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Canopy Microfungi: Function and Diversity

Abstract

Microfungi are an inconspicuous but important component of the biota of forest canopies. Within canopies, microfungi are found inhabiting living and dead foliage, bark, and wood, and are also associated with canopy epiphytes and arthropods. As epiphytes on foliage and twigs, microfungi serve to concentrate dilute organic nutrients. Biomass and annual production by epiphytic microfungi can approach 500 kg/ha and may represent a significant food resource for microarthropods. Saprotrophic decomposers contribute to in situ decomposition of perched litter. Fungal endophytes occupy healthy, asymptomatic foliage and stems. Some of these fungi also produce compounds antagonistic to insect herbivores. Canopy microfungi may also provide a minor link between soil and aquatic food webs as early colonists of live foliage and twigs that complete their sporulation cycles in soil or streams and as a portion of annual aboveground production that is assimilated in soil as litterfall. The varied components and functions of canopies with which microfungi are associated suggest that biodiversity of the microfungi biota is high and potentially a rich source of novel taxa.

Introduction

The canopies of mature, old growth forest trees present a complex, multilayered habitat that supports a rich and varied community of organisms. Microfungi are an integral component of this community, interacting in a variety of ways with the host tree as well as the other organisms that together comprise the canopy community. For two of the authors (JKS, MAS), investigating the fascinating, complex roles of fungi in the forest canopy provided an early introduction and apprenticeship in mycology that became a lifetime career interest. Microfungi in canopies are more than objects of biological curiosity, however; they play important ecological roles in mature forests: nutrient cycling, symbioses with canopy epiphytes, and symbioses and trophic interactions with arthropods and other canopy microfauna.

Much fundamental information on the roles of fungi in canopies remains fragmentary, a problem that presents many opportunities for new and significant discoveries. Microfungi in canopies form a variety of direct associations with the host trees, colonizing foliar and twig surfaces (epiphytes), internal foliage (foliar endophytes), young and old bark (bark endophytes) and wood (xylem endophytes and wood decomposers). The distribution and diversity of microfungi in forest

canopies is also influenced by epiphytic cryptogams, phanerogams, and arthropods and other canopy animals, which also interact in a variety of associations with canopy microfungi. Decomposition and nutrient cycling processes (such as in situ epiphyte decomposition, dead limbs, lodged needles, perched soil) occur within canopies, but little information has been published on these processes and the roles of microfungi in them. Although many species are uniquely adapted to biotic functions and conditions specific to the canopy habitat, the total canopy mycobiota also includes species with widespread terrestrial distribution. More intensive investigations will undoubtedly reveal a multitude of specialized, highly adapted endemic microfungi, and inevitably many new taxa.

Diversity of microfungi occurs at an exceedingly small scale—a single conifer needle may harbor several dozen different species externally and internally. Although microfungi are ubiquitous in nature, they typically are inconspicuous: usually they are present as internal, unseen, microscopic hyphae and their presence is revealed externally only when they sporulate, usually seasonally and typically ephemeral. Many are highly host- or substrate-specific. Conventional sampling methods of vegetation ecology are inadequate to

accurately enumerate microfungi, and the details of distributions of even the more familiar taxa remain sketchy. Laborious isolation procedures are generally required to detect and quantify them. Identification requires microscopic examination, and generally requires a high degree of expertise. Often identification is difficult or impossible with isolates in pure culture that fail to produce spores or identifiable structures. Conversely, certain groups do not grow or sporulate in culture (e.g., Metacapnodiales), and must be detected visually on host substrates. A particular obstacle to ecological studies of canopy fungi is that often basic taxonomic information is lacking or insufficient. This problem can only partially be overcome by integrating existing databases—fundamental biological survey work is also needed. Differentiation of individuals of a fungus species adds yet another level of complexity. Because of the ability of fungal hyphae to anastomose and become multinucleate, and the ability of many fungi to reproduce asexually, enumeration of individuals often can only be accomplished using specialized techniques of molecular genetics.

Foliar and Twig Epiphytes

Communities of epiphytic fungi in canopies develop as a result of the same types of biotic and abiotic interactions at play on non-arboreal substrates, with the exception that new uncolonized substrates are predictably and regularly added by new seasonal growth. Foliar and bark surfaces provide substrates that support characteristic assemblages of specialized microepiphytes that undergo changes in species composition and biomass as the substrates age. Particularly in more mesic habitats, microepiphyte assemblages can become well developed, especially on evergreen foliage and twigs, where they may attain a substantial biomass and annual productivity. Carroll (1979) estimated biomass of fungal foliar epiphytes in an old-growth Douglas-fir forest at 30 kg/ha, and Carroll et al. (1980) estimated fungal twig microepiphyte biomass at 12-20 kg/ha. Annual production of fungi on combined twigs and needle surfaces was estimated to be 450 kg/ha. (Carroll et al. 1980).

Although mesic, foliar surfaces experience extremes of temperature and desiccation seasonally and diurnally. Epiphytic fungi are adapted to xeric conditions and low levels of nutrients that

are either leached from foliage or intercepted in rainfall. Most fungi in exposed habitats have melanized hyphal walls, grow sporadically in response to temporally favorable conditions, and are specialized to withstand exposure and desiccation. Needle surfaces typically are colonized by familiar, ubiquitous epiphytes common on many plants: such genera as *Epicoccum*, *Alternaria*, and *Hormonema*. *Atichia millardetii* Racib., the anamorph of *Seuratia millardetii* (Racib.) Meeker, a loculoascomycete that grows as a yeast-like mass in a gelatinous matrix, is a dominant epiphytic species on twigs and needles of several conifers in the Pacific Northwest (Carroll et al. 1980). On some hosts, sooty molds (*Capnodium*, *Metacapnodium*) occur in association with scale insects and are nourished by exuded honeydew (Hughes 1976).

On conifers, such as Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), the topology of needle surfaces influences distribution of microepiphytes, with greater colonization near the needle midrib, near stomata, and along the margins of anticlinal cell walls (Bernstein and Carroll 1977; Carroll 1979). Microbial biomass tends to increase with needle age through the first three years. In this exposed habitat, these fungi are also available as a food resource to grazing microarthropods, such as oribatid mites, and grazing may help explain the decreases in microbial biomass observed on older needles. Distribution of microepiphytes also tends to decrease with increasing height in the canopy (Carroll 1979). Microbial biomass on twigs similarly increases with age (Carroll et al. 1980).

Specialized Parasites and Pathogens

Common microfungi parasites and pathogens of foliage and twigs of northwestern conifers are described in detail in Funk (1981, 1985). A recent host index (Farr et al. 1989) lists approximately 80 species of microascomycetes, 50 species of hyphomycetes, and 30 species of coelomycetes associated with the foliage and twigs of Douglas-fir alone in the Pacific Northwest. This list should be considered partial because routine isolations from Douglas-fir and other conifer hosts often yield taxa not listed (Stone, unpublished). Endemic pathogens are not uncommon in the foliage of mature trees, but they often have disjunct distributions, apparently affected by site factors and individual host genetic susceptibility.

Phaeocryptopus gaeumannii (T. Rohde) Petr. and *Rhizosphaera kalkhoffii* Bubák, for example, are commonly found infecting a proportion of the needles of mature Douglas-fir trees, but their effects are not often serious unless other sources of stress, such as drought or cold injury, are involved. In young plantations and non site-adapted genotypes, however, these fungi can cause serious defoliation.

Another group of foliar fungi are primarily superficial but also invade the inner spaces of foliage. Such colonization may be confined to stomatal chambers or may involve extensive intercellular hyphae in mesophyll parenchyma. Microthyriales or "fly speck" fungi have flattened, shield-like ascomata produced on living needles. Black mildews, such as *Meliola*, *Asteridiella*, and *Rasutoria*, are typically superficial, but sometimes produce hyphae that enter needles at the stomata or pierce epidermal cells. Again, presumably because of the exposed habitat, the hyphae of these fungi are melanized. *Phaeocryptopus gaeumannii* commonly infects needles of Douglas-fir and produces extensive superficial and internal hyphae (Stone and Carroll 1986).

Foliar Endophytes

Fungal colonization of internal tissue of apparently healthy foliage, particularly of plants with evergreen or long-lived foliage, has been well documented. Such endophytes are a ubiquitous, ecologically specialized group of symbiotic fungi and are widely assumed to be present in virtually all land plants (Carroll 1988). Inhibition of herbivory by toxic alkaloids produced by endophytes infecting certain grasses has been demonstrated (reviewed by Clay 1988), and forms the basis of a mutualistic symbiosis in these hosts. Several fungus species isolated as endophytes from coniferous foliage and bark also have been shown to produce biologically active compounds (Bills et al. 1992; Polishook et al. 1993; Stierle et al. 1993), including compounds toxic to defoliating insects such as spruce budworm (Calhoun et al. 1992.). Several of these endophyte associations are also believed to be antagonistic to insect herbivores (Carroll 1991), although endophytes encompass a variety of ecological roles (Stone et al. 1994).

Endophyte species comprise an ecological assemblage that is distinct from saprophytic epi-

phytes and decomposers. Many are host specific or have restricted host distributions, but a few species with broad host ranges are often recovered from foliage at low frequencies. *Phyllosticta abietis* Bissett & Palm is the most common endophyte of *Abies* spp. in the Pacific Northwest, and also occurs on Douglas-fir. *Pleuoplaconema* sp., possibly the anamorph of *Chloroscypha chloromela* (Philips & Harkn.) Seaver, is the most common endophyte of *Sequoia sempervirens* (D. Don) Endl. (Espinosa-Garcia and Langenheim 1990, Rollinger and Langenheim 1993), and occurs as a dominant endophytic colonist throughout the natural range of the redwood (Rollinger and Langenheim 1993). *Rhabdocline parkeri* Sherw., Stone & Carroll, the most common foliar endophyte of Douglas-fir, is benign, but its congeners *R. pseudotsugae* Syd. and *R. weirii* Parker & Reid are defoliating pathogens of Douglas-fir (Sherwood-Pike et al. 1986). Several genera are recurrently isolated as endophytes from a variety of conifer hosts, including: *Phomopsis*, *Cryptosporiopsis*, *Cryptocline*, *Phyllosticta*, *Seiridium*, *Geniculisporium*, and *Nodulisporium*. Assemblages of foliar endophytes have been examined in several conifer hosts in the Pacific Northwest (Carroll and Carroll 1978; Petrini and Carroll 1981; Espinosa-Garcia and Langenheim 1990), and in the eastern United States (Bills and Polishook 1992).

Little is known of the details of colonization of foliage by endophytes. In species that have been studied, colonization is restricted to minute, limited portions of tissue in the epidermis or mesophyll. *Phyllosticta concentrica* Sacc. on *Taxus* spp. is apparently only subcuticular, whereas *P. abietis* on Douglas-fir and *Abies* spp. form limited intercellular infections within the mesophyll (Stone 1993). Infections of *Rhabdocline parkeri* are confined to single epidermal cells in healthy needles, but colonize extensively and sporulate on galls of the midge *Contarinia pseudotsugae* Condrashoff and also senescent and abscised needles (Sherwood-Pike et al. 1986; Stone 1987). Similar intracellular endophyte infections have also been observed for an unidentified endophyte in *Sequoia sempervirens* (J. K. Stone, unpublished). Endophyte infection densities and species richness increase with foliage age (Stone 1987; Espinosa-Garcia and Langenheim 1990). Douglas-fir needles are repeatedly infected by *R. parkeri* as they age (Stone 1987). Because *R. parkeri* occurs

as discreet, separate infection loci, the number of individual infections per needle can be counted and the total per tree estimated. McCutcheon et al. (1993) conservatively estimate the number of infections by *R. parkeri* in a single tree to be on the order of 10^{11} .

An endophytic habit similar to *R. parkeri* may be widespread in the Ascomycete family Hemiphaciaceae. In the Pacific Northwest, *Didymascella thujina* (Durand) Maire, with its spotty distribution on dead needles on otherwise healthy branches of *Thuja*, is suspect; a better example would be *Fabrella tsugae* (Farl.) Kirschst. on eastern hemlock. This species can be reliably found in late winter on the oldest needles still attached to healthy hemlock trees; its appearance coincides with normal senescence. Most endophytes of conifers apparently cease growth soon after initial infection and remain quiescent until natural needle senescence or injury cause active growth to resume. These fungi have a competitive advantage in occupying foliage just prior to abscission, and are in a position to intercept translocated metabolites. As early colonists, they are also first in possession of the abscised needles and may be considered the first sere in the succession of decomposers (Stone 1987).

Bark endophytes

Many species of fungi colonize living bark on twigs and small branches of coniferous trees, but almost nothing is known of their biology. Resinous young bark of Douglas-fir generally supports *Arthopyrenia plumbaria* (Stitzenb. in Hasse) R. C. Harris and other non-lichenized members of the Arthopyreniaceae including *Mycoglaena subcoerulescens* (Nyl.) Höhn. (= *Winteria coerulea* (Ellis & Everh.) Berl & Voglino) and *Mycoglaena* sp. ("*Pseudoplea*"). *Arthopyrenia plumbaria* also occurs on red alder and other smooth-barked trees. In eastern North America, another non-lichenized member of a normally lichenized genus, *Arthonia impolita* (Hoffm.) Borrer, is ubiquitous on young bark of *Pinus strobus*. *Vestigium felicis* Piroz. & Shoem., an unusual coelomycete with "cat's paw" shaped conidia, is known only from young living twigs of *Thuja plicata* Donn ex D. Don in the Pacific Northwest (Pirozynski and Shoemaker 1972).

Ascomycetes that fruit on recently dead twigs still attached to otherwise healthy trees—notably,

members of the Hypodermataceae, but also including *Lachnellula* spp. (Hyaloscyphaceae)—are prominent on living conifers in the Pacific Northwest. *Tryblidiopsis pinastri* (Pers.:Fr.) P. Karsten, a common circumboreal species which in our area occurs on *Picea engelmannii* Parry ex Engelm., and *Discocainia treleasei* (Sacc.) J. Reid & Funk, on *P. sitchensis* (Bong.) Carrière, are representative. Both fruit in abundance in the spring on twigs that have been dead for less than a year, and thus must be suspected of routinely colonizing bark of living twigs. Other species whose biology appears to be similar are *Therrya pini* (Albertini & Schwien.) Höhn. and *T. fückelii* (Rehm) Kujala on *Pinus* spp., *Coccomyces strobil* J. Reid & Cain on *P. strobus* L., *Coccomyces heterophyllae* Funk on *Tsuga heterophylla* (Raf.) Sarg., and *Lachnellula ciliata* Dennis and *L. agasizii* (Berk. & Curtis) Dennis on *P. menziesii* and *Abies* spp., respectively. Live bark is apparently also the habitat of *Taxomyces andreanae* Strobel, Stierle, & Hess (Strobel et al. 1993), which has helped focus attention on the commercial potential of endophytes by virtue of its reported ability to produce the anticancer agent taxol *in vitro* (Stierle et al. 1993).

Bark endophytes, which then become the first successional species in the decomposition of dead branches (a process which in some conifer species proceeds to an advanced stage before the material falls to the forest floor), are potentially important in canopy ecology. Perhaps, for example, their presence excludes aggressive generalists that are actively pathogenic. On the other hand, all of the above species figure in lists of disease-causing fungi and can be found fruiting in abundance on diseased and dying trees, although generally (perhaps invariably) these trees are already severely weakened by other causes. The well-adapted parasite that is neutral or even beneficial under natural conditions can always become a serious problem in a stressed community, in artificial monoculture, when trees are introduced outside their normal range, and when closely related hosts from different parts of the world are brought into contact.

Xylotropic endophytes, fungi that are early colonists of sound wood, are another similar, apparently widespread group, although coniferous hosts from the Pacific Northwest apparently have not been examined for their presence. In Europe, healthy, attached branches of oak and beech

(Chapela and Boddy 1988; Boddy 1992), *Alnus* spp. (Fisher and Petrini 1990), and conifers (Sieber 1989; Kowalski and Kehr 1992), and in North America beech and aspen (Chapela 1989) are endophytically colonized by a mycobiota characteristic for each host (Chapela 1989). As with foliar endophytes, these fungi form disjunct, quiescent infections in healthy wood and resume active growth and eventually sporulate in response to drying of the substrate (Chapela 1989; Boddy 1992). Xylotropic and foliar endophytes have analogous life-history strategies that involve establishing early infections followed by a prolonged period of interrupted growth, which enables immediate invasion and saprophytic exploitation of the substrate at the onset of physiological stress or senescence. Facultative pathogens, such as *Hypoxyylon mammatum* (Wahlenberg) J. H. Miller on aspen, as well as many wood decay fungi, are adapted to this strategy of early endophytic occupation.

Potential Sources of New Taxa

Colonists of Epiphytic Plants

Paradoxically, although the lichen flora of the Pacific Northwest is rich in terms of both species and biomass, lichenicolous fungi from the Pacific Northwest are underrepresented in the literature. This region has apparently not been systematically sampled or investigated, and only scattered collections exist. In Europe, for example, where lichenicolous ascomycetes have been more intensively studied, a rich and diverse mycobiota is known to be specifically associated with lichens (e.g. Hawksworth 1983). Judging from the relative ease of finding parasitised lichen thalli in our area, almost certainly a large reservoir of novel species or species not known from North America await discovery in the Pacific Northwest. Lichenicolous species are well represented in the Hypocreales and Dothideales and related mitosporic genera—orders that also contain numerous fungicolous species. Approximately ten genera of hyphomycetes and roughly an equal number of coelomycete genera are obligately lichenicolous (Hawksworth 1981). Recently, Diederich and Christiansen (1994) have identified the cause of galls common on *Usnea* spp. in the Pacific Northwest as an unusual Basidiomycete related to the Tremellales (“jelly fungi”). Other gall-like bodies on Lecanorales are also apparently caused by undescribed heterobasidiomycetes

(Diederich 1990). Related lichenicolous *Tremella* spp. have been described (e.g., *T. coppinsii* Diederich & Marson on *Platismatia* spp.) and others are known to be mycoparasites of wood decomposing fungi, e.g., *Stereum*, *Peniophora* (Zugmaier et al. 1994). Some endemic species in the Pacific Northwest are *Lethariicola sipei* Grumm. on *Letharia* spp., and *Nanostictis pseudocypbellariae* Sherwood on *Pseudocypbellaria* spp. (Sherwood-Pike 1985, 1987). In addition to lichen parasites, fungal agents of in situ lichen decomposition comprise a distinct assemblage for which virtually no published information exists. Because of the specialized nature of the substrate, a highly adapted mycobiota associated with lichen decomposition is probable.

Epiphytic mosses and hepatics present another intriguing host association. Recently Weber (1995) has rediscovered *Selenospora guernisacii* (P. & H. Crouan) R. Heim & LeGal, an inconspicuous discomycete, associated with mosses in the Pacific Northwest. Döbbler (1979) has reported pyrenocarpous and pezizalean parasites of mosses in Europe. Hepatics, similarly, are known to form symbiotic intracellular associations with endophytic fungi (endomycorrhalli) in the gametophytes. Fungi belonging to Ascomycetes, Basidiomycetes, and Zygomycetes have been reported from these hosts, in a range of cytological specializations ranging from simple to complex (Pocock and Duckett 1985a,b). Arboreal mosses and hepatics may not harbor species distinct from the terrestrial habitat, but they represent a category of host well represented in mature conifer canopies, which almost certainly harbor a specialized mycobiota where new taxa might predictably be sought.

Canopy epiphytes also harbor several associated microscopic protozoa and small animals that are parasitized by specialized fungi. In recent years, discoveries of new taxa (genera and species) of fungal predators and parasites of rotifers, amoebae, nematodes, tardigrades, springtails, and other organisms have flourished. Most habitats where these animals exist, e.g. moss, rotting wood, leaf mold, have also yielded new and interesting fungal predators and parasites (Drechsler 1944; Barron 1981, 1991; Barron et al. 1990; Barron and Szijarto 1990), although relatively few groups are working on them worldwide. Ascomycetes, Basidiomycetes, Zygomycetes, and Oomycetes are represented in predators and parasites of protozoa and small animals. These fungi display an aston-

ishing degree of specialized adaptations for capture and penetration of prey species, and constitute one of the better examples of adaptive radiation in the fungi. A number of *Nematoctonus* anamorphs of Hymenomycetes such as *Hohenbuehelia* and *Pleurotus* are known to form traps for capturing nematodes (Thorn and Barron 1984), presumably an adaptation of cellulose decomposers to the low nitrogen content of the substrate (Barron 1992). Again, careful examination of canopy habitats is almost certain to add novel taxa in this group.

Interactions with Canopy Arthropods

Coniferous canopies in the Pacific Northwest are rich in arthropod species. Voegtlin (1982) reported approximately 1500 taxa from the canopies of old-growth Douglas-fir, and concluded that Douglas-fir canopies supported the greatest diversity of arthropods of any canopy system studied to date. Few of the species reported were endemic, i.e. having their entire life cycle completed in the canopy; those that are endemic are primarily mites, Collembola, and Psocoptera. The literature on arthropod—fungus interactions is enormous and beyond the scope of this paper to review, but we should at least point out that the propensity for fungi to form complex, specialized associations with insects is ancient and fundamental. Detailed reviews of fungus—arthropod interactions can be found in Batra (1979) and Wheeler and Blackwell (1984). Again, unfortunately, published information specific to the canopy habitat is almost completely lacking.

It is almost axiomatic that wherever a high degree of arthropod diversity exists, a corresponding diversity of associated fungi will be found, although many of the fungal groups that form close symbioses with insects are among the poorest documented taxonomically. The Laboulbeniales, for example, is an order of obligate ectoparasites of insects and mites and spiders (reviewed by Weir and Beakes 1995). While many genera and species of Laboulbeniales have broad host distributions, a few species have sex- and even positional specificity (Benjamin 1971). Although the Laboulbeniales, with around 2000 species, is one of the most speciose orders of Ascomycetes and is probably the largest and most highly specialized group of entomogenous fungi, only a fraction of the potential hosts have been examined, and thus the number of undescribed species is a

matter of conjecture. The Trichomycetes, a similarly neglected group of Zygomycetes, are obligate commensals or parasites found in the digestive tracts of arthropods (Moss 1979). An example of insect-fungus interaction more typical of tree-tops is that between the woodboring Scolytid beetles, which actively cultivate and are nutritionally dependent upon “ambrosia fungi,” a diverse assemblage of anamorphic Ascomycetes. The beetles have specialized anatomical structures (mycangia) for establishing new fungal cultures when a new woody substrate is invaded (Norris 1979). Vectoring of pathogenic fungi by insects is one of the better understood and most ecologically important fungus-insect interactions involving forest trees, for example vectoring Ophiostomatoid fungi by *Dendroctonus* and *Scolytus* beetles (see Harrington, 1993; Malloch and Blackwell, 1993).

Aquatic Hyphomycetes in Lodged Litter

Conidia of aquatic hyphomycetes, mitosporic fungi with tetra- or sigmoid conidia specialized for aquatic dispersal, are typically associated with senescent and decaying leaf litter from trees growing near rapidly flowing streams (Webster 1981). Conidia characteristic of these fungi also are commonly recovered from rainfall samples collected beneath mature canopies from upland sites far from streams in Oregon (G. C. Carroll, unpublished). Sigmoid, helicoid, tetra- or radiate, and branched conidia representing several anamorph genera, have been collected from rainwashed trunks of several tree species in the Pacific Northwest (Bandoni 1981). While many of the conidia thus collected can be readily assigned to existing genera and species, e.g. *Gyoeffella biappendiculata* (Arnold) Ingold, apparently undescribed taxa are not uncommon in rainfall samples. Different species seem to occur in association with different host trees, but the source of the conidia and the ecological role of these fungi in the canopy remains enigmatic. Lodged leaves and debris are a probable source. Ando (1992) has shown that some “terrestrial aquatic hyphomycetes” are endophytic leaf colonists or parasites that sporulate ephemerally in surface condensation of leaves.

Fungi on Standing Dead Wood

Depending on the species, coniferous trees may support a large volume of dead branches in the canopy, particularly at high elevations. This aerial

niche supports a diverse assemblage of unusual fungi, whose adaptations and taxonomic diversity have been discussed in detail by Sherwood (1981). Three species predominate on standing dead coniferous wood at high elevations; *Agryrium rufum* (Pers.) Fr., an unusual non-lichenized member of the Lecanorales whose closest relatives are resinicolous fungi, also occurring on living conifers; *Xylopezia hemisphaerica* (Fr.) Höhn., a taxonomically isolated loculoascomycete, and *Cryptodiscus pallidus* (Pers.:Fr.) Corda (Ostropales). Also common in this habitat are *Durella atrocyanea* (Fr.) Höhn., *Propolis* spp., *Melittosporium propolidioides* (Rehm) Rehm, *Stictis* spp., *Mycocalicium* spp., and Odontotremataceae. This habitat is unusually rich in taxa (genera and families) that include both lichenized and non-lichenized species. Basidiomycetes are not prominent in the known mycobiota on small standing dead-woody coniferous material in the Pacific Northwest. It seems improbable that Basidiomycetes are actually as little represented in nature as our present knowledge suggests. At high elevations and drier areas aerial decomposition is clearly a lengthy process providing a stable niche with considerable spatial and temporal differentiation.

Specificity to old-growth?

Many of the species included in this discussion are known from only a few collections, so that any generalizations about their specificity to undisturbed sites must necessarily be speculative. Clearly, a host-specific fungus growing only on a rare species confined to undisturbed sites is

threatened if its host is threatened. The importance of leaving some proportion of dead wood in managed forests is increasingly recognized, which should have a positive effect on preserving uncommon species of lignicolous fungi. Most of the fungus species mentioned also occur in mature second growth within the normal geographic range of the host species.

Besides the possibility of harboring unique microfungal species, old-growth stands and individual trees may also represent a large reservoir of infraspecific genotypic diversity. McCutcheon et al. (1993) provide evidence that the foliage of old-growth trees supports a large diversity of genotypes of the endophyte *Rhabdocline parkeri*, and showed that the number of unique genotypes of *R. parkeri* infecting young trees in managed stands in close proximity to old-growth stands was similar to that of the old-growth trees but much greater than in managed stands of similar age farther away from old-growth trees. A tree from an isolated site had the fewest *R. parkeri* strains. For microfungi such as *R. parkeri*, old-growth trees represent an archive of genetic diversity. Carroll (1988) has suggested that genotypic diversity of an endophyte may help confer acquired resistance against herbivorous insects to the host tree through the combined activity of a variety of antagonistic metabolites produced by the fungus. The canopy microfungi of isolated trees, urban plantings, and trees growing outside their normal range is quite different from that occurring naturally.

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