

By Christopher J. Luley, Ph.D.

et's have a frank talk about sex and reproduction in the fungi that cause decay in trees. The details may surprise some people, but the discussion will be, as they say, "safe" for work situations.

If you get this first important biological fact about sexual reproduction in decay fungi, the rest of the details will make a lot more sense. The fact is, a tree must be infected by spores twice for sexual reproduction to occur, as evidenced by devel-



Photo 1: In order for sexual reproduction to occur in the Basidomycota decay fungi, a tree must be infected twice by basidiospores. Sexual reproduction results in the formation of conks, mushrooms or brackets that produce spores for further dispersal and spread. All photos courtesy of the author.

opment of a conk or mushroom on a tree (Photo 1).

The vast majority of wood-decay fungi require a sex partner (we will leave the discussion of the Basidiomycota here, i.e., the fungi that form conks, mushrooms and/or brackets when they fruit or reproduce). This is an obvious overstatement, but it does reflect the biological fact that infection of a tree by two compatible mating types is needed for reproduction by the Basidiomycota that cause decay in trees. The technical or biological term for this mating-type requirement is heterothallism.

And, when infections are initiated by spores, sexual reproduction requires that hyphae of these two different mating types physically join within the tree. Thus, single-spore infections in different parts of the tree that never physically join together will not result in sexual reproduction. This is particularly important in the spread of



Photo 2: Sexual reproduction and the development of fruiting structures may never occur on a tree if it is only infected by a single spore of a wood-decay fungus.

wood-decay fungi because they usually do not reproduce asexually, as do many other fungal pathogens.

There is another little-known and very difficult way to verify that trees are infected without spores. Fresh wounds on trees attract many foraging insects. These insects may carry fragments of hyphae from mushrooms or other fruiting structures. These hyphal fragments are believed to be able to initiate infections. The fragments have both mating types, so only one fragment is required for sexual reproduction to occur.

Life cycle

The life cycle of decay fungi is usually broken into several phases including dispersal, infection, invasion and reproduction. Successful reproduction completes the life cycle and returns the fungus to the dispersal phase. The length of time between infection and subsequent sexual reproduction or fruiting is highly variable. It can range from less than a year, as in the case of saprophytes colonizing previously dead portions of a tree, to many years, as in the case of heartwood or root-decay fungi.

In some cases, sexual reproduction never occurs because the tree is not infected by two compatible mating types. This at least partially answers the question of why some trees with decay never have conks or mushrooms, indicative of the fungus being present on them (Photo 2).

The environmental and host factors that stimulate sexual reproduction and fruiting in the decay fungi are generally not well known. It is clear, however, that even in the annual fungi (where new mushrooms or conks may develop each year and produce another crop of spores), yearly variation is common, meaning that because an annual fungus fruits in one year does not mean it will fruit again the next year or in the future (Photo 3) on that same tree. The perennial wood-decay fungi reproduce by developing another spore layer on the same hard, woody conk each year (Photo 4).



Photo 3: Annual fruiting fungi produce new sexual fruiting structures each year. Previous years' and current year's fruiting are evident here on an annual fruiting fungus, Fomitopsis spraguei, shown here on an oak.

TREE CARE INDUSTRY – JUNE 2020



Photo 4: A perennial fruiting fungus (Ganoderma applanatum) *displaying the annual spore layers that form on the same conk each year.*

Dispersal

The life cycle of the wood-decay fungi begins as spores are released from conks or mushrooms. Basidiospores are haploid (or have the "n" nuclear state, whereas the body of most higher organisms have the "2n" nuclear state). A single conk can produce millions to perhaps billions of haploid spores (Photo 5)! As a side note, removing conks or mushrooms from trees won't affect the decay inside the tree, but will clearly reduce the potential for these fungi to disperse spores to infect other trees. Therefore, sanitation or eliminating stumps and large roots can reduce the spread of decay fungi.

Typically, spores (all spores are hap-



Photo 5: Brown basidiospores covering the wood and top of the conk of Ganoderma applanatum. A single conk can produce millions of wind-dispersed basidiospores.

loid, or only have one-half the genetic material required for sexual reproduction) are dispersed in wind. The spores are often colorless or have some brown color or light pigmentation. Their small size, thin walls and light pigmentation make them short lived in the environment (short lived as in days and hours, depending on the conditions).

Infection

Haploid basidiospores likely cause most infections in trees when they germinate on the surface of wounds or establish infections by germinating on dead branches. Most decay fungi do not have the capacity for spores to penetrate and initiate infections di-

rectly through intact bark. Because other non-decay-causing fungi are better able to compete for soluble carbohydrates and other nutritive resources produced on the surface of fresh wounds, most decay fungi establish infections after wounds have "aged." Wounds that expose the heartwood to infection, such as on larger branches where heartwood is often present, are believed to be more important in establishing decay columns in trees.

Decay also can become established in a tree through root infections. Root infections can be initiated by spores or rhizomorphs (vegetative hyphae that are massed together in a dark, protective covering that allows some Armillaria species to grow through the soil on a root surface to infect roots of nearby trees) (Photo 6). There also is evidence that some root-decay fungi can cause new root infections via root-to-root contact. However, empirical evidence does not support that this is common in urban environments, meaning we typically don't see adjacent trees in built environments all exhibiting the same decay-pathogen infections. However, in wooded areas, root-decay centers are not uncommon.

Invasion

After initial infection, invasion of wood occurs by the growth of hyphae after spore germination. All fungi are heterotrophs, meaning that all their nutrition is gained by extracting it from



Photo 6: Rhizomorphs (the black "shoestrings" on the surface of the root in this image) of Armillaria species can also initiate root infections without infection by spores.

their host. The hyphae that initiate the decay from spores are still haploid (Photo 7). The further invasion of wood in the tree can progress with the fungus in the haploid state. However, sexual reproduction cannot occur until the tree is infected by a second spore of the same fungus.

For sexual reproduction to occur, a second haploid spore and resulting hyphae



Photo 7: All fungi must get their nutrition by extracting it from their host. Wood-decay fungi of trees invade and deteriorate wood by the use of extracellular enzymes. The white mass of hyphae or mycelium is shown here (red arrow). Individual hyphae are microscopic, and significant deterioration of wood occurs before the decay is visible to the naked eye.



Photo 8: Basidiomycete decay fungi do not reproduce asexually. However, Ascomycota decay fungi, such as Kretzschmaria deusta, shown here, do reproduce asexually. The light-gray covering on the black stromatic crust contains asexual spores of this fungus.

of a different mating type must infect and establish in the tree. Initially, the hyphae fuse and become dikaryons, a term that indicates two genetic nuclear components are present in the cell but the nuclei are not fused. This is known as the (n+n) state, which is a common nuclear condition for decay fungi in wood.

Most wood-decay fungi do not reproduce asexually. Asexual reproduction is very common in Ascomycota fungi (for example, the fungus causing apple scab and other common leaf diseases, or many of the canker-causing fungi). Asexual reproduction is very important for secondary spread of the ascomycete fungi after initial infection. There are several common and important ascomycete decay fungi of urban trees, such as *Kretzschmaria deusta*, that can reproduce asexually on their host (Photo 8).

Reproduction

Sexual reproduction results in the production of spores, which completes the life cycle of decay fungi. The cycle is completed when the nuclei present in the dikaryotic vegetative hyphae fuse and then undergo meiosis that results in production of haploid nuclei. Four basidiospores are borne on a structure called a basidium, and each spore has one or the other of the original mating types. The basidia line the pores, gills, teeth or smooth surfaces that are representative of fruiting for each particular decay fungus.

Mystery of it all

There are many mysteries in the life cycle of the decay fungi, and there is so much to learn that could help us better manage decay in trees. Most arborists know that wound paints do not prevent or even slow the infection or development of decay in trees. However, there appears to be considerable promise in treating wounds with antagonistic fungi to slow or prevent decay infections. Fungi such as Trichoderma have shown promise, but no marketable or registered Trichoderma or other antagonistic fungi are now available in the United States for management of wood decay. Wound size and type are also important to decay-fungi infections. We suggested in a previous article that, where possible, avoiding large removal cuts that expose heartwood, even to the point of using heading cuts on large branches, is a way to buy time and slow decay infections. (Photos 9a and 9b)

One of the great mysteries of decay biology is what stimulates decay fungi to eventually fruit on any individual tree (Photo 10). We only know by general observation that elevated rainfall or moist environ-



Photo 9a: Large removal cuts or wounds that expose heartwood are most susceptible to infection by decay fungi. The heartwood on the branch of this section of black walnut is the dark-colored wood in the center.





9b: Delaying or avoiding removal cuts that expose heartwood can slow or prevent decay columns from developing on the main trunk of urban trees.

ments seem to promote increased fruiting. However, in any given year, the particular amount and timing of precipitation and sequence or type of environmental conditions that increases or reduces fruiting is yet to



Photo 10: What stimulates annual fruiting of wood-decay fungi is not well known, but wet weather or damp environments seem to promote fruiting of most wood-decay fungi.

be known for most of the decay pathogens. But, as you now know, when fruiting does occur, it is the result of two infections of that particular tree.

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