fungi in plantations and homes, farmers, homeowners, attorneys, and even mycologists and plant pathologists, need to understand and appreciate their potential to wreak havoc that results in huge annual financial losses.

Introduction

Fungi from the genera *Armillaria*, *Auricularia, Coniophora*, *Fomitopsis*, *Meripilus*, *Meruliporia, Polyporus*, and *Serpula* are well-known wood decomposers (Schmidt 2006). Wood-decay fungi are classified into white rot and brown rot fungi. Although these wood-decay fungi secrete enzymes during growth and colonization of substrates, their ability to decompose wood substrates is attained through both enzymatic and non-enzymatic, chelator-mediated Fenton mechanisms (Eriksson et al. 1990, Highley & Illman 1991, Ritschkoff et al. 1992, Goodell 2003, Lindahl & Olsson 2004, Schwarze 2007, Goodell et al. 2017). The absorption of these nutrients sustains vegetative growth and allows an increase in hyphal biomass, which is achieved through tip extension and elaborate branching of the hyphae. This branching hyphal biomass is collectively called mycelium (Carlile 1994). Because fungi use an absorptive mechanism to acquire their

nutrients, with time, they deplete the nutrients from the colonized substrate, after which they search for new substrates to colonize.

The search for nutrient-rich substrates is accomplished through liberated spores, and the production of mycelial strands, mycelial cords, and rhizomorphs. The constituent mycelia of the strands, cords, and rhizomorphs migrate from nutrient-poor substrates and explore the environment in search of nutrient-rich substrates and as a result translocate nutrients and water towards their tips during migration ((Hartig 1873, Falck 1912, Jennings et al. 1974, Anderson & Ullrich 1982, Eamus et al. 1985, Granlund et al. 1985, Cairney 1992). During this period of mycelial migration, the hyphae serve as a repository of absorbed nutrients, grow as a cohesive unit, but only lose this cohesive growth when they encounter a suitable substrate and spread out with a characteristic invasive pattern of growth to completely colonize the new substrate (Moore 1994, Money 2004). Apart from mycelial strands, cords, and rhizomorphs, most plants form an association with arbuscular mycorrhizal fungi through which both plants and fungi derive inorganic and organic nutrients from each other (Gerdemann 1968, Mosse 1973, Willis et al. 2012, Lekberg et al. 2015, Brundrett & Tedersoo 2018).

Since Hartig (1873) described the apical region of rhizomorph of *Armillaria mellea* (Fig. 1), several studies have highlighted the distribution, structure, and functions of fungal rhizomorphs particularly in *Armillaria* spp (Granlund et al. 1985, Garrett 1970). For example, Townsend (1954) studied rhizomorph structure in sixteen basidiomycete fungi including *Armillaria mellea*, *Marasmius androsaceus*, *Merulius lacrymans*, and *Phallus impudicus*. Although the rhizomorph structure of some of these fungi was described, Townsend (1954) acknowledged that other fungi do not produce rhizomorphs *in vitro*, and further provided some insights into the effects of natural environmental factors on their production in soil or decaying wood. A study by Yafetto et al. (2009) has expanded further the understanding of critical biomechanical attributes of the rhizomorph structure in *Armillaria gallica* that enhance its exploratory abilities; interestingly the rhizomorph morphology of *A. mellea* illustrated by Hartig (1873) bears a striking resemblance to that of *A. gallica* studied by Yafetto et al. (2009) (Fig. 1). The aim of this present paper is to review the structure of mycelial cords and rhizomorphs as agents of spread and infection in plants.
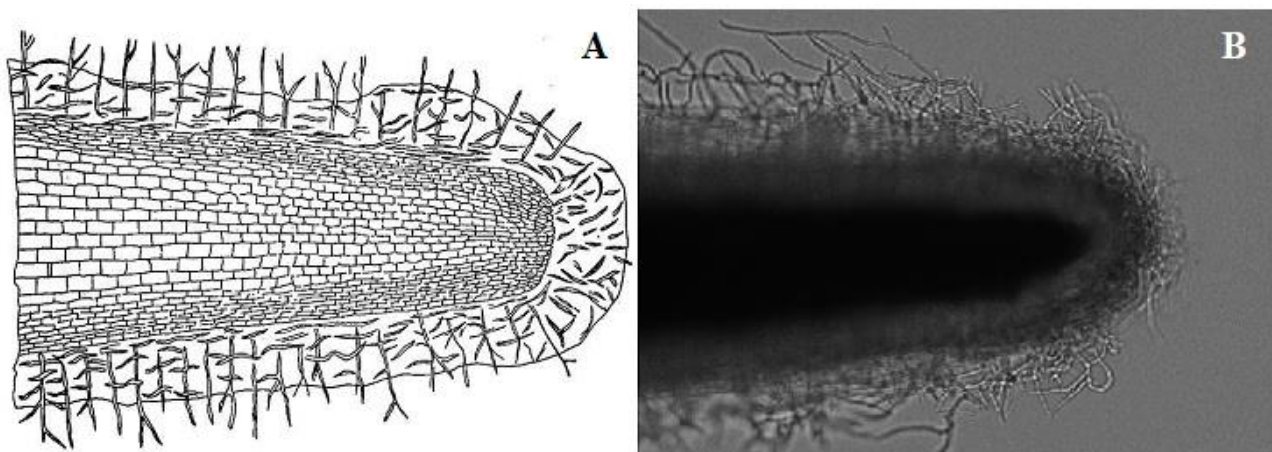

Figure 1 – A Apical region of rhizomorph of *Armillaria mellea* as described by Hartig (1873); adopted from Garrett (1970). B Apical region of rhizomorph of *Armillaria gallica* growing in an agar medium (Photo courtesy of L. Yafetto).

Mycelial cords and rhizomorphs

Hyphae aggregate to serve as *building blocks* of more complex structures in fungi. These aggregations of fungal hyphae, particularly those formed by basidiomycetes, have been named variously as *strands*, *cords*, *rhizomorphs*, or *syrrotia* (Rogers & Watkins 1938, Garrett 1970, Watkinson 1971, Thompson 1984). These terms had been used interchangeably in the literature by mycologists. To solve this situation, Rayner et al. (1985) suggested the adoption of the terms

mycelial cords and *rhizomorphs* to denote apically diffuse mycelia aggregates and apically dominant growing tips, respectively. These terms have been readily accepted and been in use since.

Three common constituent hyphal types have been identified in mycelial cords and rhizomorphs: (i) *tendril hyphae* (or narrow hyphal branches) from the older regions of the main hyphae that interlace around the other hyphae; (ii) *central vessel hyphae* (wide in diameter and thin-walled); and (iii) thick-walled, but narrow *fiber hyphae* of old cords that are formed, running longitudinally through a mature cord to provide strength (Nuss et al. 1991).

Mycelial cords and rhizomorphs of wood-decay and pathogenic fungi serve as important sources of inoculum that enable fungi to make an initial contact with newly, yet-to-be-colonized substrates. Although both mycelial cords and rhizomorphs are constructed from hyphae and function in a similar manner, they are structurally different in two respects; first, a mycelial cord is less complex than a rhizomorph; second, a mycelial cord is a linear aggregation of hyphae formed behind an advancing mycelial front where the hyphae are loosely separated and assume a fan-like mat appearance, while a rhizomorph is a complex multicellular root-like organ formed through aggregation, interlacing, and adhesion of scores of hyphae, characterized by a prominently organized tip growth (Yafetto et al. 2009, Watkinson et al. 2016, Fig. 3). The rhizomorph is uniquely characterized by a waterproof surface and a melanized rind that encloses a central open medulla cavity, which serves as a channel for the conduction of water and dissolved nutrients.

Mycelial cords, on one hand, are constituted by hyphae that are relatively loosely aggregated; they develop as a result of adhesion and growth of young branches of hyphae over an older leading hypha, which serves as the building block for the development of the mycelial cord (Moore 1994, Watkinson et al. 2016). Unlike rhizomorphs, mycelial cord formation is considered a secondary process that occurs behind growing hyphal apices distal to the colony margin, and it involves increasing aggregation of hyphae within the aging, mature mycelium (Garrett 1981). During this process of hyphal aggregation, anastomoses between the hyphae on the surface of the cords occur, fusing them into a bundle.

Rhizomorphs, on the other hand, have a similar appearance to the roots of higher plants (Fig. 2). They both function as organs of nutrient and water absorption and translocation, although rhizomorphs can pass also air along their entire lengths to prevent suffocation of the fungus while they explore the anoxic interior of substrates for nutrients (Money 2004, Watkinson et al. 2016). Like the plant roots, rhizomorphs have a highly organized apical growing tip with extreme apical dominance (Fig. 3). This apical region contains a compact growing point of tightly packed hyphae that is protected by a cap of intertwined hyphae in a mucilaginous matrix (Fig. 3). Because of these root-like appearances, rhizomorphs were initially thought to have meristems responsible for organized tip growth similar to the growth mechanism of roots (Garrett 1963, 1970, Rayner et al. 1985). This view of an apically-dominant growing tip of fungal rhizomorphs was erroneous. It is now known that rhizomorphs do not grow as a result of meristematic activity, but rather by extension of the organized apical hyphae (Yafetto et al 2009, Watkinson et al. 2016).

According to Moore (1994), the medullary region behind the tip of a rhizomorph contains vessel hyphae composed of swollen, vacuolated and often multinucleate cells surrounded by copious air- or mucilage-filled spaces. However, other studies have reported wide-lumen vessel hyphae in the medullary region of field-collected rhizomorphs which lack cytoplasmic content, and have suggested further that the major role of these vessel hyphae is for the translocation of nutrients and water over long distance (Eamus et al. 1985, Jennings 1987, Cairney et al. 1988a). Mycelial cords and rhizomorphs in *Serpula lacrymans* and *A. mellea*, respectively, have been reported to grow long distances over non-woody, nutrient-poor substrates such as concretes, rocks, metals, tiles, insulation materials (Butler 1957, 1958, Rishbeth 1968, Watkinson 1971, Jennings & Watkinson 1982, Arora 1986, Jennings 1991, Money 2004).

Mycelial cords of *Serpula lacrymans*

The extent to which hyphae are organized and differentiated varies between species (Butler

1966). Mycelial cords from *S. lacrymans* (Wulf ex Fr.) Schroet have earlier been reported to be constituted from wide, but empty vessel hyphae and narrow, but thick-walled fiber hyphae running longitudinally through the hyphal aggregate (Hartig & van Tubeuf 1902, Falck 1912). Hornung & Jennings (1981) studied the development of surface mycelium of *S. lacrymans* with emphasis on different stages of growth and observed the following hyphal types: *undifferentiated hyphae* common to all stages of mycelial development; *main hyphae* of faster growth rate that have the tendency to form hyphal aggregates; *tendril hyphae* from which hyphal aggregates originate; *fiber hyphae* which are often coenocytic, but thick-walled, and *vessel hyphae* which are often thin-walled with a wide lumen.

Figure 2 – Root-like structure of *Armillaria* rhizomorphs in potato dextrose agar medium, after 3 weeks of growth at 30°C (Photo courtesy of L. Yafetto).
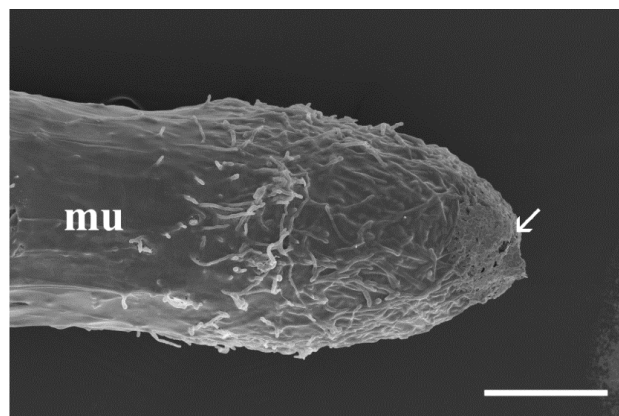

Figure 3 – Scanning electron micrograph of rhizomorph tip of *Armillaria gallica*. A protective cup of mucilage (arrow) is localized to the tip, and a mucilaginous sheath (mu) covers the entire length of the rhizomorphs. Scale bar = 100 µm (from Yafetto et al. 2009).

Jennings & Watkinson (1982) compared initial stages of mycelial cord development of *S. lacrymans* in culture with the structure of mature strands from infected wood, and reported that cultures with mycelial cords stained with 1% Nile blue at early stages of development had three types of differentiated hyphae: (i) approximately 10 µm diameter wide, empty *aseptate* hyphae that stained evenly blue; (ii) non-stained, *septate* hyphae with visible cytoplasmic contents and (iii) narrow and septate unbranched tendril hyphae with dark-stained dense cytoplasm of about 2 µm diameter. Meanwhile, a comparative transmission electron microscopy (TEM) and scanning electron microscopy (SEM) studies by Jennings & Watkinson (1982) of mature mycelial cords of

S. lacrymans obtained from an actively growing colony in a house revealed three distinguishable regions: (i) an outer surface covered by colorless thin-walled hyphae growing separately from one another; (ii) a zone lying beneath the outer surface characterized by a few hyphae that were cracked with holes; and (iii) a central portion characterized by longitudinal channels.

Rhizomorphs of *Armillaria* spp

Granlund et al. (1984) studied *A. mellea* rhizomorphs with SEM to investigate their internal and external features in relation to their reputed ability to translocate water and other solutes over long distances. The internal structure revealed the arrangement of hyphal tissues of different zones of the *A. mellea* rhizomorphs as follows: (i) peripheral hyphae that formed a layer approximately between 20 and 30 µm thick, (ii) cortical hyphae, (iii) medulla hyphae and (iv) the central space, usually occupied by a cottony pith of fine, loosely-woven hyphae. Furthermore, Granlund et al. (1984) reported that the diameter of the hyphae constituting the various tissues in *A. mellea* increased towards the center of the rhizomorph. They recorded 2.2 µm, 2.3 µm, and 13.9 µm as the mean diameter of peripheral hyphae, cortical hyphae and medulla hyphae of the rhizomorph, respectively. In addition, the distance between septa of hyphae increased towards the center; for example, while a distance of 20 µm between septa was recorded in the cortex, a 70 µm distance was recorded between septa in the medulla zone.

Yafetto et al. (2009) confirmed similar zones of hyphal tissues within *A. gallica* rhizomorphs which they described from the outside to the inside as follows: (i) an outer layer of *peripheral hyphae*, (ii) an inner cortical layer of *radial hyphae*, (iii) a medulla region, consisting of two layers of *longitudinal hyphae* – an outer layer of thick-walled, narrow lumen, tightly packed hyphae, and an inner layer of thin-walled, wide lumen, loosely packed hyphae usually called the vessel hyphae; and (iv) a *central cavity* (Fig. 4). Yafetto et al. (2009) concluded that indeed *A. gallica* has well-organized rhizomorphs characterized by strikingly arranged hyphal types. These descriptions of the hyphal tissues have undoubtedly provided more insight into the structure of rhizomorphs, which further help to elucidate their functions as organs for the translocation and transportation of nutrients and water along their lengths towards their tips. Not only did Yafetto et al. (2009) confirm findings of Granlund et al. (1984) about the structure of *A. gallica* rhizomorphs, but their study also provided better micrographs from their SEM studies, and comprehensively revised terminologies used to identify the different hyphal types, based on their arrangement, to assuage the usual confusion that normally associated rhizomorphs with their descriptions.

Rhizomorph structure and function

It is suggested that the central cavity described in Fig. 4 and those previously mentioned in studies by Granlund et al. (1984) are used as air-conducting channels, and may be generated as a result of the collapse of vessel hyphae (Fig. 5), supporting the views of Hartig & van Tubeuf (1902), Falck (1912). The arrangement of the different hyphae within a rhizomorph is of importance to the translocation in rhizomorph-forming fungi since an aseptate lumen is required for mass translocation of nutrients and water within the vessel hyphae towards the rhizomorph tip, with less expenditure of energy in the form of the application of pressure. This may also suggest why vessel hyphae are thinly walled to allow easy passage of water and osmolytes across the wall surface (Fig. 5). Eamus et al. (1985) provided evidence that supports the view that long-distance translocation in mycelial cord and rhizomorphs occurred predominantly by the movement of a solution along the vessel hyphae.

According to Granlund et al. (1984), peripheral hyphae of rhizomorphs could serve as a source of infection in plants, such that these infective hyphae could be used by *A. mellea* to make contact and invade new plant hosts, particularly through the roots. Granlund et al. (1984) further argued that the peripheral hyphae may also serve absorptive role for the rhizomorph such that they may constantly supply the rhizomorph with nutrients and water to support its active tip growth; they explained that as the tip extends, the peripheral hyphae, which provides a large surface area in the mature region, may have the potential to laterally absorb nutrient and water from the immediate

surroundings of the rhizomorph into its interior. The dissolved nutrients and water are thus transported into the inner medulla region for translocation to the tip. Yafetto et al. (2009) suggested that with such intake of nutrients and water, and the accumulation of osmolytes, an internal turgor pressure is created within the rhizomorph, which is eventually converted into the driving force for the growing tip to invade hard, compact substrates.
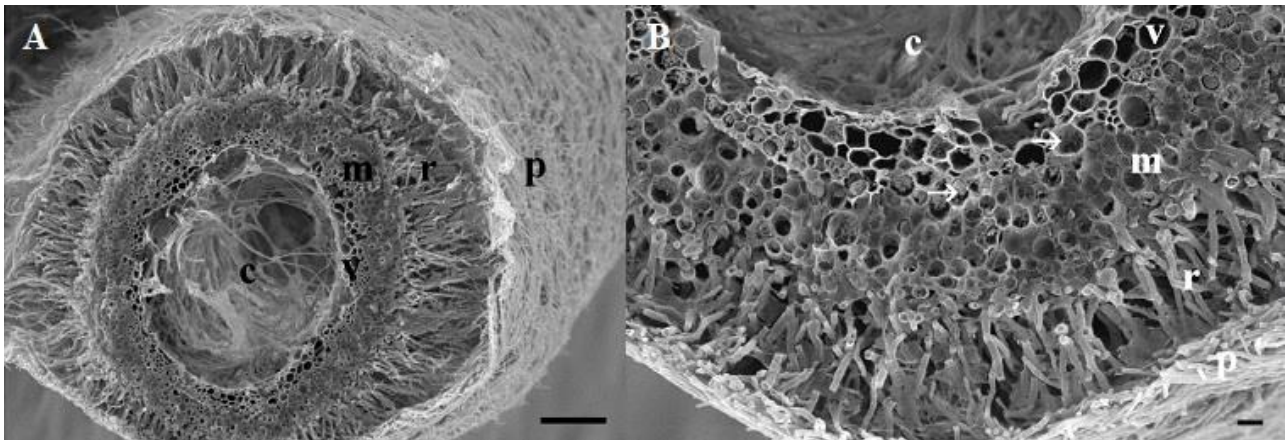

Figure 4 – Scanning electron micrograph of transverse sections of freeze-fractured rhizomorph of *Armillaria gallica*. A Complete arrangement of hyphae in rhizomorph. B A close up micrograph of hyphal arrangement: From the outer layer to the inner zones are; a cortical layer of loosely-packed, radially arranged, thin hyphae (r), covered with peripheral hyphae (p); an inner medulla of tightly-packed, longitudinally arranged, thick-walled hyphae with narrow lumens (m) with cellular contents (arrows); longitudinally arranged thin-walled vessel hyphae with wide lumens (v), and a central cavity that may be formed by degeneration of vessel hyphae (**c**). Scale bar = 100 μm (A); Scale bar = 10 μm (B) (from Yafetto et al. 2009).
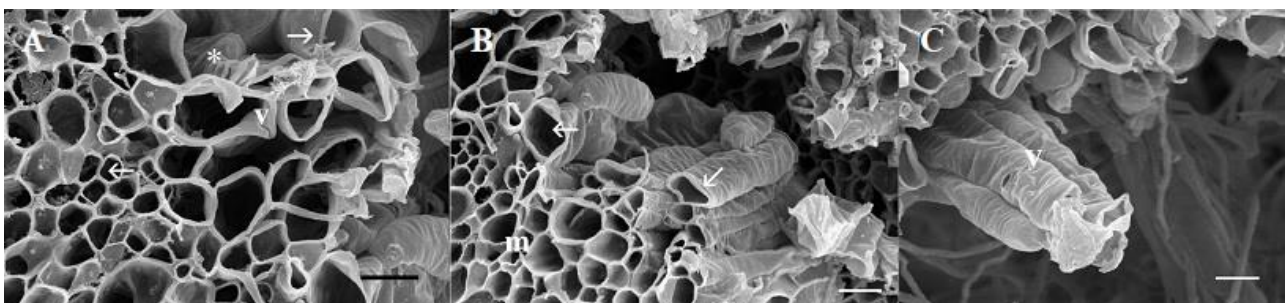

Figure 5 – Scanning electron micrographs of *Armillaria gallica* rhizomorph. A Vessel hypha (**v**) in close association with tightly packed longitudinal hyphae (Arrow ←). Some of the vessel hyphae have wrinkled wall (*****), while others have collapsing wall (Arrow →). Scale bar = 10 μm. B Wide lumen vessel hyphae (arrows) in close association with narrow lumen, thick-walled longitudinal hyphae (m) that form a rind around the vessel hyphae. Scale bar = 10 μm. (C) Wrinkled, collapsed vessel hyphae (v), protruding from the freeze-fractured surface. Scale bar = 10 μm (Micrographs courtesy of L. Yafetto).

Armillaria: A model system for the study of fungal rhizomorphs

The genus *Armillaria* (Fr.: Fr) is a cosmopolitan pathogenic basidiomycete that contains about 40 species known for causing root and butt rot diseases (Watling et al. 1991, Volk & Burdsall 1995, Pegler 2000, Baumgartner et al. 2011). The term "honey fungus" has been used to describe many species of *Armillaria* because of its yellowish caps and the sweet taste of their mushrooms. *Armillaria* has a wide range of hosts including deciduous and coniferous trees, shrubs, and vines (Smith et al. 1992), and it is considered one of the most devastating disease-causing plant

pathogens; it kills and decomposes plants in forests and plantations in both temperate and tropical regions of the world (Garraway et al. 1991).

Of all species of the genus *Armillaria*, *A. mellea* is the most pathogenic, and the best studied. Other species, including *A. luteobubalina* and *A. ostoyea*, have also been reported to be pathogenic (Fox 2000). *A. mellea,* like other *Armillaria* species has the ability to produce reddish- to black-colored rhizomorphs, which have a unique internal structure (Townsend 1954).

Interestingly, the mycelium and rhizomorphs of some *Armillaria* species have been studied over a century and are shown to be bioluminescent, but, surprisingly, not their fruiting bodies (Murrill 1915, Buller 1924, Harvey 1952, Wassink 1978, Mihail & Bruhn 2007).

As a root pathogen, the direct control of *Armillaria* spp is practically impossible to accomplish, but they are easily detected in the terrestrial environment, since they occur everywhere in the soil; they produce fruiting bodies at the base of a tree trunk as well as black rhizomorphs that are found beneath forest leaf litter and in association with roots of forest trees (Fox 1990, Schmidt 2006). In 1992, for example, Smith et al. (1992) detected *A. bulbosa* in Michigan using molecular genetics techniques. The *A. bulbosa* was reported to have occupied an area of 15 hectares, weighed about 10,000 kg and was more than 1,500 years old, making it one of the largest and oldest living organisms ever known. Similarly, clones of *A. ostoyae* and *A. gallica* have been detected in soils in Oregon (USA) and England to have colonized an area over 9 km^2 and 9 hectares, respectively (Marximüller & Holdenrieder 2000).

In most cases, *Armillaria* is a saprobe, colonizing dead tree stumps, but it becomes parasitic, either as a necrotroph or biotroph when it infects the roots of a healthy host using its networks of rhizomorphs (Watling et al. 1991, Baumgartner et al. 2011, Tsykun et al. 2012). A rhizomorph adheres firmly to root tips of healthy plants after the mucilaginous material on its tip dries, sends out mycelia and continues to grow and spread beneath the bark of the tree producing mycelial fan. Competition from neighboring trees, insect attack and the prevalence of adverse climatic factors further affect the health of the infected host. In such a compromised condition, the host is killed outright if it fails to successfully defend itself and the mycelium manages to reach the xylem to interfere with the flow of sap in the cambium (Wahlström & Johansen 1992, Woodward 1992, Schmidt 2006). Thus, rhizomorphs are used by *Armillaria* as a means to propagate itself to effect infection in other healthy trees over long distances (Hartig 1874, Garrett 1970).

Above all, the genus *Armillaria*, unlike other rhizomorph-producing genera (*Meruliporia incrassata* and *Serpula lacrymans*), readily produces rhizomorphs *in vitro* making it a suitable candidate as a model system to further study fungal rhizomorphs (Yafetto et al. 2009). Additionally, *Armillaria* spp. have been well studied in North America and Europe, but sparingly in Africa, and findings from such studies are well represented in literature, some of which are presented in Table 1.

Mycelial cords and rhizomorphs: dry rot by *Meruliporia incrassata* and *Serpula lacrymans*

The rhizomorph-forming fungus *Meruliporia incrassata* causes dry rot of wooden components in buildings. Its damage is sometimes referred to as brown-rot. Since its description from pine as *Merulius incrassatus* Berk. & Curt. in South Carolina, *M. incrassata* (Berk & Curtis.) Murr. (Family Coniophoraceae) has been recognized as a wood-decay fungus in North America (Berkley & Curtis 1849). It has a wide distribution in the southeastern United States of America and has been reported occasionally in Canada (Verall 1968, Palmer & Eslyn 1980). Its occurrence in the southern British Columbia, Canada is an interesting observation, since this region is very moist. There has been no report of the occurrence of *M. incrassata* in Arizona or New Mexico, an observation attributed to the dry climate of the desert in the southwest USA. Its distribution pattern suggests that *M. incrassata* develops best in warm climates (Burdsall 1991).

M. incrassata causes severe damage to homes in California using its rhizomorphs (Fig. 6). During attacks on homes, *M. incrassata* develops rhizomorphs from its depleted food base mostly from outside the home (tree stumps, landscaping lawns with woodchips, etc.). The rhizomorph is capable of translocating nutrients and water, under warm and moist conditions, to its tip until it

encounters a wooden component of the building. It then begins to colonize the wood swiftly by digesting and extracting cellulose, leaving behind the brown lignin component of the wood. The description of *M. incrassata* as a dry rot fungus can, therefore, be regarded as erroneous because its participation in wood decomposition is impossible without water. *M. incrassata* fungus destroys dry wood by transferring water through its rhizomorphs to the sites of active growth and decomposition (Verall 1968, Brownlee & Jennings 1981a, b).

Figure 6 – Field-collected rhizomorphs of *Meruliporia incrassata* from an infested home in California. Note the root-like, woody appearance (Specimen courtesy Luis De La Cruz Wood Preservation Services, Pasadena, CA, USA; Photo courtesy of L. Yafetto).

Possible conditions for infestations of homes in California by *M. incrassata* may include the following: first, when lands are cleared of trees for construction of homes, tree stumps are sometimes left in the soil. An array of fungi colonizes these tree stumps until the nutrients are depleted, at which time rhizomorph–forming species develop rhizomorphs in search of new sources of food; second, topsoil and wood mulch used in landscaping may often provide a combination of optimum conditions (moisture and poor ventilation) for wood-decay fungi to develop rhizomorphs. This second condition normally results from the continuous supply of water by sprinklers under low nutrient conditions. As long as the fungus has the continuous supply of water and can channel it to the tips of its rhizomorphs, it survives until it locates a nutrient-rich substrate in the building; third, an untreated wood used to construct buildings is another potential source of *M. incrassata* growth and rhizomorph development. Under all these conditions, the destructive abilities of the rhizomorphs manifest themselves when they contact wooden components of a building (Money 2004).

Meanwhile, a different fungal species, *Serpula lacrymans,* is known to be responsible for similar destruction in Europe (especially in Britain), and other parts of the world, including Japan and Australia (Money 2004). For example, *S. lacrymans,* together with other fungi, caused enormous historical damage to wood in ships, where in one instance, rotting of timber was responsible for sinking the ship *Royal George* in 1782 and necessitated rebuilding of *Queen Charlotte* in 1810 (Money 2004).

Both *M. incrassata* and *S. lacrymans* produce brown basidiomes, with brown, thick-walled, dextrinoid basidiospores; both cause brown rot of their wood substrates; both produce water– and nutrient–conducting rhizomorphs and mycelial cords, respectively (Burdsall 1991, Moore 1994).

Table 1 Selected relevant literature highlighting some key studies of *Armillaria* spp and rhizomorphs.

Area of Study	Reference
Development/Distribution	Snider 1959, MacDonald & Cartter 1961, Weinhold 1963, Motta 1967, 1969, Went 1973, Motta & Peabody 1982, Eamus et al. 1985, Cairney et al. 1988b, Masuka 1989, Twery et al. 1990, Gray et al. 1996, Horner et al. 1995, Volk et al. 1996, Tsopelas & Tjamos 1999, Baumgartner & Rizzo 2001, Mansilla et al. 2001, Otieno et al. 2003, Prange & Nelson 2006, Freymann 2008, Baumgartner et al. 2011
Ecology	Garrett 1953, 1960, Masuka 1989, Rizzo et al. 1990, Horner et al. 1995, Isaac 1995, Tsopelas & Tjamos 1999, Wallander et al. 2002, Prange & Nelson 2006, Rigling et al. 2006, Vargas & Allen 2008a, 2008b, Freymann 2008, Tsykun et al. 2012, Kubiak et al. 2017
Forest pathology	Garrett 1953, 1956, 1960, Gibson 1960, Azevedo 1976, Rishbeth 1978, Thompson & Boddy 1983, Twery et al. 1990, Tsopelas & Tjamos 1999, Coetzee et al. 2000, Wallander et al. 2002, Morrison 2004, Treseder et al. 2005, Vargas & Allen 2008b, Baumgartner et al. 2011
Molecular Characterization/ Phylogeny/Taxonomy/Systematics	Korhonen 1978, Anderson & Ullrich 1979, Guillaumin et al. 1985, Roll-Hansen 1985, Anderson 1986, Motta & Korhonen 1986, Termorshuizen & Arnolds 1987, Watling et al. 1991, Volk & Burdsall 1995, Volk et al. 1996, Zolciak et al. 1997, Ota et al. 1998, Coetzee et al. 2000, 2001, 2003, Qin et al. 2007, Tsykun et al. 2013

Future perspectives

Rhizomorphs and mycelial cords continue to play vital roles in the survival, propagation, and pathogenicity of fungi, and, as such, interest in their study should be intensified and sustained. Professor Lynne Boddy of Cardiff University, UK, and her collaborators, over the years, have extensively studied mycelial strands and cords, and have produced insightful findings of the structure, functions, and behavior of mycelial cords which (Fricker et al. 2017). To this end, some specific areas of biomechanics of *Armillaria* rhizomorphs need urgent attention. *Armillaria* species remain a well-studied group, but their rhizomorphs are excellent models for such biomechanical studies (Yafetto et al. 2009), and remain inadequately studied by mycologists and plant pathologists.

M. incrassata continues to remain one of the best candidates for rhizomorph studies, because, although it is known to produce rhizomorphs, there is no information in the literature on its ability to produce *in vitro* rhizomorphs with organized tip growth as seen in *Armillaria*. This necessitates a renewed interest in the study of *in vitro* production of rhizomorph in *M. incrassata*, the success of which shall be a breakthrough in rhizomorph studies.

Since data on profiled gene sequence of *Armillaria* already exist, work to identify genes that control the growth and development of rhizomorphs should be initiated. This can be extended to other rhizomorph-producing fungi, particularly *M. incrassata* for comparative purposes. There is a

good prospect for understanding the molecular basis of these processes in *Armillaria* and *Meruliporia* that will eventually guide the development of effective control strategies in the future.

As a crucial step, investigations that seek to address key aspects of the biomechanics of rhizomorphs should adopt a multidisciplinary approach. This multidisciplinary approach is critical since there are biological, molecular, physical and mathematical components necessary for better understanding of rhizomorph growth, development and invasive behavior.

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