Chapter 20

Armillaria root diseases of diverse trees in wide-spread global regions

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1. Species and identification

The taxonomy of annulate [possessing a ring-like structure on the stipe (stem) of the basidiocarp (mushroom, fruiting body, basidioma) that is the remnant of the ruptured veil on the underside of the cap] *Armillaria* (Figs. 20.1E–J, 20.2, and 20.3) and its exannulate (without an annulus) sister genus *Desarmillaria* (Fig. 20.1K) is constantly changing. However, at least 40 species are currently recognized around the world (Baumgartner et al., 2011; Koch et al., 2017; Heinzelmann et al., 2019; Antonín et al., 2021; Kedves et al., 2021), and most *Armillaria* spp. have a wide host range. In many cases, species of *Armillaria* are distinct between the Northern and the Southern Hemispheres. Historically, the identification of *Armillaria* was largely based on the morphology of the basidiocarp, and interfertility or mating compatibility (e.g., Korhonen, 1978; Anderson and Ullrich, 1979; Heinzelmann et al., 2019). In recent decades, recognition and identification of *Armillaria* species has become increasingly reliant on DNA sequences, such as phylogenetic analyses representing multiple gene regions, which elucidate the evolutionary relationships among the species (e.g., Guo et al., 2016; Klopfenstein et al., 2017; Koch et al., 2017; Antonín et al., 2021). Recently, genome-level phylogenetic analyses have been used to provide high-resolution discrimination among *Armillaria* spp. (Kedves et al., 2021), but such analyses are restricted to species with sequenced genomes.

2. Life cycle and spread

Armillaria typically produce basidiocarps on a seasonal basis, but basidiocarps may be produced only sporadically in some situations (Figs. 20.1E–K and 20.2). Basidiospores, which are considered to have short-to-moderate viability (e.g., weeks to a few months), are produced from basidia on the mushroom gills (Rishbeth, 1970) (Fig. 20.3). Basidiospores of most *Armillaria* species are haploid, although some species may produce diploid or heterokaryotic basidiospores (e.g., Guillaumin et al., 1991; Ota et al., 1998). Most *Armillaria* spp. have a bifactoral, tetrapolar heterothallic mating system (individuals are self-incompatible and sexual reproduction requires the mating of two compatible individuals) (Fig. 20.3), but some species are homothallic (sexual reproduction takes place in a single thallus, self-compatible) or have a unifactorial, bipolar mating system. In most cases, basidiospores travel only a short distance (e.g., Dutech et al., 2017). A basidiospore and/or a germinating hypha from a basidiospore must fuse with a compatible basidiospore and/or hypha to form a transient, heterokaryotic/dikaryotic mycelium (Larsen et al., 1992). Over time, the heterokaryotic mycelium becomes diploidized to form homokaryotic/monokaryotic, diploid mycelium, which is the primary vegetative state (e.g., Kim et al., 2000, 2001) (Fig. 20.3). In nature, the long-term establishment of new *Armillaria* genotypes derived from sexual recombination is somewhat rare because established *Armillaria* genets (vegetative clone or individual) tend to competitively exclude new

FIG. 20.1   Symptoms and signs of Armillaria root disease. (A) Disease mortality center caused by *A. solidipes* in Idaho, USA. (B, C) Mycelial fans that develop under the bark on lower boles and roots of infected trees. (D) Rhizomorphs of *Armillaria* sp. (E–J) Annulate basidiocarps (mushrooms, fruiting bodies, basidiomata) of (E) *A. mexicana*, (F) *A. solidipes*, (G) *A. ostoyae*, (H) *A. mellea*, (I) *A. cepistipes*, and (J) *A. luteobubalina*. (K) Exannulate basidiocarps of *Desarmillaria ectypa*. *Photo credits: (A), (B), (D), John W. Hanna; (E), Rubén Damián Elías-Román; (F), Rainy C. Rippy; (C), (G), (H), Renate Heinzelmann; (I), Stephen Woodward; (J), Richard Robinson; (K), Yuko Ota.*
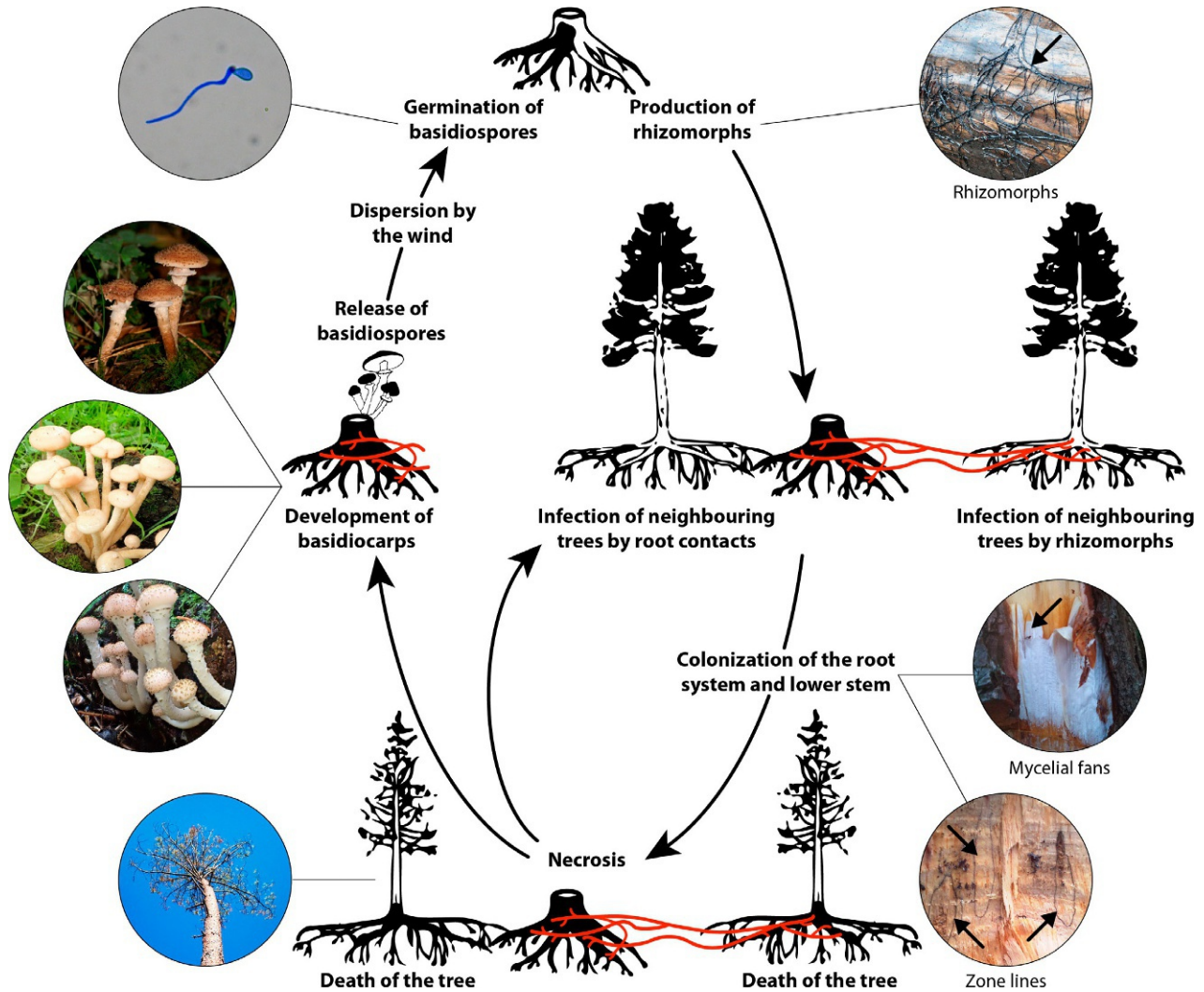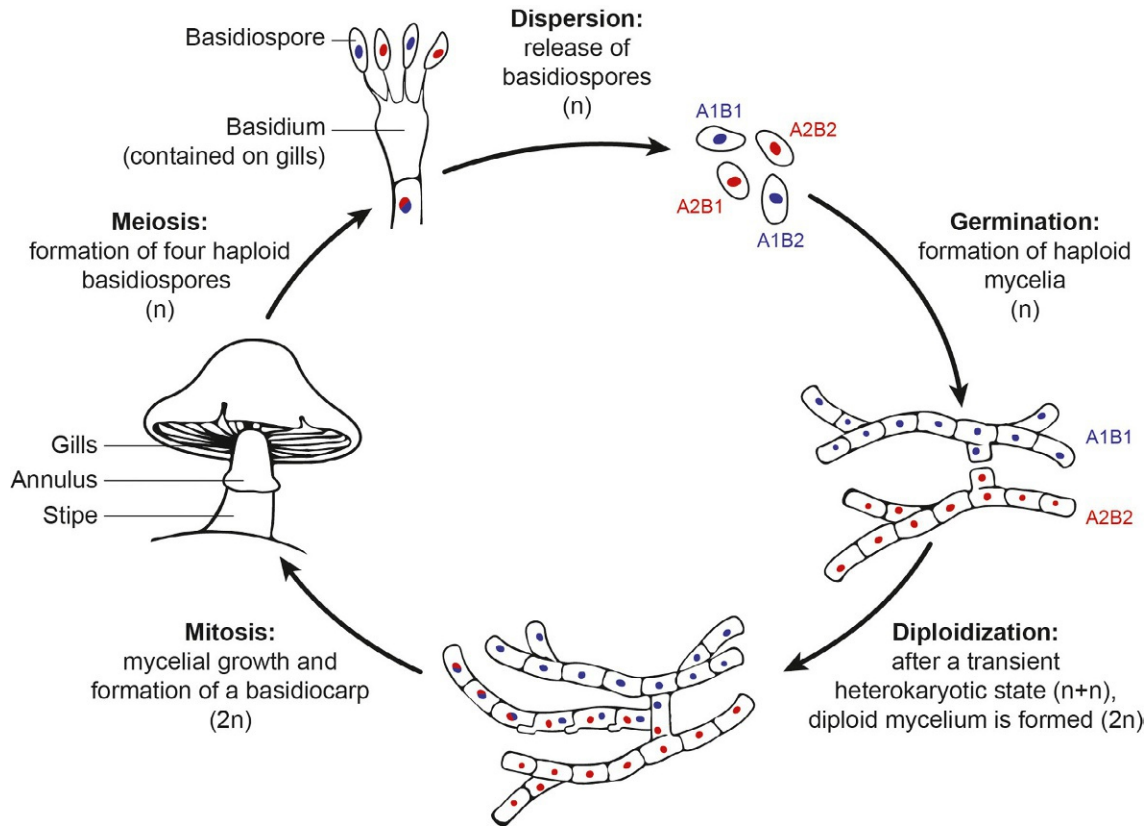
FIG. 20.2 Life cycle of *Armillaria* species. Basidiocarps (fruiting bodies, mushrooms, basidiomata) develop on a seasonal basis and release wind-dispersed basidiospores that germinate on a woody substrate to generate a haploid mycelium that can mate with a compatible haploid basidiospore/mycelium for heterothallic species, or diploid mycelium for homothallic species. *Armillaria* then spreads vegetatively underground via rhizomorph growth (indicated in red) or mycelial growth (root-to-root contact). Entry through the root bark can be facilitated by wounding, but host penetration by virulent *Armillaria* spp. can also occur via mechanical and/or enzymatic means with the aid of secreted phytotoxins. After successful penetration through the bark, *Armillaria* spp. produce mycelial fans beneath the bark of living trees that begin to degrade cellular components of the woody host. After host tissue/organs die, *Armillaria* spp. are sustained by deriving nutrients obtained by colonization and degradation of host-derived materials. *Armillaria* causes a characteristic wet/stringy, yellowish wood decay with zone lines that may serve to protect *Armillaria* inside the rotten wood. *Photo credits: Renate Heinzelmann, Rubén Damián Elías-Román, Frédéric Labbé, and Tyson Ehlers.*

genotypes of the same species from a site over time (e.g., Legrand et al., 1996; Ferguson et al., 2003; Prospero et al., 2003; Warwell et al., 2019). However, natural and anthropogenic disturbances could foster the creation of niches that allow for the establishment of new genotypes.

Armillaria spread typically occurs in the leaf-litter layer (duff) or underground via vegetative growth of rhizomorphs (dark, root-like mycelial structures) or mycelia (root-to-root contact) (Figs. 20.1D and 20.2; see Section 4). Rhizomorphs generally grow at a rate < 3 m per year, depending on the nutritional substrates, climate, and other environmental factors (e.g., Rishbeth, 1968; Kable, 1974; van der Kamp, 1993; Labbé et al., 2017b). In some situations, the radial growth of *Armillaria* results in an Armillaria root disease center or mortality center (e.g., Fig. 20.1A), but *Armillaria* often causes root disease that is more diffuse or scattered throughout the site. Notably, some individual genets of *Armillaria* have been dubbed as the "humongous fungus" and are considered among the largest and longest lived organisms on Earth (e.g., Smith et al., 1992; Ferguson et al., 2003). A single genet of *A. solidipes* (as *A. ostoyae*) in the northwestern USA was estimated to

FIG. 20.3 Sexual reproductive cycle of heterothallic *Armillaria* species (e.g., *A. solidipes*, *A. ostoyae*). Basidiocarps (fruiting bodies, mushrooms, basidiomata) release wind-dispersed basidiospores that germinate to form a haploid mycelium (n). Two separate, compatible hyphae (e.g., A1B1 and A2B2 mating types of the tetrapolar bifactoral mating system) fuse to form a transient, heterokaryotic/dikaryotic mycelium (n + n). Over time, the heterokaryotic mycelium becomes diploidized to form diploid, homokaryotic/monokaryotic mycelium (2n), which is the primary vegetative state (e.g., rhizomorphs, mycelial fans). Under suitable environmental conditions, basidiocarps can develop, and basidiospores are formed on each basidium (pl: basidia), which is produced on the gills under the basidiocarp cap.

cover 965 ha, with an estimated age of 1900–8650 years (Ferguson et al., 2003). Long-range dispersal can occur via wind-dispersed basidiospores that are produced in abundance by the basidiocarps (Figs. 20.1E–K, 20.2, and 20.3).

***Armillaria* lifecycle terminology[a]**

Annulate—stipe possessing an annulus, ring-like or collar-like structure (see Figs. 20.1 and 20.3).
Basidium (pl. basidia)—a microscopic, spore-producing structure found on the basidiocarp (mushroom, fruiting body, basidioma) of basidiomycete fungi.
Bifactorial, tetrapolar mating system—a mating system controlled by two unlinked mating loci termed *A* and *B*, which can both be multiallelic, and successful mating can occur between two haploid individuals that are compatible at both mating loci.
Dikaryotic—possessing two nuclei per cell.
Diploid—having two homologous (representing each mating type of the mated gametes) copies of each chromosome.
Exannulate—stipe lacking an annulus (see above).
Haploid—each nucleus contains the number or set of chromosomes normally found in a gamete (reproductive cell).
Heterokaryotic—containing genetically different nuclei within a single cell.
Heterothallic—fungal species of which isolates can only mate with other isolates of a compatible mating type.
Homokaryotic—possessing genetically identical nuclei.
Homothallic—fungal species of which isolates possess the capability to mate with themselves.
Monokaryotic—possessing one nucleus per cell.
Rhizomorph—mycelial cords with a dark outer surface that resemble plant roots, grow in leaf litter, underground or on the surface of trees and other plants, and can conduct water and nutrients (see Figs. 20.1D and 20.2).
Stipe—stalk-like supporting structure.

[a]Definitions are modified information derived from Wikipedia, https://en.wikipedia.org.

2.1   Infection process

Armillaria is typically widespread and persistent across a site, and it frequently co-occurs as rhizomorphs or mycelia in proximity to the roots of woody plants. Entry through the root bark can be facilitated by wounding, but host penetration by virulent *Armillaria* spp. can also occur via mechanical (e.g., pressure from rhizomorph growth) and/or enzymatic means with the aid of secreted phytotoxins (e.g., Cleary et al., 2012a, 2012b; Kedves et al., 2021; Devkota and Hammerschmidt, 2020). Multiple families of wood-decomposing enzymes (e.g., cellulose-, hemicellulose-, lignin-, and pectin-degrading enzymes) and related pathogenicity factors (e.g., expansins, cerato-platanins, salicylate hydroxylases, secondary metabolites, small-secreted proteins, and others) are central to the pathogenicity and wide host range of *Armillaria* (Heinzelmann et al., 2019). During the *Armillaria* infection processes, the host will typically produce a range of responses to limit the pathogen, such as the production of defensive compounds, compartmentalization of the pathogen, and callusing over the infection site. The success of *Armillaria* infection depends on numerous interacting factors, including the level of *Armillaria* virulence and inoculum potential, host tree health and vigor, and many other biotic/abiotic factors. In general, *Armillaria* infection tends to be more successful in susceptible hosts that are weakened, stressed, and/or maladapted to the current conditions on the site. After successful penetration through the bark, pathogenic *Armillaria* spp. produce mycelial fans in the vascular cambium beneath the bark of living trees, and these mycelial fans begin to degrade cellular components of the woody host (Figs. 20.1B, C, and 20.2); however, saprotrophic *Armillaria* spp. can also produce mycelial fans on dead trees or other woody materials. As infection progresses, roots and/or basal boles can be partially or fully girdled, and the tree continues to lose vigor, which also increases susceptibility to other pests and environmental stresses. After the host tissue dies, *Armillaria* is sustained by deriving nutrients obtained by colonization and degradation of dead wood and other organic matter. *Armillaria* is also capable of causing wood rot, such as heart rot, that can weaken the structural integrity of the basal bole and/or lateral roots. Trees with such wood rot represent hazard trees that are susceptible to structural failure and/or wind throw, which can threaten life, limb, and property.

3.   Geographic distribution, host range, and impact (or damage)

Distinctive sets of *Armillaria* species are found in each continent, as listed in Heinzelmann et al. (2019) (Fig. 20.4). Currently, more than 40 *Armillaria*/*Desarmillaria* species have been officially described and recognized (e.g., Heinzelmann et al., 2019), but studies of species richness based on DNA sequences in public databases suggest that 50–60 *Armillaria* species may occur (Koch and Herr, 2021). Notably, the same *Armillaria* species rarely occurs in both the Northern Hemisphere and Southern Hemisphere (e.g., Heinzelmann et al., 2019); however, rare movement of *Armillaria* species between the Northern and Southern Hemispheres can represent an invasive pathogen threat (e.g., Coetzee et al., 2001; Coetzee et al., 2003b; Coetzee et al., 2018a; Mwenje et al., 2006).

3.1   Europe—*A. borealis*, *A. cepistipes*, *A. gallica*, *A. mellea*, *A. ostoyae*, *D. ectypa*, and *D. tabescens*

In Europe (Fig. 20.4), *Armillaria* is widespread and occurs in most places with woody vegetation, such as forests, tree plantations, parks, orchards, gardens, and vineyards. Five annulate species (*A. borealis*, *A. cepistipes*, *A. gallica*, *A. mellea*, and *A. ostoyae*) and two exannulate species (*D. ectypa* and *D. tabescens*) occur in Europe, but each species differs in its geographic distribution, host preference, and biological niche (Guillaumin et al., 1993; Marxmüller and Guillaumin, 2005). *Armillaria borealis* and *A. cepistipes* have a northward-orientated distribution range that stretches far into Scandinavia; whereas, *A. mellea* and *D. tabescens* have a more southward-oriented, distribution that extends beyond southern Europe into northern Africa. European *A. ostoyae* and *A. gallica* are more central in their distributions, with *A. gallica* being more thermophilic than *A. ostoyae*. In large parts of western Europe, central Europe, southeastern Europe, and eastern Europe, the distribution ranges of multiple *Armillaria* species overlap. Species with a preference for relatively cooler climates, such as *A. borealis*, *A. cepistipes*, and *A. ostoyae*, are usually restricted to higher altitudes in their southern ranges. *Desarmillaria ectypa*, an extremely rare species confined to marshes and peat bogs, is absent from southern Europe and has a very discontinuous distribution in the rest of Europe.

Among the *Armillaria* species occurring in Europe, only *A. ostoyae* and *A. mellea*, and to some extent *D. tabescens*, are considered aggressive primary pathogens (Guillaumin et al., 1993). All other *Armillaria* species in Europe primarily act as opportunistic pathogens, which infect hosts that are predisposed by other biotic/abiotic factors, and saprotrophs that degrade deadwood. In northern, central, eastern, and parts of western Europe, *A. ostoyae* is usually the primary cause of Armillaria root disease in coniferous forests and plantations, whereas *A. mellea* is the primary cause of disease in southern Europe, where it causes damage in fruit-tree plantations and vineyards. In plantations of exotic eucalypts (*Eucalyptus* spp.) in France, *D. tabescens* is regularly identified as a primary cause of root disease.

FIG. 20.4 Geographic distribution of *Armillaria* and *Desarmillaria* species. *Indicates species that only occur in the one continent or region. §Indicates species that were presumably introduced into the geographic region. #Indicates species without a formal description.

More recently, the less virulent *Armillaria* species, *A. gallica* and *A. cepistipes*, have gained attention in Europe, because of their interaction with the invasive pathogen (*Hymenoscyphus fraxineus*) that causes ash dieback (Gross et al., 2014). This ash-dieback pathogen causes crown dieback and root collar lesions of narrow-leafed ash (*Fraxinus angustifolia*) and European ash (*F. excelsior*) (Husson et al., 2012; Chandelier et al., 2016). Often those ash trees affected by *H. fraxineus* become secondarily infected by *A. gallica* or *A. cepistipes* (Marçais et al., 2016; Enderle et al., 2017; Madsen et al., 2021). Subsequently, tree stability is reduced, and ash tree decline is further accelerated, which is a major concern.

3.2 Asia—*A. borealis, A. cepistipes, A. duplicata, A. fuscipes, A. gallica, A. jezoensis, A. mellea, A. mellea* ssp. *nipponica, A. nabsnona, A. omnituens, A. ostoyae, A. sinapina, A. singula, D. ectypa, D. tabescens,* and Nag. E (unnamed *Armillaria* biological species)

At least 16 *Armillaria* species occur in Asia (Heinzelmann et al., 2019) (Fig. 20.4). Of these, *A. duplicata*, *A. fuscipes*, and *A. omnituens*, which are described from India (Chandra and Watling, 1982), lack biological and phylogenetic information. In addition to these 16 species, another 8–9 biological species or phylogenetic lineages have also been recognized in China (Guo et al., 2016). The *Armillaria/Desarmillaria* species in Asian regions other than China, Korea, and Japan have not been sufficiently investigated.

In East Asia (China, South Korea, and Japan), three *Armillaria* taxa are recognized as the most pathogenic species. *Armillaria ostoyae* has been found frequently in northeastern China and it may also be widely distributed in northwestern and southwestern China, where it has caused serious damage in plantations of Korean pine (*Pinus koraiensis*) and larch (*Larix* spp.) (Qin et al., 1999). *Armillaria ostoyae* is widely distributed in South Korea; however, serious forest damage caused by *A. ostoyae* has only been reported from the northern part of the country (Park et al., 2018). In Japan, severe Armillaria root diseases caused by *A. ostoyae* were reported in the 1950s and 1960s in plantations of hinoki cypress (*Chamaecyparis obtusa*), Japanese/Korean red pine (*P. densiflora*), and Japanese larch (*Larix kaempferi*). At that time, more than 1500 ha of young Japanese larch plantations were affected. In recent years, Japanese larch has died in large numbers (≈ 3000 ha) in Hokkaido, Japan, due to the interactions of *A. ostoyae* infection, drought stress, and bark beetle (*Ips cembrae*) attack (Wada et al., 2020).

Desarmillaria tabescens is the second most important Armillaria root disease pathogen in China, where it has been found in Beijing and in provinces of central China (e.g., Shandong, Hebei, and Jiangsu) (Yuan, 1997). *Desarmillaria tabescens* is also one of the most important Armillaria root disease pathogens in Japan, where it is mainly distributed in Honshu and southward. Each year, this pathogen kills many trees of economic value, such as fruit trees and woody ornamentals (Qin et al., 2007). In South Korea, despite its widespread distribution, no severe forest damage caused by *D. tabescens* has been reported to date.

Armillaria mellea is considered to be a saprotroph or weak pathogen in China and Korea, but it is a virulent pathogen of hinoki cypress in many orchards, gardens, and young plantations within Japan. The homothallic form of *A. mellea* is distributed in Japan and China, while the heterothallic form only occurs in China.

3.3 North America—*A. altimontana, A. calvescens, A. cepistipes, A. gallica, A. gemina, A. mellea, A. mexicana, A. nabsnona, A. sinapina, A. solidipes* (as *A. ostoyae*), and *D. caespitosa* (as *D. tabescens*)

Each of the 11 known *Armillaria* spp. in North America (Fig. 20.4) has a distinctive distribution pattern. In the USA, *A. mellea* is a prominent pathogen of broad-leaved trees and other woody plants in the eastern, southeastern, central, and southwestern regions (e.g., Bruhn et al., 2000), and it is also a prominent pathogen of broad-leaved and coniferous trees in California and Arizona (e.g., Baumgartner and Rizzo, 2001a, 2001b). *Desarmillaria caespitosa* (formerly *D. tabescens/A. tabescens* in North America) is a primary pathogen of diverse horticultural and forest trees in the southeastern, eastern, and central USA (e.g., Bruhn et al., 2000; Schnabel et al., 2005; Kelley et al., 2009; Antonín et al., 2021). In coniferous regions of the northern USA, high elevations of the southwestern USA, and southern Canada, *A. solidipes* (frequently reported as *A. ostoyae*) is considered the most important Armillaria root disease pathogen of coniferous trees (e.g., Morrison et al., 1985; Mallett, 1990; Banik et al., 1996; Bérubé, 2000; Worrall et al., 2004; Cleary et al., 2012a, 2012b). *Armillaria sinapina* can also cause tree mortality in the northwestern USA and southwestern Canada (e.g., Dettman and van der Kamp, 2001). Other species, such as *A. altimontana, A. calvescens, A. cepistipes, A. gallica, A. gemina*, and *A. nabsnona*, occasionally behave as pathogens or secondary/opportunistic pathogens of diverse woody hosts in the USA, especially when host trees are under stress (e.g., Bérubé and Dessureault, 1989; Banik et al., 1996; Volk et al., 1996; Brazee and Wick, 2009; Brazee et al., 2012). However, *Armillaria* taxonomy continues to change over time, as exemplified by a recent recognition of *D. caespitosa*, a North American vicariant of *D. tabescens* (Antonín et al., 2021).

In Mexico, *A. solidipes* (as *A. ostoyae*), *A. mellea, A. gallica, A. mexicana*, and *D. caespitosa* have been identified (Shaw, 1989; Elías-Román et al., 2013; Elías-Román et al., 2018; Antonín et al., 2021). In natural forests, only sporadic tree mortality has been associated with these *Armillaria* species (Alvarado-Rosales, 2007). In orchards and forest plantations, *Armillaria* can cause significant damage, especially in areas where the native forest was cleared and/or in forests associated with high disturbance (Alvarado-Rosales, 2007; Valdés et al., 2004). For example, tree deaths were associated with *D. caespitosa* (as *A. tabescens*) in teak (*Tectona grandis*) plantations of southern Veracruz. Armillaria root disease has continued to increase in these orchards even after inoculum reduction measures were implemented, which suggests that other management strategies are likely required (Cibrián-Tovar et al., 2013). In pine-oak forests of Ixtlán de Juárez, Oaxaca, a high incidence of *A. mellea* has been associated with high disturbance and inadequate forest management, compared to plots within a conserved secondary forest (Valdés et al., 2004). In fruit orchards in several states of México, high tree mortality due to *Armillaria* spp. has been reported, resulting in patches of symptomatic and dead trees that continuously increase in size. In peach orchards affected by *A. mexicana* and *A. mellea* in Michoacán and the State of México, the use of resistant rootstocks (e.g., "Mondragon") has been suggested (Rivas-Valencia et al., 2017; Elías-Román et al., 2018). In avocado orchards in Michoacán, a main avocado-producing region in México, *Armillaria* spp. (*Armillaria* sp., *A. mellea*, and *A. gallica*) were shown as etiological agents of decline and death of avocado trees (Ordaz-Ochoa, 2017). For the avocado orchards of that region, strategies to manage Armillaria root disease include aboveground root collar excavation, balanced nutrition, application of resistance inducers (e.g., acibenzolar-*S*-methyl), biocontrol agents (*Trichoderma koningiopsis*), tree pruning, and other strategies (Michua-Cedillo et al., 2016).

3.4 Africa—*A. gallica, A. mellea*, African lineage (composed of *A. fuscipes = A. heimii* and potentially other species), and *D. tabescens*

In sub-Saharan Africa (Fig. 20.4), an endemic African *Armillaria* lineage is present, along with *A. gallica* and *A. mellea*. The latter two species are confined to the area of Cape Town, South Africa, where early European settlers likely introduced these species (Coetzee et al., 2001; Coetzee et al., 2003b). The gradual escape of those two species from planted gardens to

natural woody ecosystems poses a risk for the native vegetation in this area (Coetzee et al., 2018a). A different lineage of *A. mellea*, characterized by a homothallic life cycle, is present in Ethiopia, Kenya, Tanzania, and Saõ Tomé and Príncipe. This *A. mellea* lineage occurs predominately on tea (*Camellia sinensis*) that was introduced from Asia together with *A. mellea* (Mwenje et al., 2006).

The native African *Armillaria* lineage is widespread on the African continent. Whether this lineage represents one or multiple species is an unsettled debate (Pérez-Sierra et al., 2004; Coetzee et al., 2005; Coetzee et al., 2018b). One species recognized by all authors within the African *Armillaria* lineage is *A. fuscipes*, which is currently treated as synonymous with *A. heimii*. Based on a limited number of molecular markers, some authors propose the existence of at least one other species within the African lineage that is named African Clade B (Coetzee et al., 2005) or *A. camerunensis* (Koch et al., 2017; Petchayo et al., 2020). In contrast, Pérez-Sierra et al. (2004) suggested that the African lineage comprises just one genetically variable species (*A. fuscipes* = *A. heimii*), because of similar morphology and somatic compatibility among isolates from the different genetic groups. Further studies are required to conclusively resolve the taxonomy of the African *Armillaria* clade.

In native forests, taxa from the African lineage primarily behave as opportunistic pathogens and only occasionally cause Armillaria root disease. In contrast, in plantations of exotic plant species, predominately established on previously forested sites, native African *Armillaria* is reported as a major cause of Armillaria root disease. The host range includes tea and American pines (*Pinus* spp.) in East Africa, rubber tree (*Hevea brasiliensis*) in the Democratic Republic of the Congo (= Congo-Kinshasa) and Gabon, cassava (*Manihot esculenta*) in the Republic of the Congo (= Congo-Brazzaville), pepper (*Piper nigrum*), and cacao (*Theobroma cacao*) in Cameroon, and American pines in South Africa (Onsando et al., 1997; Coetzee et al., 2000; Laflamme and Guillaumin, 2005; Petchayo et al., 2020).

3.5 Australia/Oceania—*A. aotearoa, A. fumosa, A. hinnulea, A. limonea, A. luteobubalina, A. novae-zelandiae*, and *A. pallidula*

In Australia/Oceania, seven well-characterized *Armillaria* species occur (Fig. 20.4). The most widespread species is *A. novae-zelandiae*, which is present in Australia, New Zealand, New Guinea, and Fiji. *Armillaria novae-zelandiae*, or a closely related species, is also reported from Indonesia (Coetzee et al., 2003a; Maphosa et al., 2006). *Armillaria hinnulea* occurs in Australia and New Zealand; whereas *A. luteobubalina*, *A. fumosa*, and *A. pallidula* are native to Australia, and *A. aotearoa* and *A. limonea* are native to New Zealand.

In Australia, *A. luteobubalina* is the dominant pathogenic species responsible for widespread Armillaria root disease in natural and planted eucalypt forests, where it infects eucalypts and neighboring trees and shrubs. *Armillaria luteobubalina* also actively shapes forest ecosystems by suppressing susceptible hosts, while permitting the growth of other, less susceptible species (Shearer et al., 1997). Armillaria root diseases in fruit-tree and exotic pine (e.g., *P. radiata*) plantations are also predominantly caused by *A. luteobubalina*. Other *Armillaria* species present in Australia are mostly known from areas with indigenous forests where these species act as saprotrophs or weak pathogens.

A different situation is observed in New Zealand, where most *Armillaria* root disease is caused by *A. limonea* and *A. novae-zelandiae* within plantations of introduced tree species (e.g., *P. radiata*). Armillaria root disease impact is highest in first-generation plantations established on sites cleared of indigenous forest, but the disease incidence normally is reduced over the following rotations. The *Armillaria* epidemics observed in kiwifruit (*Actinidia deliciosa*) orchards are also caused by *A. novae-zelandiae* (Homer, 1992). In contrast, other *Armillaria* species in New Zealand are only known to occur within smaller geographic areas containing indigenous southern beech (*Nothofagus* spp.) forests; little is known about their ability to cause disease.

3.6 Central and South America—*A. affinis, A. griseomellea, A. limonea, A. mellea-rubens, A. montagnei, A. novae-zelandiae, A. paulensis, A. procera, A. puiggarii, A. sparrei, A. tigrensis, A. umbinobrunnea, A. viridiflava*, and *A. yungensis*

At least 14 *Armillaria* species have been reported from Central and South America (Volk and Burdsall, 1995; Pildain et al., 2010) (Fig. 20.4). The systematics and taxonomy are moderately well studied for *Armillaria* in the temperate forests of the Patagonian Andes in Argentina and Chile; however, little is known regarding *Armillaria* taxa of central and northern South America. Earlier taxonomic studies of *Armillaria* include Spegazzini (1889), Singer (1953, 1956, 1969, 1970, 1989), and Lima et al. (2008), but few other reports are available about *Armillaria* taxa from these regions.

Armillaria species were found attacking roots of native trees, such as southern beeches (*Nothofagus*) and *Araucaria* spp., among others. Symptomatic Dombey's beech/coihue (*N. dombeyi*) was associated with the Patagonian *Armillaria* species, *A. sparrei* (Molina et al., 2020). Specific pathogenicity studies for *A. sparrei* are lacking and much needed. *Armillaria* species have been reported as a cause of root disease in commercial plantations of several exotic pines and eucalypts (Lima et al., 2008; Pildain et al., 2009). While some *Armillaria* species that are native to Patagonia, such as *A. novae-zelandiae* and *A. montagnei*, can act as beneficial saprotrophs, these species can also behave as aggressive root-disease pathogens on introduced crops, such as pines, eucalypts, and grapevines, especially on land that was previously occupied with the native forest in Chile (Ramírez, 1990; Ramírez et al., 1992).

4. Symptoms and signs

Symptoms of Armillaria root disease depend on the host and associated environmental conditions. Because this disease impacts the root system, host symptoms, which share some similarity to those caused by drought stress, can be evident as a thinning crown/foliage loss, wilting, chlorosis, basal resin flow on conifers or gummosis on hardwood trees, decayed wood/ heart rot, distress cone production on conifers, frequent tree mortality over time, and/or rapid mortality with the foliage remaining on the tree (Table 20.1). In some situations, Armillaria root disease is evident as a disease center with active disease spreading outward (Fig. 20.1A). Alternatively, infections by *Armillaria* may not show readily observable, aboveground symptoms, except for reduced growth (e.g., Morrison et al., 2000; Cruickshank et al., 2011), which can only be observed over time or by examining the growth rings of the trees.

Observation of signs (structures produced by the pathogen) of Armillaria root disease often requires excavation of the root crown and/or cutting into the basal bole or lateral roots (Table 20.1). A clear sign of *Armillaria* infection is the presence of mycelial fans (Fig. 20.1B, C) under the bark of symptomatic/asymptomatic living trees or dead trees that show symptoms of the tree response to the fungal infection, such as resinosis/gummosis or other mechanisms to compartmentalize the pathogen (e.g., Cruickshank et al., 2006). Most *Armillaria* species produce root-like rhizomorphs (Figs. 20.1D and 20.2), which are flat or round (< 4 mm diameter) and reddish, brownish, or blackish in color on the outer surface, that frequently adhere to the root surface and extend into the soil and organic matter. Sometimes, rhizomorphs are also found under the bark of standing dead trees or stumps. *Armillaria* causes a characteristic wet/stringy, yellowish wood decay with zone lines that may serve to protect *Armillaria* against potential competing fungi inside the rotten wood (Fig. 20.2). Trees with basal heart rot in the bole and/or lateral roots frequently break, which may be associated with tree failure and/or windthrow. Characteristic basidiocarps on the base or lateral roots of the tree are the most prominent signs of *Armillaria*; however, these basidiocarps are typically produced only sporadically and seasonally. For establishment in pure culture, *Armillaria* can be isolated from rhizomorphs, mycelial fans, basidiocarps, or host tissue with visible signs.

TABLE 20.1 Symptoms and signs of Armillaria root disease.

Symptoms of Armillaria root disease	Signs of Armillaria root disease
Reduced height/diameter growth	*Armillaria* basidiocarps (mushrooms) on tree base
Chlorotic foliage	Mycelial fans
Slow loss of foliage	Rhizomorphs
Distress cones	Yellow wet/stringy decay, papery when dry
Slow crown decline	Zone lines
Abundant basal resin flow on conifers	
Gummosis on hardwood trees	
Sudden or slow death of tree	

5.   Ecological function

In natural forests, *Armillaria* performs several beneficial ecological roles as a saprotroph, such as decomposition, nutrient recycling, and potential biological control against pathogenic *Armillaria* spp. In a northern Idaho western white pine (*P. monticola*) planting site, *A. altimontana* behaves as a long-term *in situ* biological control agent against pathogenic *A. solidipes* (Warwell et al., 2019). Competitive exclusion of *A. solidipes* by *A. altimontana* suggests that *A. altimontana* has a competitive advantage in its saprotrophic niche and this competitive advantage could be maintained by interspecific antagonism (Warwell et al., 2019). However, several ecological benefits are also obtained even when *Armillaria* behaves as a parasite that causes tree mortality. Benefits of pathogenic *Armillaria* include eliminating maladapted trees, creating openings for regeneration, enhancing forest succession, and providing wildlife habitat (e.g., Steeger and Hitchcock, 1998; Parsons et al., 2003).

Armillaria has some interesting, but disparate, features related to its ecological functions. For example, *Armillaria* is known for its bioluminescence, which is the subject of many hypotheses, but the ecological function of this property remains largely unverified (e.g., Baumgartner et al., 2011; Mihail, 2015). In eastern Asia, *Armillaria* spp. can form unique mycorrhizal relationships with achlorophyllous, mycoheterotrophic orchids, such as *Galeola*, *Gastrodia*, and *Cyrtosia*, which contain species that are important in traditional medicine (e.g., Baumgartner et al., 2011; Guo et al., 2016; Suetsugu et al., 2020). In other situations, *Armillaria* can participate in symbioses with other fungi, where it can serve as the host (e.g., *Entoloma abortivum*) or parasite (e.g., *Wynnea*) (Baumgartner et al., 2011). As mentioned previously, *Armillaria* can display very long-term and wide-spread occupancy of a site (e.g., Smith et al., 1992; Ferguson et al., 2003).

6.   Interactions between *Armillaria* and insects

Armillaria and insects typically co-occur and exhibit strong interactions that are often difficult to interpret (Kedves et al., 2021). In some geographic areas, such as the western USA, *Armillaria* infections are associated with predisposing conifers to attack by bark beetles, such as mountain pine beetle (*Dendroctonus ponderosae*) and western balsam bark beetle (*Dryocoetes confusus*) (e.g., Hertert et al., 1975; Kulhavy et al., 1984; Tkacz and Schmitz, 1986; Lalande et al., 2020; Sierota and Grodzki, 2020). Further evidence suggests that *Armillaria* infection of spruce (*Picea*) can induce the production of volatile compounds that attract bark beetles, such as engraver beetles (*Ips* spp.) (Madziara-Borusiewicz and Strzelecka, 1977; Sierota and Grodzki, 2020). Because both *Armillaria* and bark beetles tend to attack stressed trees, interactions among *Armillaria* and bark beetles are common, but temporal and causal relationships cannot always be definitively determined.

Another type of *Armillaria*-insect association includes defoliating insects, such as spongy moth (*Lymantria dispar*), eastern spruce budworm (*Choristoneura fumiferana*), maple webworm (*Tetralopha asperatella*), and saddled prominent caterpillar (*Heterocampa guttivitta*) (Kedves et al., 2021). In these interactions, insect defoliation is believed to predispose trees to *Armillaria* infections (e.g., Wargo and Houston, 1974). Attack by root collar weevils (*Hylobius* spp.) has also been hypothesized to facilitate *Armillaria* infection by providing wounds that serve as points of entry for the pathogen (e.g., Warren and Singh, 1970). In many other cases, *Armillaria* and insects may simply co-occur without any direct interaction, while other *Armillaria*-insect interactions are yet to be examined. Kedves et al. (2021) include a comprehensive section on interactions among *Armillaria* and insects.

7.   *Armillaria* and climate change

Several reports and studies have addressed the impact of climate change, environmental change, and extreme weather on Armillaria root disease (e.g., Wargo and Harrington, 1991; Wargo, 1996; Desprez-Loustau et al., 2006; La Porta et al., 2008; Dukes et al., 2009; Klopfenstein et al., 2009; Woods et al., 2010; Kliejunas, 2011; Sturrock et al., 2012; Kolb et al., 2016; Dempster, 2017; Kubiak et al., 2017; Labbé et al., 2017a; Aslam and Magel, 2018; Heinzelmann et al., 2019; Kim et al., 2021; Murray and Leslie, 2021). Definitive interpretations of climate impacts on Armillaria root disease are complex because of numerous other abiotic and biotic influences and the lack of long-term studies. In general, bioclimatic models predict that climate change will likely lead to changes in the suitable climate space or potential distributions of *Armillaria* spp. and their woody hosts over the long term (e.g., Klopfenstein et al., 2009; Kim et al., 2021).

Host tree stress caused by climate maladaptation is a likely outcome of climate change and extreme weather events, such as drought or unusually high temperatures, and such host tree stress can predispose host trees to Armillaria root disease (e.g., Desprez-Loustau et al., 2006; Dukes et al., 2009; Sturrock et al., 2012; Kolb et al., 2016; Dempster, 2017). The degree of maladaptation is dependent on the phenotypic plasticity of the host and other interacting factors, such as spacing, associated pests, soil properties, tree size, and root architecture. Based on these factors, it is likely that Armillaria root disease

will continue to increase under changing climates in the future, and forest managers should consider climate change in their strategies to manage Armillaria root disease. Management options include selecting or planting trees that are tolerant or adapted to climate change and Armillaria root disease, and using silvicultural methods to reduce the tree stress, such as increasing tree spacing (see Section 9).

8. Molecular and genomic studies

Genomic and transcriptomic studies of *Armillaria* face many challenges related to the number of *Armillaria* species, the numerous hosts, and the wide diversity of environmental conditions and geographic locations where *Armillaria* occurs. Such work is complicated due to the different ecological roles of *Armillaria*, ranging from beneficial saprotrophic decomposer to virulent pathogen. In 2013, the first *Armillaria* genome (*A. mellea*; Europe) was published (Collins et al., 2013). Subsequently, genomes of *A. cepistipes* (Europe), *A. gallica* (Europe), *A. ostoyae* (Europe), and *A. ostoyae* (North America = *A. solidipes*) were published (Sipos et al., 2017), genomes of *A. solidipes* and *A. altimontana*, both endemic to North America, were compared (Ibarra Caballero et al., 2022), and the genome of an endemic African species, *A. fuscipes*, was published (Wingfield et al., 2016). In addition, unpublished, genomic sequences of other *Armillaria* spp. are available on public databases, including the Joint Genome Institute (JGI) Genome Portal (https://genome.jgi.doe.gov/portal/). Genome and transcriptome research has provided insights into expressed genes involved in lignocellulose and pectin degradation, fruiting body formation, rhizomorph growth, pathogenicity, and overcoming plant defenses (e.g., Ross-Davis et al., 2013; Sipos et al., 2017; Heinzelmann et al., 2019; Ibarra Caballero et al., 2022). The increasing availability of genomic and transcriptomic information will provide further insights regarding the ongoing processes at the pathogen–host interactions and the genomic specificities of *Armillaria* species with different ecological strategies (e.g., saprotrophic vs parasitic) (Ibarra Caballero et al., 2022).

9. Management

Armillaria root disease is notoriously difficult to manage because *Armillaria* has an extremely wide host range. *Armillaria* can also persist for decades on a site using dead organic matter as a nutritional substrate (e.g., Roth et al., 1980; Redfern and Filip, 1991), and it can survive on a site for thousands of years (e.g., Ferguson et al., 2003; Bendel et al., 2006). For these reasons, it is typically considered unreasonable that *Armillaria* can be eradicated from most sites. Instead, management approaches for Armillaria root disease typically involve methods that shift the balance of ecosystem dynamics to reduce the likelihood of damage.

9.1 Reducing root disease susceptibility

Because *Armillaria* seems to attack trees that are stressed due to climate maladaptation or other stress factors, a primary strategy for managing Armillaria root disease is to plant, select, or naturally regenerate trees that are well-adapted to the site and exhibit adaptation to a broad range of environments. In some situations, planted trees appear more susceptible to Armillaria root disease than naturally regenerated trees, especially if planted trees are not adapted to the site. Because drought stress can be associated with Armillaria root disease, seral species, such as pines or larch, tend to be less susceptible in conifer forests of North America (e.g., Morrison, 2011; Kubiak et al., 2017; Murray and Leslie, 2021), and it is also prudent to maintain an adequate spacing of trees on a site, which could also limit tree-to-tree spread of *Armillaria* and reduce moisture stress. In contrast, forest management practices (thinned and fertilized vs. thinned and unfertilized vs. no treatment) resulted in no differences in *Armillaria* occurrence across both wetter and drier sites of eastern Washington, USA (Kim et al., 2010). Care must also be taken to avoid wounding trees that remain after thinning and use other methods to increase host vigor. In some horticultural situations, *Armillaria*-resistant rootstock may be available (e.g., Elías-Román et al., 2019). Under horticultural conditions, the removal of soil surrounding the root crown may offer protection against *Armillaria* (Baumgartner, 2004: Schnabel et al., 2012).

9.2 Reducing *Armillaria* inoculum

Several studies have focused on stump extractions as a method to manage *Armillaria* by reducing *Armillaria* inoculum and/or nutritional substrates for the *Armillaria* pathogen. Studies of stump extraction have yielded mixed results, depending on the location and tree species. In southern interior British Columbia, Canada, stump extraction prior to planting Douglas-fir (*Pseudotsuga menziesii*) and associated conifers typically improved growth and reduced Armillaria root disease-caused

mortality at 40-years post-planting (Morrison et al., 2014). A similar trend was noted in other long-term (21–50 years) studies for coniferous forests of Canada and Scandinavia (Cleary et al., 2013). In a different study in British Columbia, extraction of birch (*Betula*) and neighboring stumps was associated with promoting bacteria that appeared beneficial in suppressing Armillaria root disease (Modi et al., 2021). However, a different result was obtained from a study of an *Armillaria*-infested site with ponderosa pine (*P. ponderosa*) in Washington, USA. After 35 years, the influences of stump extraction and inoculum reduction measures were only marginal at best for improving the growth of the remaining trees, and the benefits did not appear to warrant the costs associated with the stump extraction (Shaw et al., 2012). Even where stump extraction is effective at reducing Armillaria root disease, considerations should be given to (1) disturbances may allow new *Armillaria* inoculum to become established, (2) cost effectiveness, and (3) deleterious ecological consequences, such as reduced organic compounds/nutrients, soil erosion, and other long-term effects of mechanical disturbances (McDonald, 2012; Heinzelmann et al., 2019).

9.3   Biological control

Biological control of Armillaria root disease is of considerable interest, not least because of potential environmental disturbances associated with other management methods (e.g., Pearce and Malajczuk, 1990; Chapman and Xiao, 2000; Raziq, 2000; Chapman et al., 2004). Biological control of *Armillaria* pathogens offers great potential; however, such approaches are likely site-specific and involve complex microbial interactions. The application of biocontrol agents must consider regulatory approval processes, producing sufficient inoculum, and matching the specific ecological requirements of a potential biocontrol agent to the site. Furthermore, the high cost associated with the application of biological control agents would make such treatments uneconomical in most situations, except for targeted, high-value sites.

An economical and environmentally friendly approach to biological control is the use of management practices to favor native, *in situ* biological control agents [e.g., *Trichoderma* spp. (fungi) and *Pseudomonas* (bacteria)] that are already present on the site, while discouraging the *Armillaria* pathogen (e.g., Stewart et al., 2021; Ibarra Caballero et al., 2022). In one situation, the establishment of nonpathogenic *A. altimontana* appeared to competitively exclude the pathogenic *A. solidipes* within a western white pine plantation (Warwell et al., 2019). Using management practices to favor native, *in situ* biological control agents does not require regulatory approval, and it focuses on the native biological control agents that are already adapted to the site. Methods, such as metagenomics and metabarcoding, can be used to determine fungi and bacteria present in the forest soil; however, knowledge of the microbiome and associated analyses are needed to determine which treatments (Ibarra Caballero et al., 2022) (e.g., applications to adjust soil organic matter, N, and pH, and/or prescribed fire) favor the biological control agents and discourage the *Armillaria* pathogen.

9.4   *Armillaria* as an invasive pathogen

When introduced to a new area, *Armillaria* can become established and behave as an invasive pathogen. Because *Armillaria* spreads slowly, apparent symptoms of Armillaria root disease can take years or decades to develop, which makes exotic/invasive *Armillaria* difficult to detect in the short term. Furthermore, accurate identification of *Armillaria* is needed before it can be recognized as an invasive species; however, the invasiveness of *Armillaria* has been previously established on multiple sites (e.g., Coetzee et al., 2001, 2003b, 2018a; Mwenje et al., 2006; Wingfield et al., 2010). These examples of the invasiveness of *Armillaria* demonstrate that precautions are critical to avoid moving *Armillaria*, which can be associated with plants, soil, or wood, into new geographic areas.

10.   Concluding remarks

Armillaria root disease occurs around the world in many places where woody plants grow. Depending on the environmental conditions, host plant, and host condition, different *Armillaria* species occur in different geographic regions, and each *Armillaria* species displays distinct ecological behaviors, ranging from a virulent primary pathogen, secondary pathogen, beneficial saprophyte, or beneficial mycorrhizal symbiont of orchids in Asia. Even as a pathogen, *Armillaria* provides benefits to forest ecosystems, such as eliminating maladapted trees, creating openings for regeneration, fostering forest succession, and creating wildlife habitat. Trees that are stressed due to maladaptation or other disturbances are frequently more susceptible to Armillaria root disease, as are many trees that are planted on previously forested sites. Climate change is predicted to exacerbate Armillaria root disease as host trees become stressed due to climate maladaptation. Single genets of *Armillaria* can spread in the duff and underground via root-like rhizomorphs or mycelia from root-to-root contact of host trees/shrubs to create disease centers. Because *Armillaria* can inhabit a site for centuries or millennia, it cannot

easily be managed. Management of Armillaria root disease can focus on (1) selecting or planting site-adapted tree/shrub species with less susceptibility to *Armillaria*, (2) reducing the stress on potential hosts, (3) reducing inoculum of pathogenic *Armillaria*, and/or (4) implementing management practices that favor natural biological control agents of *Armillaria*. Because *Armillaria* spp. can represent an invasive species threat, movement of *Armillaria* via plants, soil, or colonized wood should be avoided. Currently, DNA sequence-based methods provide the most reliable method to identify *Armillaria* spp. Genomic and transcriptomic studies of *Armillaria*, and metagenomic and metatranscriptomic studies of soil microbial communities offer promising new approaches toward understanding the Armillaria root disease and the development of novel approaches for disease management.

11.   Exercises or study questions

(1) What characteristics of *Armillaria* spp. make it hard to manage?
(2) How does *Armillaria* spread?
(3) What are the signs of Armillaria root disease?
(4) What are three potential management approaches for Armillaria root disease?
(5) How is climate change expected to affect Armillaria root disease?
(6) How can *Armillaria* species be identified?
(7) Name two *Armillaria* species that have been recognized as primary pathogens?
(8) Are *Armillaria* species in the Southern Hemisphere the same as those in the Northern Hemisphere?

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