**Armillaria:**
A Pathogen of Trees and Natural Component of Oak Woodlands

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*Armillaria*, known as the oak-root fungus and honey mushroom, causes a root and butt rot disease of over 700 species of woody plants (Sinclair et al. 1987). It was first recognized as a pathogen in the late 1800s in Europe and early 1900s in the United States when attempts to develop nurseries, orchards and vineyards failed due to the disease. The genus *Armillaria* has come into prominence recently because it contains the world’s largest living organisms. An individual clone of *A. gallica*, a species distributed in much of eastern North America, was thought to be giant when researchers discovered that it covered about 15 ha (38 ac.) in Michigan’s Upper Peninsula (Smith et al., 1992). Since then, an immense clone of another *Armillaria* species, *A. ostoyae*, has been found covering 869 ha (2,200 ac.) in mixed conifer forests of Oregon’s Blue Mountains (G. Filip, Oregon State Univ., pers. comm.). This clone is believed to be at least 2400 yrs. old! The role an organism so large and long-lived plays in plant communities must be substantial, although it is not often considered due to its mostly subterranean and therefore, invisible existence. In this paper I discuss the biology of *Armillaria* and describe its diagnostic features to assist in its identification and increase awareness of how it may impact, or be impacted, by efforts to manage and preserve oak woodlands. Specific guidelines for controlling *Armillaria* root rot are provided at the close of the paper.

**Armillaria Pathology and Biology**

*Armillaria* is now understood to be a collection of species, about 40 worldwide, that exhibit varying degrees of pathogenicity (the ability to cause disease). Aside from their primary role as decomposers assisting in nature’s grand scheme of sequestering and recycling carbon, *Armillaria* kills trees. Trees of all ages can be attacked and the progression of disease is as follows: first small roots are infected, then the cambial region beneath the bark of large roots, and the lower trunk or butt log is colonized-often belowground. Colonization of the entire root system may take months to decades depending upon the size and susceptibility of the host, the aggressiveness of the *Armillaria* species, and soil conditions. New trees may become infected as healthy roots come in contact with colonized roots or rhizomorphs (dark, root like infective structures that grow in soil, along roots and underneath bark). Rhizomorphs may grow up to 2 m (6 ft) a year and are found primarily in the upper 30 cm (1 ft) of soil and rarely below 60 cm (2 ft) (Morrison, 1976; Redfern, 1973). They also may grow underneath the bark of dead and dying trees to a height of several meters. Eventually *Armillaria* begins fruiting, i.e., producing mushrooms, on or around its host and over time and following host death, *Armillaria* will begin to cause a white rot of the wood. Few pathogens can colonize both living and dead tissue; *Armillaria* is one of them!

The likelihood of root rot increases substantially in trees stressed from drought, defoliation, other diseases, over watering, soil compaction, construction damage, and numerous other abiotic and biotic factors. Native species and exotics alike are more susceptible to infection when planted in plantations and artificial landscapes that are subjected to multiple stress factors. Exotic species are inherently at risk because they have not evolved a “balance” with the endemic *Armillaria* species, and the presence of several species or clones of *Armillaria* further broadens the range of susceptible hosts.

Stress predisposes otherwise healthy plants to disease in part because of the need for plants to reallocate energy reserves away from defense against pathogens (Bazzaz, et al. 1987; Herms and Mattson, 1997). Some specifics of this phenomenon have been described for *Armillaria*-host interactions. For example, compared to healthy trees, maples and oaks stressed by gypsy moth defoliation had lower levels of antifungal enzymes and higher levels of

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Armillaria-stimulating sugar in roots (Wargo, 1972; 1981). Stressed trees are unable to maintain biochemical barriers that block the enzymes Armillaria produces during infection (Wargo, 1984). Like gypsy moth, other defoliators including the oak leaf roller and powdery mildew fungi, reduce photosynthesis and predispose oak trees to infection (Day, 1927; Staley, 1965). Numerous other insect pests and fungi that attack tree trunks and branches and pathogens that cause wilts can worsen or be worsened by Armillaria. Examples include Nectria canker, twolined chestnut borer, Leptographium root rot and bark beetles (Wargo and Harrington, 1991). Managing these pests and diseases will help to manage Armillaria.

Severe drought is the most common abiotic (non-living) stress that predisposes oaks in woodlands and forests to Armillaria root disease. This has been well documented in the mixed oak forests of the Eastern United States. The legendary drought of 1925, in which annual precipitation was 40% less than normal, and the 1985-88 droughts, in which annual precipitation was 25% less than normal, were followed by widespread Armillaria-induced mortality of scarlet, red and black oak (Clinton et al., 1993; Hursh and Haasis, 1931). Of course, drought and other naturally occurring weather events cannot be prevented. However, root disease can be minimized if efforts are directed at maintaining plant and community health before and after stressful events occur. This requires periodic assessment of tree health and should include more than above ground measures. Evaluation of the “landscape below ground”, including root biomass, soil structure, soil nutrient status, occurrence of mycorrhizae and soil-borne pathogens such as Armillaria, will provide an accurate picture of the true health of an individual tree or a woodland community.

Man-made stresses may act like other abiotic and biotic stresses to augment Armillaria disease. Forests and woodlands that are over-thinned have hotter, drier soils, and more sunscald and winter injury compared to unmanaged stands. These conditions collectively were found to stress mixed oak stands and encourage Armillaria disease (Gottschalk, 1989). Fire suppression and logging and the resulting build-up of stumps and debris led to increased Armillaria root and butt rot in national forests and parks in the United States (Byler et al. 1990; Slaughter and Rizzo, 1999). The practice of periodic burning of woodlands and forests may help keep Armillaria at bay due, in part, to the burning of potential substrates that Armillaria needs for food and by directly killing rhizomorphs (Filip and Yang-Erve, 1997). At the Morton Arboretum in Illinois, we have found that annual burning of a dry mesic oak woodland not only kills rhizomorphs, but appears to reduce Armillaria mushroom production (Table 1).

Table 1.
Comparative abundance of Armillaria mushrooms in 10 burned and 10 unburned plots.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>2000</th>
<th>2001</th>
<th>2000</th>
<th>2001</th>
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<tbody>
<tr>
<td>Unburned</td>
<td>0.3</td>
<td>0.5</td>
<td>2.0</td>
<td>8.0</td>
</tr>
<tr>
<td>Burned</td>
<td>0.3</td>
<td>0.3</td>
<td>1.0</td>
<td>2.3</td>
</tr>
</tbody>
</table>

Burning may also inhibit Armillaria indirectly by the alkaline pH of post-burn ash leachates and the influx of antagonistic microbes including Trichoderma spp. (Reaves et al., 1984;1990). Perhaps periodic burning and even targeted burning of stumps and debris may be a useful tool for natural areas land managers who identify an Armillaria problem.

Over watering is the most common stress leading to Armillaria outbreaks in landscaped areas that are usually watered in accordance with the needs of turfgrass. Too much moisture can have a detrimental effect on trees because it reduces root growth due to the lack of soil oxygen (Kozlowski and Pallardy, 1997). Trees adapted to woodland conditions, e.g. oak, are
Figure 1. 1880 map of the distribution of *Quercus* in North America (excluding Mexico) showing the numbers of oak species in each region, beginning with one species in the lightest zone and ending with 14 or more species in the darkest zone. 


especially vulnerable. In contrast, dry conditions can kill mycelial fans of *Armillaria* and for this reason control guidelines sometimes state that partial excavation of soil around infected trunks will delay the progression of disease (Horne, 1914; Shurtleff, 1987). In fact, ethanol that forms in the rhizosphere of over watered and flooded plants may actually stimulate *Armillaria* growth (Weinhold, 1963). Replacing turf with a 7.5-10 cm (~3-4 in) mulch layer (kept away from the trunk) below the dripline of trees in landscapes may help to reduce overwatering stress and keep the balance between tree and *Armillaria* in favor of the tree.
Armillaria and Oak

The affinity of Armillaria for moist, cool conditions is an important factor in its distribution worldwide. Most Armillaria species occur in temperate and boreal forests and woodlands, and those existing in tropical regions are found at upper elevations (Kile et al., 1991). On a local scale, Armillaria diseases occur on wooded sites or sites that were once wooded. An association of Armillaria with native woody plants, including the genus Quercus, was noted long ago by pathologists such as the pioneering Robert Hartig who noted the commensalistic (neither detrimental nor beneficial) relationship between Armillaria and native trees and first described Armillaria root rot on introduced pines in Germany (Hartig, 1874). He wrote “Armillaria is found especially frequent on roots and crowns of native beech, hornbeam, oak, birch and mountain ash...of a completely secondary nature”. Similar early references may be found from the United States. Hendriksen (1925) in speaking about California and Oregon states that “Armillaria exists in an oak tree, but does not kill it...” and “so long as its native host is alive, the fungus does not leave it to attack fruit trees”. It was in California that Armillaria was labeled the oak-root fungus and the relationship between oak woodlands and Armillaria root disease became legend (Gardner and Raabe, 1963). Indeed, the general distribution map of Quercus in North America created by C.S. Sargent for the U.S. Census in 1880 (fig 1) overlaps with reports of Armillaria disease in economic hosts (fig 2).

![Figure 2. Armillaria infections recorded on hosts planted in parks, gardens, former woodlands, etc.](image-url)

How long has there been an association between Armillaria and Quercus? Ancestors of both appear to have emerged some 50 to 80 million years ago. Fossils of mushroom-like gilled fungi have been discovered in 80 million year old (Cretaceous) formations and, based on DNA evidence, are believed to be the earliest ancestor of modern mushroom fungi (Hibbett et al, 1997). The earliest oak fossils appear somewhat later during the Eocene and Oligocene epochs (55-25 million years ago) (Crepet and Nixon, 1989). Perhaps the movement of ancestral Armillaria species was, in some cases, linked to that of Quercus that extended into Eurasia from the North American continent via Tertiary period land bridges (Crepet and Nixon, 1989). Indeed, two modern Armillaria species (A. mellea and A. gallica) are widely distributed in mixed hardwood forests containing oak on both continents. Current host specializations and the varying degrees of parasitism existing between Armillaria and oak are descendents of
ancestral plant-fungi interactions and the result of co-evolution (see Pirozynski and Hawkesworth, 1988). Early plants probably relied upon nutrients released from saprophytic (decomposer) fungi while the plants provided fungi with a source of fixed carbon (Taylor and White, 1989). Armillaria, unusual in their capacity to be both saprophytic and parasitic, would have been well-prepared to co-evolve with plants and ensure their evolutionary survival.

Three Armillaria species prevail in oak woodlands and are commonly found on oak: A. mellea, A. gallica (=A. bulbosa), and to a lesser degree, A. tabescens. All three species infect many other genera and it is difficult to determine if oak is, in fact, a preferred host. Anecdotal evidence suggests that oaks are often the foci of large disease centers, and it appears that species in the red or black oak subgenus are most vulnerable to attack. However, comparative studies of the susceptibility of different oak species are scarce and additional data are needed. Many Armillaria species worldwide are not pathogens of oak. A. ostoyae, for example, may grow in mixed oak forests but it attacks, almost exclusively, conifers. Australian species, including A. luteobalina, are partial to the indigenous Myrtaceae found 'down under'.

It's safe to assume that most oak woodlands, forests and their derived landscapes can claim at least one Armillaria species. In natural areas, Armillaria contributes to a balanced, or endemic, level of disease that drives succession by creating small canopy gaps and influencing stand structure and composition. (Castello et al., 1995; Lundquist and Negron, 2000; van der Putten et al. 1993). However, Armillaria may overwhelm a community that is exposed to prolonged, or numerous, stresses. For example, in Australian coastal woodlands in which A. luteobalina is the primary pathogen and Banksia and Acacia are its indigenous hosts, an entire woodland nearly collapsed from attack by Armillaria and detrimental factors associated with its proximity to urban areas. Armillaria killed off dominant tree species and produced too many canopy gaps and bare ground that encouraged increases in sedges/ground cover species, wind erosion and weed invasion (Shearer et al., 1997).

Identifying and Managing Armillaria

In the Chicago metropolitan area most urban woodlands are (or were) dominated by oak and are likely harbor at least one Armillaria species. Its presence magnifies the effects of other pressures imposed upon the urban forest by urbanization. These include heavy visitation, soil compaction, vegetation damage, construction disturbance, alteration of site hydrology, increased number and variety of invasive plants, etc. Vital socio-economic and environmental benefits of sustaining the urban forest are recognized (Dwyer et al., 1994) and Armillaria ought to be considered as one of many potential threats to this goal.

Armillaria can be managed, but it is unlikely to be eradicated. The first step toward management is recognizing its signs and symptoms. There is a certain amount of variation among these global toadstools, but they can be readily identified to genus by several macroscopic features (no need for a microscope):

- honey-colored mushrooms (fig 3) that produce white spore prints and are formed (mostly) in clusters;

![Figure 3. Clusters of Armillaria mushrooms at base of tree.](Photo courtesy of author)
• blackened (sometimes reddish) rhizomorphs (fig. 4), the so called “shoe-strings” that develop from fans or mushrooms and grow along roots, through the litter layer, soil, and underneath bark;
  • a creamy white mycelial mat or “fan” (fig. 5) confined to the cambial region underneath bark of tree trunks and large roots;
  • white rot of wood produced in the basal log and large roots of trees after they have died.

Mushroom characteristics including the presence and form of a ring on the mushroom stem (stipe), scales on the cap and host species can help to determine the species of *Armillaria* present. This is important for assessing the relative disease threat in an area as some species, e.g. *A. mellea*, are more pathogenic than others, e.g. *A. gallica*. Dr. Tom Volk, University of Wisconsin, has developed a website (TomVolkFungi.net) with pictures and descriptions of all *Armillaria* species in North America.

Sometimes infected trees may appear to die suddenly, like a wilt, even though colonization of the roots and above ground symptoms has been developing for a long time (years or decades). The first clue to a problem is usually seen in the canopy. Symptoms result from root death and include: yellow or off-color, sparse foliage; slowed growth manifest as shorter stem internodes; gradual twig and branch death; and gradual canopy decline. On the surface of infected trunks, bark may be loose, and on coniferous hosts especially, bark may be cracked with resin and exudates present. If there are no signs of

*Armillaria* (remember that mushrooms are produced only once a year during autumn in Illinois and the Eastern U.S.), but a tree is declining, look for rhizomorphs in the soil around the trunk and mycelial fans underneath the bark of the trunk and large roots below the soil line. Unfortunately, there isn’t a strong correlation between above-ground symptoms and the extent of root colonization and it is hard to predict when an infected tree will die. If the basal portion of a tree has mycelial fans, death can be assumed to be imminent. See The Morton

**Figure 4. Black *Armillaria* rhizomorphs and underlying white rot of wood.**
*Photo courtesy of author.*

**Figure 5. White mycelial fan of *Armillaria.***
*Photo courtesy of Univ. of California*
Below is a list of guidelines for managing Armillaria:

1. Invest in preventative measures to minimize stress. This is the single most important tool for managing Armillaria disease, as it will help prevent colonization in the first place. For example,
   - Avoid drastic thinning practices that might increase the likelihood of winter injury, wind damage, etc.
   - Reduce weeds (especially woody invasive plants) to diminish competition for resources. Be aware that incomplete removal of stumps and resprouts may provide substrate to Armillaria (we have found this to be the case for buckthorn, Rhamnus cathartica, in Illinois).
   - Prevent construction damage to trees that causes soil compaction and alters a site’s hydrology when building on or near woodland habitats.
   - Prune moderately as over-pruning (e.g. more than 1/4 to 1/3 of a tree’s canopy at one time) is stressful and has been directly related to increased Armillaria disease.
   - Do not over water or wound trees in landscapes.
   - Practice good planting practices and horticultural care, e.g. mulching, watering and fertilizing only if necessary.
   - Encourage root system development by planting smaller trees and using container stock. The increased surface area that comes from great numbers of small roots can help to alleviate stress from droughts.

2. Remove dead and dying trees, stumps, woody debris, roots and rhizomorphs from the upper soil layers. Armillaria can utilize the host materials as a food base for many years.

3. Replant with tolerant or resistant hosts that are suited to a given site. See the University of Illinois Report on Plant Disease (http://www.ag.uiuc.edu/~vista/pdf_pubs/) and Raabe (1962, 1979 a,b) for lists.

4. Monitor regularly for insect pests and diseases in order to respond rapidly to outbreaks. Remove winter-killed and cankered branches and diseased leaves. If need be, apply least toxic insecticides at appropriate times to control defoliating and boring insects.

5. Ask for and support development of environmentally-sound methods of controlling Armillaria and other predisposing diseases and pests. Biological control mixtures of antagonistic fungi and nematodes have been proven to be effective against Armillaria, but remain only available experimentally.

6. Trees already infected with Armillaria can be treated by removing soil from around trunks bases to expose the fungus to drier and hotter conditions. The longevity of this treatment is unknown.

7. Treating stumps with fungicides and soils with fumigants has been useful in orchards and plantations. Be sure to follow the label restrictions. Spot burning of stumps and debris may be an alternative means of getting rid of Armillaria and potential substrates.
Literature Cited


Jacobs, 8