Spray coating is the newest commercially available coating method available. The method uses several spray nozzles that can be rotated during operation for cleaning to prevent down time. With spray coating, a wide range of coat weights are possible. Good coverage with minimal stress to the base sheet can be obtained. As with curtain coating, several issues remain with regard to formulation and uniformity of the final coating layer. However, each method shows promise as lower stress coating methods.

Concluding Remarks

The introduction of new coating technologies and new coating materials into the market place is increasing the level of competition between coated grades. Machines are running faster and more efficiently. Quality is improving and printers are reaping the benefits as they continue to demand and receive more from their suppliers. Advances in printing technology will continue to drive the coated paper markets as printers seek to print more colors using multiple printing technologies. To keep pace, the papermaker must stay knowledgeable of not only innovations in coating material and process technology, but also new printing technologies and trends.

See also: **Packaging, Recycling and Printing**: Packaging Grades; Printing. **Papermaking**: Overview; Paper Grades; Paperboard Grades.

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PATHOLOGY

Contents

Diseases of Forest Trees

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Introduction

Plant diseases have been recognized for as long as plants have been cultivated. There are many references to plant diseases in early Greek and Hebrew writings. In these early times, diseases were believed to result from the wrath of God and it is not surprising that the Bible contains many references to plant diseases.

The discovery that fungi could cause diseases of plants was made by the chemist Anton de Bary in 1853, when he showed that rust and smut fungi (Uredinales and Ustilaginales) were the causal agents of cereal diseases. De Bary was also responsible for showing that late blight of potato, a disease responsible for reducing the human population of Ireland by half in five years, was caused by the fungus *Phytophthora infestans*. This is perhaps the most famous (or infamous) of all plant diseases. De Bary is appropriately recognized as the 'father' of modern plant pathology.

Although understanding that plant diseases are caused by microbes might seem to be rather obvious to us today, the process of enforcing this understanding was by no means simple. During the first half of the nineteenth century, the doctrine of spontaneous generation was well established, with strong support for the view that microbes emerged from decaying plant and animal matter. Understanding that microbes were the cause and not the result of decomposition emerged relatively slowly. This was through substantial experimentation by scientists including De Bary and Pasteur.

Forest pathology and the study of diseases of trees followed relatively soon after the recognition that microbes can cause diseases of plants. The science of forestry had its origins in Europe and it is not surprising that the 'father' of forest pathology was German. Thus, Robert Hartig (1839–1901) produced the first textbook of forest pathology in 1874. The importance of this book was recognized rapidly as is evident from its rapid translation by the famous British plant pathologist Marshall Ward and the publication of an English edition in 1894.

Plant pathology is hugely important to human health and welfare, yet ironically it is not a subject that has attracted adequate support. It is difficult to know exactly how many active plant pathologists there are in the world but the International Society for Plant Pathology records approximately 6000 names. It is worrying to know that there are certainly no more than 300 active forest pathologists in the world today. These scientists are mostly specialists interested in particular groups of pathogens or aspects of forestry.

This article presents a brief overview of the role of pathogens in forests. This is clearly a very broad topic, which has been treated in various levels of detail and focus in a number of excellent textbooks. It is obviously impossible to provide detail concerning any particular disease. Rather, the aim is to present an introduction to other articles that deal more specifically with various categories of disease.

Diseases in Natural Forests and Plantations

Forest pathology generally treats three broad categories of trees:

- natural, generally undisturbed forests
- intensively managed plantations of native or exotic species
- amenity or ornamental trees.

Diseases tend to act differently in these distinct situations and their management is also generally different. This article specifically treats diseases of native trees, mostly in natural ecosystems or in managed woodlands or forests. Diseases in intensively managed plantations of exotic trees such as the millions of hectares of *Pinus*, *Acacia*, and *Eucalyptus* found in the tropics and the southern hemisphere are treated elsewhere (*see* **Pathology**: Diseases affecting Exotic Plantation Species).

Categories of Tree Disease and their Causal Agents

Virtually every treatment of tree diseases classifies them somewhat differently. If we use Manion's definition of diseases any 'disturbance in the normal physiological functioning of a plant,' then diseases include both those caused by biotic factors as well as those associated with abiotic factors. Biotic factors include microbes and other organisms that have the ability to spread and are thus considered to be infectious. Most forest pathologists study these diseases because they have the ability to cause devastating losses. Diseases caused by abiotic factors such as air pollution, soil contamination, and other environmental factors can also result in very substantial damage. Diseases associated with air pollution, for example, have grown in importance in recent years and this is a trend that is likely to continue as the world population grows.

Most biotic tree diseases are caused by fungi. These fungi include: (1) basidiomycetes such as the decay fungi with mushrooms and brackets as fruiting bodies and the rusts; (2) ascomycetes which are the most numerous causal agents of tree disease; and (3) the oomycetes or water molds such as species of *Phytophthora* and *Pythium* which are best known as root pathogens of forest trees. Tree diseases are also caused by many other biotic agents such as bacteria, phytoplasmas, viruses, nematodes, and parasitic plants.

Disease Epidemics

There are numerous examples of tree disease epidemics that have caused devastating losses to natural ecosystems. Most of these have occurred on trees in natural ecosystems into which pathogens have been introduced. Generally these pathogens occur on the same genera of trees in areas, separated geographically from those that are affected. Typical examples are Dutch elm disease caused by *Ophiostoma ulmi* and *O. novo-ulmi*, chestnut blight (*Cryphonectria parasitica*), white pine blister (*Cronartium ribicola*), and pine wilt caused by the pine wood nematode (*Bursaphelenchus xylophilus*).

The first recorded tree disease epidemics date back to the beginning of the twentieth century. That was also the time when worldwide trade in and movement of forest products began to increase. Today there are increasing numbers of tree disease epidemics appearing. This is likely to be a trend that will continue, with the increasing movement of people and products around the world.

Vascular Wilt Diseases

Vascular wilt diseases are broadly defined as those that result from a blockage of the vascular tissues. Symptoms generally include chlorosis of the foliage and a rapid wilt (*see* **Pathology**: Vascular Wilt Diseases). These diseases are best known in hardwood trees that have xylem vessels that are easily blocked, particularly in the case of ring porous trees where trees depend on large xylem vessels at the start of the growing season. Vascular wilt diseases are less clearly defined in the conifers that have tracheids, which are less easily colonized and blocked.

Blockage of the vascular tissues can be due to the physical presence of fungal structures. The production of tyloses in the xylem vessels is a typical response to infection by vascular wilt pathogens. Production of these structures represents an attempt to slow the movement of the invading pathogen and also blocks the vessels, giving rise to wilt symptoms. Some vascular wilt pathogens are known to produce toxins, which are also involved in the development of the wilt symptoms.

Vascular wilt diseases are caused by ascomycete fungi, nematodes, bacteria, and phytoplasmas. A large number of these disease agents are carried by insects and some are soilborne. Vascular wilt diseases tend not be caused by pathogens typically dispersed in water or via airborne inoculum.

Some of the best-known fungal vascular wilt pathogens are transmitted by insects. In this regard, there are two main categories of insects that carry these pathogens. Thus, the devastating Dutch elm disease pathogens *O. ulmi* and *O. novo-ulmi* are carried by bark beetles (Coleoptera: Scolytidae) which produce maturation feeding wounds in the branch crotches of healthy trees, enabling infection to occur. The same would be true for black stain root disease caused by *Leptographium wageneri*, which can be vectored by insects such as *Hylastes* spp. that undergo maturation feeding on healthy conifer roots. In contrast, various vascular wilt pathogens are carried by casual insects such as flies (various families of Diptera) and picnic beetles (Coleoptera: Nitidulidae) that are attracted to the sap produced by freshly made wounds on trees. Typical examples of this group of insect-vectored fungi causing vascular wilt are the oak wilt pathogen *Ceratocystis fagacearum* and *Ceratocystis fimbriata*, which causes vascular wilt on a wide range of hardwood trees.

Pine wilt caused by the nematode *B. xylophilus* is an extremely important disease of pines in Asia. This is an unusual disease because it occurs in the upper parts of trees and has many similarities to vascular wilts caused by fungi. The pathogen is vectored by longhorn beetles (Coleoptera: Cerambycidae) which, prior to the recognition of the cause of pine wilt in 1971, had been generally considered to be secondary wood-boring insects of minor importance. However, these insects and particularly species of *Monochamus* undergo maturation feeding on twigs of healthy *Pinus* spp. allowing the nematodes to enter the vascular tissues of the trees. The exact mechanism of tree death is not fully understood but is thought to include physical nematode feeding and the production of toxins by nematodes or bacteria associated with them.

Fungal vascular wilt pathogens that are typically soilborne include species of *Fusarium* and *Verticillium*. Both these genera of pathogens are also well known causal agents of serious diseases of agronomic crops. Thus, *Verticillium albo-atrum* is an important pathogen of potatoes but also causes a serious vascular wilt disease of hardwood trees such as maples and ash. Host specialized forms of *Fusarium oxysporum* also cause serious wilt diseases on a wide array of agronomic crops, such as panama wilt disease of bananas caused by *F. oxysporum* f. sp. *cubense*. There are fewer examples of this group of pathogens in forest trees, but they are relatively common on legumes such as species of Acacia.

Serious vascular wilt diseases are caused by various bacteria and phytoplasmas. A serious wilt disease of trees including for example *Eucalyptus* is caused by the bacterium *Ralstonia solanacearum*.

This pathogen occurs in various forms on a wide range of mainly agronomic crops and is generally recognized as being soilborne, entering wounds on roots. In contrast phytoplasmas such as the causal agent of the serious ash yellows disease are xylem limited bacteria and are typically vectored by leaf hoppers (Homoptera).

Root Diseases

Root diseases are most typically caused by fungi belonging to all the major groups, although perhaps the basidiomycetes are best known and most common. Root diseases are also caused by nematodes although there are few examples of serious nematode problems in native trees. Root diseases are often recognized by patterns of disease development arising from the gradual movement of the causal agents through the soil (*see* **Pathology**: Root and Butt Rot Diseases). Thus, for example, in the case of species of *Armillaria* and *Heterobasidion*, this movement is generally from a single point of infection resulting in discrete patches of dying trees, with the most recently killed trees at the periphery of the disease centers. Trees will die slowly or might appear to wilt and die rapidly, but they have generally been infected for a considerable time prior to the appearance of symptoms. Species of *Armillaria* are well known to produce huge infection centers caused by a single clone of the fungus, which has led to the discovery that these fungi represent the largest and the oldest living organisms.

Fungal root pathogens have various infection strategies. Some disperse through the production of large numbers of airborne spores. Typical examples are the species of *Armillaria* and *Heterobasidion annosum*. In the case of these pathogens, spores can infect the surfaces of stumps of freshly cut trees or wounds at the bases of these trees. The fungi then consume the stumps and roots of the infected trees to build up inoculum potential that enables them to move from tree to tree by root contacts or grafts. *Armillaria* species also produce bootlace-like rhizomorphs, which grow on the surface of roots and through the soil, facilitating infection of adjacent trees.

Waterborne and soilborne pathogens and particularly species of *Phytophthora* are amongst the most important root pathogens of trees (*see* **Pathology**: *Phytophthora* Root Rot of Forest Trees). These fungi produce motile zoospores which enable them to move through water. They also produce thick-walled sexual spores that facilitate their survival in the soil for extended periods. *Phytophthora cinnamomi* is by far the best-known tree pathogen in this category and its introduction into native woody ecosystems in Australia has resulted in severe disease epidemics.

An unusual and interesting root pathogen that requires heat to become active is the conifer pathogen *Rhizina undulata*. This pathogen is an ascomycete that disperses its spores actively and these appear to infest the soil, or possibly the fungus lives epiphytically associated with conifer roots. However, heat from fire and occasionally lightning is needed before *R. undulata* becomes active. The disease can result in substantial damage after forest fires and is also commonly associated with patches of dying trees, where camp-fires have been made; among forest workers in the UK it was often known as the coffee-break disease.

Insects can be responsible for the dispersal of tree root pathogens. The best examples are species of *Leptographium* that are asexual states of *Ophiostoma*. These fungi produce sticky spores in the galleries of bark beetles and weevils (Coleoptera: Curculionidae) and the fungi are thus transmitted to tree roots by these insects. The most serious pathogen in this category is the black stain root disease pathogen, *Leptographium wagneri*, which occurs in three forms and is restricted to conifers in western North America.

Canker Diseases

Canker diseases are most commonly caused by ascomycetes and occur on branches and stems of trees (*see* **Pathology**: Stem Canker Diseases). The most serious of these are stem cankers, which girdle the lower parts of stems, resulting in tree death. Canker pathogens tend to infect the cambium and trees can respond by producing callus to seal off the infected tissue. In the case of perennial cankers the pathogen is most active during one period and the tree responds during the remainder of the year. This results in target-like cankers with concentric rings of callus on the stems of trees. In contrast, annual cankers infect the cambium and in severe cases will often girdle the trees.

Although not strictly considered canker pathogens, many rust fungi cause perennial infections on the stems of trees. The rust fungi are unique obligate plant pathogens, having up to five stages in their life cycles, which can occur on two different hosts. Thus white blister rust caused by *Cronartium ribicola*, which has devastated white pine in the North America, gives rise to its most severe damage on the stems of white pines, but has *Rubus* species as alternate hosts. Likewise, serious damage is caused to the stems of various *Pinus* species by the fusiform rust pathogen *Cronartium quercinum* f. sp. *fusiforme*, while various species of oak serve as alternate hosts.

Most canker pathogens are dispersed by spores that are produced during moist weather and that are dispersed by wind. Certainly the best known and most devastating canker disease is caused by the chestnut blight pathogen which has virtually eliminated the American chestnut, *Castanea dentata*, from its native range. There are many other fungi that cause serious canker diseases and these include species of *Botryosphaeria*, the poplar canker pathogen *Hypoxylon mammatum*, and the pitch canker pathogen *Fusarium circinatum*, to name but a few. These pathogens all tend to infect natural or artificially caused wounds on trees, or they are endophytes in healthy trees that proliferate after the onset of stress.

Insects can be important associates of some canker pathogens. For example, the pitch canker pathogen is closely associated with twig and cone feeding insects. Pitch canker is one of the most serious diseases of pines and is responsible for a devastating disease of *Pinus radiata* in California. The pathogen occurs in countries such as Chile and South Africa but is restricted to nurseries. The absence of shoot and cone insects in these countries is thought to be the reason why the disease has not developed into a major problem on large trees.

An interesting recent example of an oomycete pathogen able to cause cankers on trees is *Phytophthora ramorum*. This pathogen is infecting many genera and species of trees in the western USA and is thought to have been introduced into that country from Europe where it occurs on leaves and shoots of *Rhododendron* spp. The sporangia of *P. ramorum* are dehiscent and dispersed by air, after which zoospores are produced in moisture and these directly infect the cambium of susceptible trees, to cause annual cankers.

Leaf and Shoot Diseases

As is true with all plants, trees have a very large number of leaf and shoot diseases (*see* **Pathology**: Leaf and Needle Diseases). These are most commonly caused by ascomycete pathogens but many are caused by rusts (Basidiomycetes: Uredinales) and in a small number of cases *Phytophthora* spp. These pathogens can infect shoots where severe dieback and damage can occur. They can also give rise to the death of large areas of leaf surface causing blight and severe defoliation. Although a single defoliation generally does not kill trees, repeated infections are common and can cause growth loss and even tree death. In other cases, leaf diseases cause discrete spots or localized symptoms on the leaves.

Ascomycete leaf and shoot pathogens have a number of different dispersal strategies. Some have exclusively airborne spores that tend to be actively discharged from fungal fruiting structures. Typical examples are for example in the sexual states of *Mycosphaerella* and the powdery mildews that cause leaf diseases on many trees. Many asexual states of ascomycete leaf and shoot pathogens produce spores that are discharged in association with rainfall. Typical examples amongst more serious tree pathogens are found in the needle blight pathogen *Dothistroma septospora* and the dogwood anthracnose pathogen, *Discula destructiva*.

The rust fungi cause leaf and shoot diseases as well as the cankers discussed above (*see* **Pathology**: Rust Diseases). Spores associated with most of these stages are powdery and windborne although moisture is generally required for the production of basidiospores and insects are known to be involved in fertilization of pycnia. Many rusts are important leaf and shoot pathogens of forest trees. These for example include needle rusts on conifers caused by *Coleosporium* spp., the aecial state of cedar apple rust on apples caused by *Gymnosporagium juniperi-virginianae* and eucalyptus rust caused by *Puccinia psidii*.

Insect Associated Diseases and Blue Stain

Many species of conifer infesting bark beetles are known to carry fungi that impart blue stain to the sapwood of infested trees (*see* **Pathology**: Insect Associated Tree Diseases). Most of these fungi are species of *Ophiostoma* and *Ceratocystis* and their asexual states. They are generally known to be nonpathogenic or only mildly pathogenic. However, their role in killing trees is poorly understood and deeply debated. Certainly some of these fungi such as *Ceratocystis polonica*, associated with the aggressive European spruce bark beetle *Ips typographus*, are highly pathogenic and appear to contribute substantially to tree death.

Irrespective of their pathogenic role associated with bark beetles, species of *Ophiostoma* and *Ceratocystis* that infest conifers impart substantial damage to timber products. After the insects have killed these trees, the sapwood typically becomes severely discolored with so-called blue stain. This discoloration is not strictly a stain in the sense that it is caused by a product of the fungi. It rather arises from the darkly pigmented hyphae of the fungi which colonize the tracheids and ray parenchyma. The fungi do not result in any weakening of the timber but the discoloration is aesthetically unattractive to wood markets and associated financial losses can be great.

Wood Decay

Decay and so-called heart rot in standing trees is most typically found in old-growth forest where trees are sufficiently old to develop columns of decay at their centers (*see* **Pathology**: Heart Rot and Wood Decay). Decay fungi enter wounds on the stems of trees or through broken branches and gradually consume elements of the heartwood. This decay is caused by basidiomycete fungi belonging to, for example, species of *Phellinus* and *Ganoderma*. Various important root pathogens such as species of *Armillaria*, *Heterobasidion annosum*, and *Phellinus weirii* also cause heart rot and decay after they have killed trees or roots.

There are various different types of decay and these arise from the different nutritional habits of the fungi that cause them. For example the white rot fungi consume approximately equal amounts of cellulose and lignin thus causing a relatively evenly spread softening of the wood, which is often stringy. Brown rot fungi utilize chiefly cellulose and the remaining wood is almost pure lignin that appears in a cubical pattern known as brown cubical rot. Another relatively common pattern of decay is white pocket rot where all the lignin is removed from small pockets that contain virtually pure cellulose.

Avoidance and Management of Tree Diseases

Management of diseases in native forests and woodlands is extremely difficult and in some cases virtually impossible. This is very different to disease management in plantations where many options exist for disease avoidance.

One of the most important components of tree disease management lies in excluding pathogens from new environments. As mentioned previously, some of the most devastating diseases have been caused by pathogens introduced into new environments. Exclusion of pathogens from new environments depends on quarantine regulations that ensure that they are not moved across borders. This objective can be very difficult to achieve, particularly where countries have large boundaries, especially with countries having less rigorous regulations. Island countries such as Australia and New Zealand have invested substantially in quarantine and they have achieved remarkable success. However, on the whole, plant quarantine commonly fails, and new and devastating diseases must be expected to continue to move between countries and continents as global trade and travel continue to grow.

Another strategy used to reduce the impact of disease is through eradication of pathogens after they have been introduced into new areas. This approach is complicated and depends on early recognition of the disease, a clear understanding of the biology of the causal agent, and intensive efforts to eliminate it. Various tree disease eradication programs have been launched and have failed. The best example was the program in the USA between 1930 and 1965 aimed at eradicating the alternate host of white pine blister rust. There are, however, more positive examples such as the virtual eradication of Dutch elm disease from New Zealand.

Chemical control or protection to reduce the impact of tree diseases is not commonly used in forestry. This is due to the fact that forests represent extensive, ecologically sensitive environments where most fungicides cannot be used responsibly. There are, however, some examples of very effective chemical control of tree pathogens. One of the best of these is the regular chemical control of *Dothistroma* needle blight in countries such as New Zealand, Australia, and Chile. Chemicals or biological products are used to protect conifer stumps from infection by the root rot pathogen *H. annosum*, and chemical control in nurseries is commonly applied.

An effective and commonly used strategy to manage tree diseases is through avoidance. Avoiding disease can be achieved through silvicultural methods aimed at reducing inoculum. For example, the efficient removal of dying elm trees that are infested with insects carrying the Dutch elm disease pathogen can be effective. Avoidance of wounds on trees at the time when they are likely to become infected is also an effective means of reducing diseases such as for example oak wilt. Natural forests can also be managed in such a way as to favor certain species that are not susceptible to the pathogens present, or management can include the removal of alternate hosts such as scrub oak, in the case of fusiform rust.

In the future, we might expect many new opportunities to reduce the impact of diseases. For example, DNA based techniques for disease diagnoses are becoming increasingly available and are likely to play an important role in quarantine. Biological control has not been particularly effective in tree disease management in the past, but new advances at the molecular level, for example in the use of fungal virus associated hypovirulence, are also likely to emerge in the future. Genetic modification of trees is also likely to advance to a point where trees previously eliminated from the landscape, such as in the case of the American chestnut, might be reintroduced. Furthermore, it is likely that new and nondamaging fungicides will be discovered in the future and that these will contribute to reduction in the impact of tree diseases.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Pathology**: Diseases affecting Exotic Plantation Species; Heart Rot and Wood Decay; Insect Associated Tree Diseases; Leaf and Needle Diseases; *Phytophthora* Root Rot of Forest Trees; Pine Wilt and the Pine Wood Nematode; Root and Butt Rot Diseases; Rust Diseases; Stem Canker Diseases; Vascular Wilt Diseases. **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

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Root and Butt Rot Diseases

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Introduction

Diseases caused by root rots figure prominently amongst the most-studied pathologies of forest trees. Indeed, root and butt rots cause more economic damage to commercial forestry in the temperate world than any other known type of disease. While this notoriety underlines the negative impact of this type of disease on timber production, a much more dynamic and positive role can be assigned to root rots in natural ecosystems. Root rots are one of the driving forces ensuring spatial and temporal diversification of forests. While root rots as a whole encompass both generalistic and host-specific pathogens, aggressive primary microbes, and secondary opportunistic ones, their overall effect at the stand level is to accelerate, and sometimes cause, a patchiness in which some tree species are preferentially affected and weaker individuals culled. Because of their selectivity at the species and at the individual tree level, root diseases play a significant role in determining the structure and composition of a forest. Individual trees and/or clusters of individuals are taken out, and the gaps created allow for tree regeneration. Often, more resistant seral species will substitute the more susceptible pioneering species leading to forest succession. Ecotones between gaps and closed canopy offer rich and diverse habitats, home to a substantial amount of the local biodiversity. Finally, a further outcome of root rots is nutrient recycling: this is achieved by breaking down the chemically complex woody substrate in a synergistic activity with other wood decay fungi, bacteria, and wood-boring insects.

As stated above, concerns about root rots become serious when timber production is involved. Unfortunately, most habitat modifications, including but not limited to those related to logging, appear to increase the damage caused by root rots. In many cases, human activities allow for the establishment of or increase in root rots. Once disease is established, an irreversible process starts in which root rots will play a significant role in shaping the future of that forest. When root diseases affect ecosystems characterized by poor soils, limited host variability, or limiting climatic conditions, their impact may be significant even in the absence of further human activities.

Causal Agents of Root Rots: Establishment Strategies and Population Genetics

Root diseases can be caused by a wide range of organisms including oomycetes, ascomycetes, and basidiomycetes. Root and butt rots, instead, are exclusively caused by fungi belonging to the homobasidiomycetes. The three genera *Armillaria*, *Heterobasidion*, and *Phellinus* have broad worldwide distribution and probably are responsible for the majority of root diseases in temperate forests. Other less frequently encountered genera include *Inonotus* and *Phaeolus*.

All of the known root rotting organisms reproduce sexually. A fertile cell layer (called the hymenium) borne by the sexual fruit bodies of these fungi produces haploid meiospores. Hymenia can be porous or gilled (**Table 1**). Fruit bodies produced by root rot fungi can be an excellent diagnostic clue and include true mushrooms (*Armillaria*), bracket or shelflike conks (*Heterobasidion*), and relative inconspicuous resupinate fruit bodies entirely supported by the surface on which they are growing (*Phellinus weirii*) (**Table 1**). It should be noted that by the time the fruit bodies are produced, root rots are already in an