
MACROFUNGI ON WOODY SUBSTRATA

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GENERAL CONSIDERATIONS

Wood-inhabiting macrofungi inhabit substrata that differ in size, state of decay, and moisture content. Thus, the ecologies of fungi growing on wood differ. Wood-inhabiting species include fungi that were in or on the wood when a tree or tree part fell to the ground (e.g., pathogens and nonpathogenic endophytes of living tissue, heart rots), as well as the succession of fungi that follow in an organized fashion as the wood deteriorates.

In addition, many putative and known ectomycorrhizal species “climb up” on wood to fruit and simultaneously may obtain nutrients from the wood by degrading organic compounds (Read et al. 1989). Although we do not know how most wood-inhabiting ascomycetes function, some have been shown to be pathogens, endophytes, or saprobes. Thus, surveys of wood-inhabiting fungi will not be limited strictly to wood-decaying species (Figs. 8.32 and 8.33).

All of the decay fungi, to some degree, recycle lignocellulosic and mineral nutrients back into the ecosystem. In addition, their decay activities soften the woody tissues, making them more amenable to bird and small-mammal habitation and use by arthropods, nematodes, and other invertebrates as well as other fungi. It also has been shown that wood in advanced stages of decay on the ground is important for establishment of mycorrhizal associations with seedlings, and that decayed woody debris acts as a moisture sink for the maintenance of mycorrhizal fungi in seasonally dry forests (Harvey et al. 1978; Larsen et al. 1982; Jurgensen et al. 1986). In forests, brown-rot residues can be a major soil component. In standing trees, decay fungi can be root-, butt-, or heart-rot organisms, which are generally mutually exclusive. Those fungi cause decay of the roots and/or stems and thereby predispose the tree to wind throw or trunk breakage.

Different groups of wood-inhabiting fungi use quite different volumes of substratum (resource bases) for the production of sporocarps. Consequently, fungal sub-



FIGURE 8.32 Some of the macrofungi, such as *Armillaria tabescens* shown here, are plant pathogens. (Photo by G. Mueller)



FIGURE 8.33 Many of the large macrofungi, such as this species of *Volvariella*, are wood decomposers. (Photo by G. Mueller)

strata from tiny twigs to large trunks must be sampled if a majority of fungal species within the study area are to be found. The optimum size of employed plots or subplots will vary from one to several thousand square meters depending on the density of downed wood at a sampling site. In addition, live woody-stem and trunk substrata support conks or other fruit bodies arising from decaying parts of the tree or bark.

In general, gymnosperm hosts/substrata support a more restricted mycota than do angiosperm hosts/substrata (S. M. Huhndorf and H. H. Burdsall, personal observation). The numbers of species of wood-inhabiting fungi in a given area probably depends more on the range of decay classes of substrata than the number of species of phanerogams present because the majority of those fungi probably are not particularly host-genus or host-species specific.

Although numerous standardized surveys have been conducted on terrestrial macrofungi, few have been conducted on the inhabitants of wood. Examples of surveys of wood-inhabiting fungi include the studies of Scandinavian pyrenomycetes (Mathiassen 1993); wood-rotting basidiomycetes (Renvall 1995); and basidiomycetes, ascomycetes, and slime molds (Heilmann-Claussen 2001). Ryvarden and Nuñez (1992) and Lindblad (2000, 2001) studied polypores in the tropics, and Heinrich and Wojewoda (1976) studied the effects of air pollution on basidiomycetes. Additional references are available in Vogt and associates (1992).

Mycodiversity, as with all other subsets of biodiversity, exhibits distinct patterns in both space and time. Such fungal patterns are to a large extent unexplored, as evidenced by the almost complete lack of mycological examples in the increasing body of biodiversity literature

(see Rosenzweig 1995 for a comprehensive and taxonomically broad treatment of species richness patterns). A number of ecological and evolutionary questions related to wood-inhabiting fungi need investigation. A sample of such questions follows:

- What are the shapes of the species-area curves of wood-inhabiting fungi in various environments or on woody substrata of different size and decay class?
- How do habitat variety and woody-plant diversity affect mycodiversity?
- How do forest productivity and substratum abundance influence mycodiversity?
- Does the local species richness of wood-inhabiting fungi exhibit mainland-island patterns?
- Does the species richness of wood-inhabiting fungi follow a latitudinal gradient, as is found in many other taxa (low latitudes being richer)?
- How does sporocarp production (sexual reproduction) vary within and between years?
- How do species composition and richness change through the course of decay?
- How do natural disturbances, such as hurricanes and fires, perturb species composition and richness patterns?
- How do anthropogenic disturbances, such as logging and wood removal, affect diversity of wood-inhabiting fungi?

ISSUES OF IMPORTANCE WHEN DESIGNING SAMPLING PROTOCOLS

In the following section we cover concepts specific to studies concerned with sampling macrofungi found on woody substrata. The material supplements the general information presented in the next section ("Approaches to Sampling Macrofungi").

As with other groups of macrofungi, the number of species of fungi on wood increases with the size of the area sampled, or more specifically, the amount of substratum sampled. The distribution and amount of substratum present therefore will dictate the size of the area to be sampled at a particular site. Small-size woody debris generally is encountered much more frequently than large-diameter wood. Thus, the area that must be searched to obtain an adequate sample of macrofungi will depend on the distribution and frequency of the different diameter classes of downed wood, as well as the frequency of the fungi under study. Discovery of cryptic fungi is often aided by more intensive searching of designated sampling areas or subplots. Fungi fruiting on large-diameter wood (logs and standing-live and stand-

ing-dead trees) are easily undersampled if collecting is confined to small subplots because of the low density of large pieces of wood in those subplots and because few of those large pieces will be in the right stage of decay to support fungal fruiting. For a complete survey of macrofungi on all classes of woody debris, we recommend augmenting small subplot-based samples of small debris with another method for surveying many large pieces of wood. Even when many logs were surveyed for macrofungi in Scandinavia, the species-substrata curve did not reach an asymptote, indicating that many more species would be discovered if additional logs were sampled (Fig. 8.34; Lindblad 1998). Had those samples been stratified by diameter class, decay class, or tree species, however, they might have produced flattened species-substrata curves within strata. Aggregating samples from different habitats tends to produce steadily increasing species-effort curves. A gradient analysis of communities of macrofungi and slime molds on beech logs of different ages and decay classes in Denmark (Heilmann-Clausen 2001) showed that the correlated factors of age, decay stage, and contact with soil, together with microenvironmental variables such as exposure to sun, moss cover, and soil moisture were the most strongly correlated with community structure. Studies in Puerto Rico have indicated that diameter class and microclimate are among the most important factors influencing wood-inhabiting macrofungal community

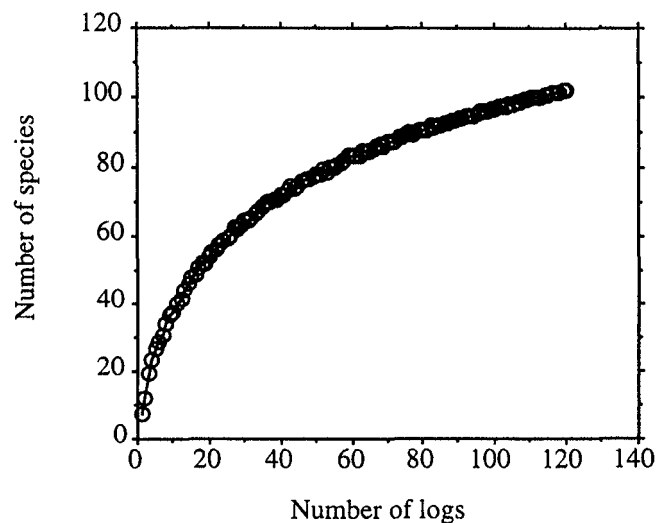


FIGURE 8.34 This graph shows the positive correlation of cumulative species diversity with substratum quantity. The number of macrofungal species (Polypores, Corticiums, Agarics, Heterobasidiomycetes, Hymenochaetaceae, and a few other groups) are plotted as a function of substratum quantity (dead logs of *Alnus*). Each point represents an average of 100 random samples drawn from a pool of 150 logs inspected twice in a Norwegian study area. (Adapted with permission from Kauserud 1995.)

composition in tropical climates (Lodge and Cantrell 1995b; Lodge 1996; S. M. Huhndorf and D. J. Lodge, unpublished data). Inspection of higher reaches of trees may add new species, but most of the canopy species probably also will be found on fallen branches or in gaps (Ryvarden and Nuñez 1992; Lodge and Cantrell 1995b).

INCONSPICUOUS AND INDISTINGUISHABLE SPECIES

Two main problems arise when sampling fungi on wood. First, many resupinates, inconspicuous basidiomycetes, and small ascomycetes either are not detectable or not recognizable in the field. That problem can be resolved by removing all woody substrata to the laboratory for examination. Although doing so precludes resampling of the same subplot, that problem can be solved, as discussed later. Second, it frequently is difficult to determine whether or not a species has been collected already, either within a subplot during one sampling or in previous samplings. More than one individual of a species may be taken from one piece of substratum when only one is intended because different stages of maturity of some species are difficult to recognize. However, some species look so similar in the field that species may be missed. No assumptions should be made regarding the identity of the small ascomycetes and other inconspicuous fungi, and all separate patches of those fungi should be collected.

PLOT SIZE

Small to Medium-Size Woody Debris

Collecting macrofungi in randomly or regularly spaced subplots is an effective way to sample fungi on small to medium-size (1.0–15.0-cm diameter) woody debris. The investigator examines each piece of debris or stem for macrofungi that produce recognizable fruiting structures and collects one specimen of every species from each piece of substratum within the plot. The data outlined later in this chapter (see “Data Collection”) are recorded for each specimen. Portions of hosts or substrata that protrude into a subplot also are sampled. Samples of each species present on each class of substratum should be sufficient to enable identification. After sampling, a substratum should be returned to its original position for future sampling. Substrata from which specimens are taken may be tagged for future recognition. For fungi that cannot be seen easily or distinguished to morphospecies with the naked eye, all woody debris should be

collected from a subplot for examination under a dissecting microscope. Small ascomycetes and resupinate heterobasidiomycetes fruiting on small woody debris are examples of taxa that require such destructive sampling. If the subplots are to be sampled repeatedly, they should be divided into halves or quadrants so that debris is collected from each sector only once. Subplots should be sampled throughout the growing season.

A few forests have been surveyed and gridded in such a way that grid cells may be selected as sample plots, but new plots will need to be established for most studies. Circular plots are usually the most efficient to set up and sample. The precisely oriented, 90-degree corners of square plots are unnecessary, and the only required equipment is a string premeasured to the desired radius extending from a center pole. The diameter of the plots depends on the density of fallen wood in the diameter classes of interest and the type of fungi under study. For example, although detecting small ascomycetes on branches and twigs is difficult, those fungi have been sampled successfully using 0.5-m² circular plots positioned at the central core of larger plots (S. M. Huhndorf, personal observation). Plots 10 m in diameter can be used to sample medium-size pieces of wood, although larger plots may be needed if fallen branches are rare. The practical upper limit for the diameter of a circle plots is between 10 and 20 m (78.5–314 m²).

Large Woody Debris, Standing Trees, and Recent Treefalls

It is often advantageous to use large woody substrata or dead trees instead of plots as the sample units for fungi that fruit on those types of substrata. A fallen tree or log can be sampled for visible fruiting structures from base to top, and the location of each specimen and the type and decay class of the tree or log noted. Specimen collection sites can be tagged or mapped and resampled periodically.

If plots or subplots for sampling fungi on small debris are set up along transect lines, sample units can be selected and density of large fallen or standing-dead trees in the area estimated using the point quarter method (Cottam and Curtis 1956). In that technique, points are identified along the transect line at distances selected using a random numbers table. Then, the distance from each point to the base of the nearest fallen log or dead tree in the northwest, northeast, southeast, and southwest quarters is measured. Those distances are used to calculate density of standing or fallen trees. Recording the diameters and heights or lengths of the trees and logs and the compass orientation on which they fell is useful for relocating them. Alternatively, if the forest is gridded, or if parallel transect lines are established at regular inter-

vals, then the locations of large woody debris, tree falls, and snags can be mapped. If the sampling area is large, global positioning systems (GPS) can be used to identify the locations of logs and dead trees, and locations can be mapped using latitude and longitude in a geographic information system (GIS). Logs to be sampled are selected from the mapped ones. One or more of the recently developed adaptive sampling protocols (see “Adaptive Sampling,” later in this chapter) may prove useful when sampling those relatively rare substrata (Thompson 1992; Thompson and Seber 1996).

FREQUENCY OF SAMPLING

How often a plot should be sampled depends on the amount of species turnover between sampling dates (see discussion of complementarity under “Determining Adequate Sampling,” later in this chapter, and in Colwell and Coddington 1994). For Xylariaceae and small ascomycetes in the tropics, 3-month sampling intervals appear to provide optimal balance between discovery of previously unrecorded species and sampling effort. Turnover in fruiting agaric species is high in both temperate and tropical forests such that these species should be sampled at weekly or biweekly intervals. Corticioid and polypore fungi, however, may be sampled at approximately 2-month intervals (H. H. Burdsall and D. J. Lodge, personal observation).

DATA COLLECTION

In addition to date of sampling, macrohabitat information (e.g., forest type, plant association, climatic zone, elevation), host, plot number, and other standard collection data, the following information should be collected when sampling from woody substrata:

1. Substratum/host class: information on substratum type (e.g., trunk, branch, twig, stump, or root), condition (e.g., living, dead, or dead on living plant), and position (e.g., vertical, $>60^{\circ}$ – 90° ; prostrate; on ground; or suspended (<1 m or >1 m above ground)).
2. Substratum preference(s) (from Mathiassen 1993): where the fungus is fruiting, for example, on wood only (W), mainly on wood but some on bark (Wb), equally frequent on wood and bark (wb), mainly on bark but some on wood (Bw), or on bark only (B).
3. Substratum size class: diameter of the substratum, using the following size classes: less than 1.0 cm, 1.0–2.5 cm, 2.6–5.0 cm, 5.1–10 cm, 10.1–20 cm, or more than 20 cm.
4. Decay class: condition of the wood; for example, as hard and not decayed; hard but decayed and either discolored or not; softened and punky (light weight, fibrous, spongy; this condition is termed white rot); well decayed (humus-like; dark; friable or, if the remaining wood is primarily of lignin, breaking into small hard blocks; this condition is termed brown rot).
5. Condition of bark: tight, loose, or off.

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Front cover: The slime mold *Physarum roseum* on a decaying leaf. Slime molds are fungal-like organisms traditionally studied by mycologists. Photo by Ray Simons.

Back cover: A species of *Mycena* found in Yunnan, China. Species of the mushroom genus *Mycena* are commonly encountered throughout the world. Photo by Gregory M. Mueller.