What Do We Know about Fungi in Yellowstone National Park?

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C. CRIPPS

Agaricus species in grassland.

Fungi are the fabric that holds most ecosystems together, yet they are often forgotten, ignored, underestimated, or even reviled. Still it is the fungi in all their diverse roles that weave organisms, organic matter, soil, and rocks together. The Kingdom Fungi includes an estimated 1.5 million species worldwide (Hawksworth 2001)—molds, yeasts, plant pathogens, aquatic fungi, coral fungi, teeth fungi, bird's nest fungi, stinkhorns, cup fungi, morels, truffles mushrooms, boletes and more. Fungi were once thought to be related to plants but they lack chlorophyll and cellulose cell walls. Instead, fungi have chitin cell walls, a key fungal characteristic. DNA reveals that fungi are most closely related to animals. Like animals they are heterotrophs and must obtain food from an outside source; in fungi this is accomplished by absorption. Unlike bacteria, fungi have a nucleus and are multicellular (except for yeasts).

Fungi facilitate the establishment and survival of forbs, grasses, and forest trees in numerous ways and, in essence, are a link between the biotic and abiotic. Fungi may be saprophytic (decomposing dead plants and returning nutrients to the soil), mycorrhizal (attached to roots where they provide nutrient conduits for plants, shrubs, and trees), and/or pathogenic (thinning weak plants and allowing the strong to survive). Once in a while, a human-introduced fungus wreaks havoc as an invasive species that can devastate forests. The pathogenic white pine blister rust (*Cronartium ribicola*), accidentally imported from Europe in the early 1900s, is currently decimating whitebark pine forests.

The bodies of all fungi except yeasts are comprised of hyphae, tiny microscopic threads that permeate soil, roots, leaves, and wood, feeding off the richness of forests and meadows. The mycelium (a mass of hyphal threads) can exist out-of-sight almost indefinitely. The fleshy fruiting bodies (i.e., mushrooms) are the reproductive part of the fungus, ephemeral structures designed to lift the fungus out of the soil or wood in order to disseminate its reproductive propagules as spores.

How many fungi species occur in Yellowstone National Park? How are they distributed? What is their importance in ecosystem processes? Our goal was to synthesize information about Yellowstone fungi from collection records and to make recommendations for expanding the knowledge of fungi in the park. Delving into the literature and fungal herbaria in the United States and Europe, we compiled reports and records of fungi from the park over the last 130 years. Our findings were interesting not only for their historical value, but because they provide valuable baseline data to guide future research efforts. Management decisions often depend on this kind of basic knowledge.

COURTESY NEW YORK BOTANICAL GARDEN HERBARIUM

The first recorded fungus for Yellowstone National Park is *Hymenochaete* (now *Veluticeps*) *fimbriata*, a crust fungus collected on wood by Frank Tweedy in 1885 and deposited in the New York Botanical Garden Herbarium.

The History of Fungi Collecting in Yellowstone

The first fungus recorded from Yellowstone, *Hymenochaete fimbriata* (now in the genus *Veluticeps*), was collected in 1885 by botanist Frank Tweedy, who wrote the park's first botanical guide, *Flora of the Yellowstone National Park,* in 1886. It is a tough leathery bracket or crust fungus found on dead pine. This is one of the few Type specimens from Yellowstone, it was described for the first time from a collection which is now in the New York Botanical Garden's Fungal Herbarium.

Mycological priorities have changed over time. Until the mid-1970s, most of the fungi collected in the park were plant pathogens; more than 90% were rusts. Around 1900, Wyoming botanist Aven Nelson made numerous collections of plants and fungi, most of which are rust fungi. Nelson's specimen from Yellowstone is *Puccinia annulata*, a rust found on *Epilobii* species. Other collectors who contributed to our knowledge of rusts in the park include Hedgecock (1902–1909), Bartholomew (1913), Conard (1924-1926), Overholts (1926), Pady (1941), and Sprague (1941). Overholts was one of the few to collect small Ascomycota in the park.

Rusts were of interest not only for their pathogenic nature, but because species and strains often associate with a particular plant species. Rusts and other pathogens could be easily pressed flat along with plant leaves, and many fungal herbaria got their start this way. It was only later that large fleshy fungi (mushrooms) were dried and stored, at first pressed flat like plants, then later dried whole and stored in packets or boxes.

Large fleshy fungi (mostly Basidiomycota) were not seriously collected in the park until the 1960s, perhaps because of a lack of interested mycologists, but access and the ability to dry fungi quickly were still problematic. Fungal fruiting bodies are ephemeral and appear only after rainfall or in high humidity and, unless special techniques are used, that is the only time the fruiting bodies can be collected. Special drying methods are necessary to preserve the fleshy fungi, otherwise they quickly melt into a slimy mass. Portable dehydrators for specimens did not exist early on and were not common until the 1950s, and even then many field camps lacked the electricity to run them. Although adventurous backcountry mycologists know it is possible to dry fungi over campfires, even using dried herbivore dung as fuel in woodless areas, larger fungi collected far from roads are more likely to be lost to decay. Today fungi are described and photographed when fresh, then dried on electric dehydrators before being packaged for posterity.

About 100 fungi were collected every 25 years until 1976, when the number increased dramatically (fig. 1). Dr. Kent McKnight of Brigham Young University, Utah was an important collector of fungi in Yellowstone from the 1960s through the 1980s. He was sometimes accompanied by Prof. Meinhard Moser of the University of Innsbruck (Austria) and Dr. Joseph Ammirati of the University of Washington. Their collecting trips produced the spike in records after 1976 and culminated in the publication of "A Checklist of Mushrooms and Other Fungi in Grand Teton and Yellowstone National Parks," published in 1982. This list, while valuable, unfortunately does not indicate which fungi were found in which park, although many likely occur in both parks. Today, some of the collections (vouchers) from McKnight's checklist are in Yellowstone's Heritage and Research Center, but others have been deposited elsewhere. Many of McKnight's collections, housed at Brigham Young, are currently inaccessible. Moser's numerous collections at the University in Innsbruck are housed in the herbarium there.

A large portion of the mushroom flora in the Rocky Mountains, including most of the fungi likely to be fruiting in Yellowstone in autumn, are from the large and difficult

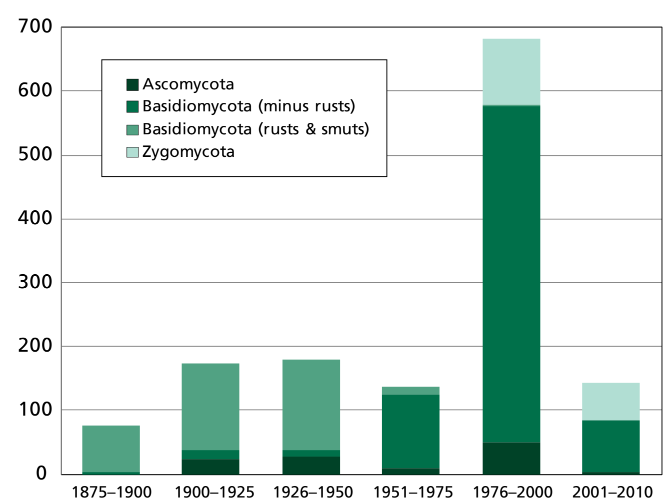

Figure 1. Number of fungi collected in Yellowstone National Park from 1875 to 2010. Zyggomycota collections are all of *Pilobolus*. Yellowstone's bioblitz in 2009 netted at least 82 species of macrofungi.

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Mycology crew for Yellowstone National Park's first bioblitz in August 2009.

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The first record of *Tricholoma cingulatum* for the region was found during Yellowstone's first bioblitz.

genus *Cortinarius*—rusty, brown-spored mushrooms with a cobweb-like veil. There are few specialists for this genus, but fortunately the three men noted above pooled their expertise for the benefit of the park. Their checklist contains more than 64 taxa of *Cortinarius*, and our database extends this to 103 species (McKnight 1982, 1986; Moser and McKnight 1984; Moser et al. 1999).

The lichenologist Sharon Eversman of Montana State University made a major contribution by collecting lichens in the park over many years (Eversman 2004). While lichens are often called dual organisms and not traditionally included in fungal databases, in recent years they have been classified as fungi because they are comprised mostly of ascomycete fungal hyphae with a layer of algal cells that produce food for the symbiotic partners. Eversman deposited 524 well-referenced specimens in 81 genera and as 255 species—a sufficiently extensive collection to suggest the range of a species within the park.

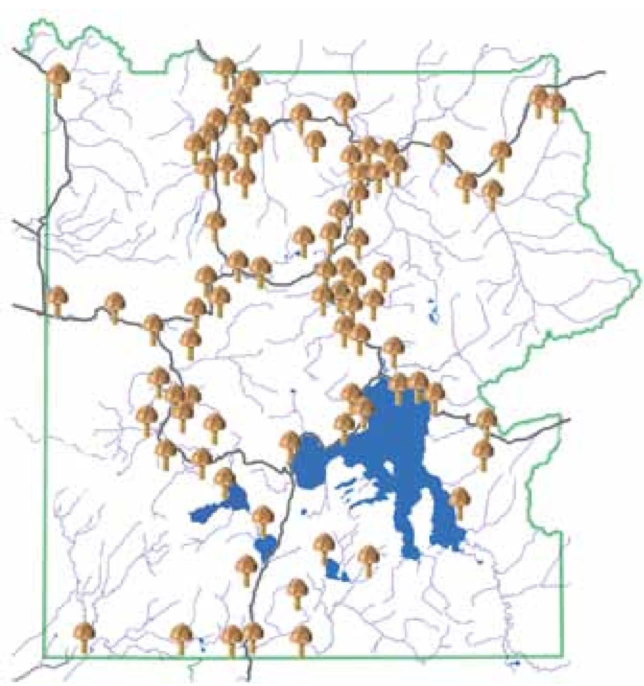

Figure 2. Most sites where fungi have been collected and recorded from 1885 to 2010 are near park roads.

In August 2009, when 125 researchers came from all over the country to collect as many different specimens as possible during Yellowstone's first "bioblitz." Dr. Cripps led the mycology crew from Montana State University and the Southwest Montana Mycological Association in Bozeman. Despite the dry conditions at that time of year, the crew netted more than 80 species of fungi during the 24-hour period, including two which were previously unreported in the park and one which was new for both Montana and Idaho. This was the first report of *Tricholoma cingulatum*, which occurs only with willows, in the Rocky Mountain region.

Fungi Sites in Yellowstone

Fungi have been collected at about 80 sites in the park, often near lakes, creeks, rivers and falls (fig. 2). This may be because fungi often fruit in moist habitats and Yellowstone is seasonally dry in many areas, or it might reflect the larger diversity of plants and microhabitats in these areas; a significant portion of Yellowstone's plant diversity is found in riparian areas (*Yellowstone Science* 2004). Perhaps this pattern merely reflects the propensity of mycologists, like tourists, to stop near these refreshing locations.

All forest trees in Yellowstone depend on mycorrhizal fungi (literally "fungus root") in one way or another. The presence of appropriate mycorrhizal fungi appears critical to forest health and sustainability. While some mycorrhizal fungi will attach to the roots of any woody plant, many have co-evolved with a particular tree species over thousands of years. Certain species of *Suillus* (slippery jacks) are restricted to five-needle pines, which in Yellowstone means whitebark and limber pine (Mohatt et al. 2008). An example would be the Siberian suillus (*S. sibiricus*) found on whitebark pine at

Suillus sibiricus (below) is mycorrhizal with five-needle pine species such as these whitebark pine on Dunraven Pass.

All forest trees in Yellowstone depend on mycorrhizal fungi in one way or another. The presence of appropriate mycorrhizal fungi appears critical to forest health and sustainability.

Dunraven Pass as well as on stone pines in Europe and Asia. Researchers have found that some ectomycorrhizal fungi prefer young trees and others mature forests. This means that when fire resets the successional clock for plants, it does the same for fungi. The records of many fungi from the park list them simply as "with pines," although specialized habitats such as whitebark pine forests (Mohatt et al. 2008; Cripps and Trusty 2007), thermal areas (Redman et al. 1999), and subalpine conifer forests (Cullings et al. 2000) have been the focus of some research.

Yellowstone is well known for its geothermal areas and the unique forms of life that thrive at high temperatures. The bacteria *Thermus aquaticus*, discovered in Yellowstone's lower geyser basin, contains an enzyme stable at high temperatures (Brock 1985) that has been used in molecular research and in determining fungal relationships. What about thermophilic (heat-loving) fungi? Brock, who discovered *Thermus aquaticus*, reported a few thermophilic and thermotolerant fungi from Yellowstone (Tansey and Brock 1971, 1972), and more recent researchers have discovered others in the park (Sheehan et al. 2005). Two thermotolerant and 16 thermophilic fungi have been reported from Amphitheater Springs (Redman et al. 1999; Hensen et al. 2005). *Curvularia protuberata*, a fungus that lives in the roots of *Dichanthelium lanuginosum* (hot springs panic grass), appears to give the grass its tolerance to hot soils (Redman et al. 2002). At least this is true when a virus first infects the fungus (Marquez et al. 2007) which then infects the plant.

Other researchers have found arbuscular mycorrhizal fungi (Glomeromycota) that can exist on plant roots in geothermal soils in the park (Bunn and Zabinski 2003; Appoloni et al. 2008). A few ectomycorrhizal fungi are recorded with conifers near thermal features (Cullings and Makhija 2001). There are likely other fungi yet to be discovered that thrive in and around the park's hot springs, geysers, fumaroles and geothermal areas.

In Yellowstone, fungi are mostly observed as mushrooms, puffballs, or bracket fungi on trees during certain parts of the year. Mushrooms and puffballs are of special interest because some are edible. Although park rules prohibit people from collecting and removing any mushrooms from the park without a permit, deer, elk, bear, squirrels, voles and insects are among the many animals that eat the fruiting bodies. Edible fungi documented in the park include king boletes (*Boletus edulis*), black morels (*Morchella elata*), golden chanterelles (*Cantharellus cibarius*), slippery jacks (*Suillus* species), oyster mushrooms (*Pleurotus* species), orange milky cap (*Lactarius deliciosus*), shrimp russula (*Russula xerampelina*), shaggy manes (*Coprinus comatus*), meadow mushroom (*Agaricus campestris*) and giant western puffball (*Calvatia booniana*). Toxic species include those in genus *Amanita*, such as *A. muscaria* (yellow variety of fly agaric) and *A. pantherina* (brown panther)

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This giant western puffball (*Calvatia booniana*) is about one foot in diameter, edible, and a decomposer of grass.

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Meadow mushroom (*Agaricus campestris*) occurs in open grasslands.

(McKnight 1982). Others, such as *Psilocybe merdaria* (non-psychoactive) are found on substrates such as bison dung.

In addition to the mushrooms that sprout out of bison dung in the park are tiny, dung-loving fungi that go unnoticed by most people. On hands and knees, the researcher Michael Foos found *Pilobolus*, the only fungus in Zygomycota recorded in the park, on herbivore dung everywhere in Yellowstone (Foos 1989). This fungus, whose name literally means "hat thrower," shoots its spore packet out of the "zone of repugnance" (a scientific term for a bison paddy or elk duds) onto vegetation at a g-force of 20,000 to 180,000, one of the fastest flights in nature (Yafetto et al. 2008). If eaten by a grazing ungulate, the spores travel through the animal's digestive tract and land back in the manure, ready to do their job of reducing the pile. While *Pilobolus* itself appears to be an innocuous decomposer, Foos (1987) discovered that lungworms can infect elk by hitching a ride on the spore packets.

Gaps in Our Knowledge of Fungi

Our investigative work revealed more than 1,489 records of fungi (not including lichens) collected in the park that are now deposited in various herbaria or mentioned in scientific papers. This translates into 520 species (186 genera) (table 1). The total number of recorded fungi appears minimal given that mycologists estimate that there are typically six times more fungi than plants in most areas (Hawksworth 2001). This suggests that at least 7,680 species of fungi would be expected in the park in proportion to Yellowstone's plant flora of 1,280 known species (*Yellowstone Science* 2004). That leaves a great deal more for us to discover.

Although subsequent identification of fungi sites is sometimes difficult, especially for fungi recorded before GPS, most of the recorded sites are near roads—the pattern typical of other fungal surveys in which mycologists have taken advantage of easy collecting before undertaking

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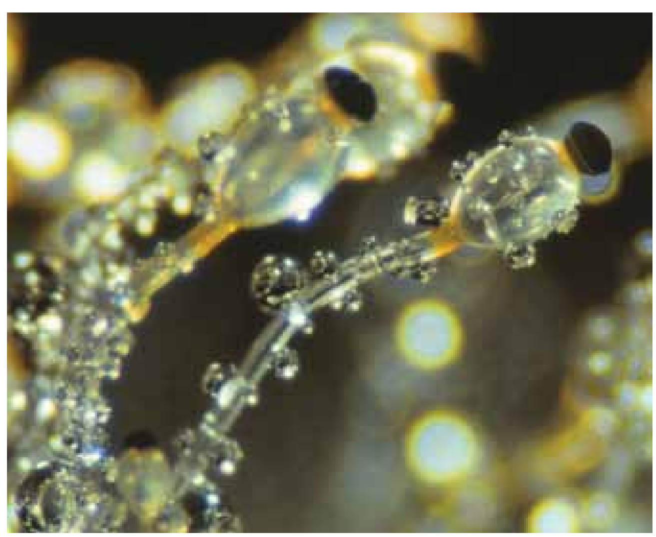
The inedible and non-psychoactive *Psilocybe merdaria* is a decomposer of bison dung.



M. FOOS

Pilobolus (highly magnified) fruits on dung and decomposes it. Note the dark spore packets which are shot off.

time-consuming hikes and expeditions. Other areas of the park remain as mycological blank spots. According to the database we developed, the most studied groups of fungi in Yellowstone are the rusts (Uredinales), mushrooms to some extent (particularly the genus *Cortinarius*), the dung fungus *Pilobolus* (Zygomycota), and lichens (Cripps 2011). These are basically researcher-driven results, dependent on the interests of specific collectors in the park. Most of the collecting has been of fungal fruiting bodies, with no major efforts to culture fungi from particular substrates except dung and thermal pools.

In some cases, fungal presence has been detected on roots (as mycorrhizae) and in thermal areas using molecular techniques and the data are catalogued as DNA sequences in Genbank (Cullings et al. 2001). But little to nothing is known of microfungi within other substrates, e.g., soil fungi, endophytes (inside plants), and little is known of the micro-ascomycota as pathogens or decomposers. Most of the fungal species recorded for Yellowstone are known from a single recorded specimen in the database and therefore, except for lichens and perhaps *Pilobolus*, accurate distributions are not known, even for the more well-studied groups.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Wolf lichen (*Letharia vulpina*) is among the more studied fungi that occur in Yellowstone.

Table 1. Genera and number of species of fungi reported in Yellowstone National Park from 1885 to 2010.

Genera					
Absida-1	Chrysomphalina-2	Galerina-2	Leccinum-3	Peziza-1	Sarcodon-1
Acaulospora-4	Chrysomyxa-4	Gastropila-1	Lentinellus-1	Phaeogalera-1	Sarcosphaera-1
Acremonium-2	Cintractia-1	Gautieria-2	Lepiota-2	Phaeolus-1	Scolecobasidium-2
Aecidium-4	Clavaria-1	Geastrum-2	Lepista-3	Phaeomarasmius-2	Scutellinia-1
Agaricus-7	Clavariadelphus-2	Gigaspora-2	Leptoporus-1	Phanerochaete-1	Scutellospora-1
Agrocybe-2	Claviceps-1	Gloeophyllum-4	Leratiomyces-1	Phellinus-1	Septoria-1
Albatrellus-2	Clitocybe-7	Glomus-9	Leucopaxillus-1	Phialophora-1	Sporothrix-1
Albugo-1	Clitocybula-1	Golovinomyces-3	Lindbladia-1	Pholiota-5	Steccherinum-1
Amanita-7	Coleosporium-2	Gomphidius-2	Loreleia-1	Phragmidium-11	Strobilurus-1
Amylocystis-1	Coltricia-2	Guepiniopsis-1	Lycoperdon-4	Phyllachora-2	Stropharia-1
Anthracobia-2	Coprinopsis-1	Gymnomyces-1	Lyophyllum-1	Pilobolus-4	Suillus-15
Antrodia-1	Cortinarius-103	Gymnopilus-3	Marssonina-1	Piloderma-1	Syncarpella-1
Armillaria-1	Cronartium-5	Gymnopus-1	Megacollybia-1	Plectania-1	Taphrina-1
Ascobolus-1	Cryptoporus-1	Gymnosporangium-7	Melampsora-10	Pluteus-1	Tarzetta-1
Aspergillus-2	Cumminsiella-1	Gyromitra-3	Melampsorella-2	Podosphaera-1	Tephrocybe-2
Astreus-1	Cunninghamella-1	Hebeloma-5	Melanoleuca-3	Psathyrella-3	Thelebolus-1
Auricularia-1	Curvularia-1	Helvella-1	Morchella-4	Pseudeurotium-1	Thelephora-1
Bankera-1	Cylindrosporium-1	Herpotrichia-1	Mycena-5	Psilocybe-1	Thermomyces-1
Blumaria-1	Cyptotrama-1	Hyaloperonospora-1	Naohidemyces-2	Puccinia-52	Tilletia-3
Boletopsis-1	Cystodermella-1	Hydnellum-4	Naucoria-1	Pucciniastrum-2	Torula-1
Boletus-1	Dilophospora-1	Hydnum-1	Neolecta-1	Pycnoporellus-2	Tranzschelia-1
Botryobasidium-1	Discina-1	Hygrocybe-2	Neolentinus-1	Ramaria-2	Tranzscheliella-1
Bovista-1	Endocronartium-1	Hygrophorus-12	Nidula-1	Ramularia-4	Trichaptum-1
Brauniellula-1	Entoloma-4	Hypholoma-4	Onnia-2	Rhizina-1	Tricholoma-10
Calvatia-5	Entyloma-3	Hypocrea-1	Orbilia-1	Rhizogene-1	Tricholomopsis-2
Calyptospora-1	Erysiphe-3	Inocybe-7	Otidia-1	Rhizophagus-3	Truncocolumella-1
Cantharellus-1	Flammulaster-1	Kuehneromyces-2	Pachylepyrium-1	Rhizopogon-7	Tyromyces-1
Cenococcum-1	Floccularia-4	Laccaria-2	Paraglomus-2	Rhodocollybia-2	Uromyces-9
Cercosporella-2	Fomitopsis-1	Lachnellula-1	Penicillium-1	Rhodocybe-2	Ustilago-3
Chaetomium-1	Fuligo-2	Lachnum-1	Peniophora-1	Royoporus-1	Veluticeps-2
Chroogomphus-2	Funneliformis-2	Lactarius-13	Peridermium-3	Russula-16	Wilcoxina-1

Caloscyphe fulgens is a spring cup fungus that can be pathogenic on spruce seeds.

Only 5% of the estimated 1.5 million species of fungus in the world have been named, making the description of unknown species time-consuming and creating bottlenecks in species identification.

Most collections of Yellowstone fungi are in the New York Botanical Garden, the US Department of Agriculture, National Fungus Collection in Beltsville, Maryland, and Yellowstone's herbarium at the Heritage and Research Center in Gardiner, Montana. Although Hawksworth emphasized the importance of fungal culture collections in his 2004 article, "Fungal diversity and its implications for genetic resource collections," much of what he says translates to the importance of dried herbarium collections. For example, the DNA of rusts in the park is available in chronological order. Have the genetics of rusts changed over time? What is the epidemiology of fungal pathogens in the park? Have some fungal species declined or disappeared as they have in Europe? These are some of the many questions that can be answered with herbarium specimens. The herbarium represents an important aspect of our natural history: in human terms (the collectors), in genetic terms (DNA repositories), in chemical terms (record of pollutants) and in fungal terms (biodiversity past and present). Without knowledge of our fungal history, we go blindly forward into the ecological future.

Recommendations for Field-Based Inventory

How can we learn more about fungi in Yellowstone National Park? Mycologists are testing new survey methods, combining bioblitzes that invite the public with the expertise of specialists. This has added to our knowledge of fungi in Point Reyes, Rocky Mountain, and Great Smoky Mountains national parks. In the latter, an "all taxa survey" of fungi was attempted (Hughes and Peterson 2007) during which fungi were collected by many means, including culturing and detection with DNA probes (Rossman 1994; Mueller et al. 2004). These methods can reveal the fungi in soil, inside plants, on roots, and in the air, adding greatly to the diversity count, but they do not always provide reference material for herbaria and they are time-consuming, resource exacting, and often expensive.

The exhaustive all taxa survey is a "holy grail" for fungi, but usually needs to be tempered because of limited financial resources and the availability of mycologists. Only 5% of the estimated 1.5 million species of fungus in the world have been named, making the description of unknown species time-consuming and creating bottlenecks in species identification. In addition, the character of the particular park to be surveyed is an important consideration. While fungi may fruit nearly year round and be easily accessible in some parks, dry and/or cold conditions limit fungal fruiting to particular seasons in each elevation zone, resulting in small windows of opportunity for collection in Yellowstone. Many areas of the park are inaccessible because of difficult terrain or wildlife habitat (grizzly bear, moose, wolves, bison), and trampling by large herbivore herds is detrimental to fruiting structures. Repository and curation needs are also a consideration. Yellowstone's Heritage and Research Center in is an excellent facility for this purpose given sufficient resources for curation. These factors need to be taken into account in future fungal surveys in the park.

A survey of the park's fungi might be accomplished most effectively using a stratified sampling strategy that takes into consideration habitat type (including elevation), age class of over-story vegetation, and disturbance (fire) along with spatial, seasonal, and climatic factors. With lodgepole pine

Guepiniopsis alpinus (lemon drops) is a wood decomposer that relies on moisture from spring snow for fruiting.

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Pholiota molesta fruits prolifically on burned soil a few years after a forest fire. It is a decomposer only found in this specialized habitat.

covering 80% of the park, these forests should be stratified into age classes and into burned/unburned areas for sampling. Riparian areas, which account for 38% of the park's plant species diversity, may be of special interest for fungi, especially during the dry season.

We recommend three sampling strategies for fungus collection, two of which require significant resources. One method is for collection of fruiting fungi, the second for isolation of fungi from substrates, and the third includes the use of molecular techniques to detect and identify fungi (Rossman 1994; Mueller 1994). Collection should be timed to correlate efficiently with high seasonal precipitation or rain events (generally a few days after), and the fruiting period for each group or species. The seasonal progression of fruiting generally starts with grass saprophytes in open grasslands at low elevations followed by fungi on burns and around remnant snowbanks in June (Cripps 2009). Forest fungi begin fruiting at the lower elevations and progress upward from Douglas fir to lodgepole, spruce-fir, whitebark pine, and finally alpine tundra (table 2). Droughts or low rainfall in July can seriously reduce fruiting at lower elevations. In years when fall precipitation is minimal, it can be difficult to find fungi fruiting at all.

Instead of relying on fungi fruiting in nature, fungal surveys can be accomplished or enhanced by culturing fungi from substrates (Rossman 1994; Mueller 1994). Although a significant portion of fungi will not grow on petri dishes in the laboratory, this method can be used to isolate some micro-fungi, pathogens, soil fungi, endophytes, mycorrhizal fungi, and aquatic fungi from substrates such as woody material, leaves, needles, soil, roots, algae, and dung. While this method takes significant resources and needs to be applied or supervised by experts, it has the potential to increase the diversity of fungi recorded in an area.

Molecular methods, which are particularly applicable to fungi that do not fruit or grow in culture, are currently being used for soil fungi, mycorrhizal fungi, and thermal fungi (Mueller et al. 1994). Molecular methods can be used to identify population level diversity in fungi, to delineate fungal "individuals", determine relationships, and identify unique organisms or sequences for patent purposes (Varley 2005). This method is time and resource consuming and can only be applied by experts. However, it holds the promise of discovering some of Earth's more unique and cryptic organisms. YS

Acknowledgments

We wish to thank Mary Hektner and Jennifer Whipple for their support of this project and all the mycologists who have made contributions to information on fungi in Yellowstone National Park.

Table 2. A generalized model showing where and when fungi are likely to fruit in Yellowstone National Park (Cripps 2011) with monthly precipitation averages for Mammoth Hot Springs, 1971–2000.

Habitat type	Ecological group	Apr 1.17”	May 1.96”	June 1.99”	July 1.56”	Aug 1.47”	Sept 1.35”	Oct 0.96”
Low elevation sage & grasslands	grass saprophytes	x	x	x				
Douglas fir & limber pine forests	saprophytes, mycorrhizal			x		x		
Low & mid elevation burns	burn fungi		x	x				
Lodgepole pine forests with remnant snowbanks	snowbank fungi			x	x			
Riparian areas before flood stage	willow fungi		x	x	x	x	x	
Aspen & cottonwood cover areas	saprophytes, mycorrhizal		x	x	x	x	x	
Lodgepole pine forests	saprophytes, mycorrhizal		x	x			x	
Spruce-fir forests	saprophytes, mycorrhizal				x	x	x	x
Whitebark pine forests	saprophytes, mycorrhizal				x	x	x	x
Alpine tundra	saprophytes, mycorrhizal				x	x	x	
Geothermal areas		x	x	x	x	x	x	x

Data compiled from information on fungi in the Greater Yellowstone Area (Cripps 2001; Cripps & Antibus 2011; Cripps & Ammirati 2010; Cripps & Eddington 2005; Cripps & Horak 2008; Mohatt et al. 2008).

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Literature Cited

Appoloni, S., Y. Lekberg, M.Tercek, C. Zabinski and D. Redecker 2008. Molecular community analysis of arbuscular mycorrhizal fungi in roots of geothermal soils in Yellowstone National Park (USA). *Microbial Ecology* 56(4):649–659.

Brock, T.D. 1985. Life at high temperatures. *Science* 230(4722):132–138.

Bunn, R.A. and C. Zabinski. 2003. Arbuscular mycorrhizae in thermal-influenced soils in Yellowstone National Park. *Western North American Naturalist* 63(4):409–415.

Cripps, C.L. 2001. Mycorrhizae of aspen forests: Ecology and potential application. In *Sustaining aspen in western landscapes: Symposium proceedings, June 13-15, 2000, Grand Junction, Colorado.* p. 285–298. Fort Collins, CO: US Dept. of Agriculture, Forest Service, Rocky Mountain Research Station.

Cripps, C.L. 2009. Snowbank Fungi revisited. *Fungi* 2:47–53.

Cripps, C.L. and R. Antibus. 2011. Native ectomycorrhizal fungi of limber and whitebark pine: Necessary for forest sustainability? In *The future of high-elevation, five-needle white pines in western North America.* Proceedings of the High Five Symposium. June 28–30, 2010, Missoula, MT. R. E. Keane, D.F. Tomback, M.P. Murray, and C.M. Smith, eds., 37–44. Fort Collins, CO:US Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Cripps C., and Ammirati J. 2010. Eighth international symposium on Arctic-Alpine mycology (ISAM 8), Beartooth Plateau, Rocky Mountains, USA 2008. *North American Fungi* (5):1–8.

Cripps, C.L. and L.E. Eddington 2005. Distribution of mycorrhizal types among alpine vascular plant families on the Beartooth Plateau, Rocky Mountains, USA, in reference to large-scale patterns in Arctic-alpine habitats. *Arctic, Antarctic and Alpine Research* 37(2):177–188.

Cripps, C.L. & Horak, E. 2008. Checklist and Ecology of the Agaricales, Russulales and Boletales in the alpine zone of the Rocky Mountains (Colorado, Montana, Wyoming) at 3000–4000 m a.s.l. *Sommerfeltia* 31:101–123.

Cripps, C.L. and P. Trusty. 2007. Whitebark pine restoration, Dunraven Pass (Monitoring mycorrhizal status of seedlings). Final report to the Greater Yellowstone Coordinating Committee.

Cullings, K., V. Parker, S. Finley and D. Vogler. 2000. Ectomycorrhizal specificity patterns in a mixed *Pinus contorta* and *Picea engelmannii* forest in Yellowstone National Park. *Applied and Environmental Microbiology* 66:4988–4991.

Cullings, K. and S. Makhija 2001. Ectomycorrhizal fungal associates of *Pinus contorta* in soils associated with a hot spring in Norris Geyser Basin, Yellowstone National Park, Wyoming. *Applied and Environmental Microbiology* 67(12):5538–5543.

Eversman, S. 2004. Macrolichens of the forests of Montana and Yellowstone and Glacier national parks. In *Fungi in forest ecosystems: Systematics, diversity and ecology.* C.L. Cripps, ed. 213–232. New York, NY:New York Botanical Garden Press.

Fetig, W. 1999. Aven Nelson's 1899 Yellowstone expedition. *Castillejà, A publication of the Wyoming Native Plant Society* 18(4):4.

Foos, K.M. and J.A. Royer. 1989. A survey of *Pilobolus* from Yellowstone National Park. *Mycotaxon* 34:395–397.

Foos, M.K. 1997. *Pilobolus* and lungworm disease affecting elk in Yellowstone National Park. *Mycological Research* 101:1535–1536.

Hawksworth, D. 2001. The magnitude of fungal diversity: The 1.5 million species estimate revisited. *Mycological Research* 105:1422–1432.

Hawksworth, D. 2004. Fungal diversity and its implications for genetic resource collections. *Studies in Mycology* 50:9–18.

Henson, J., R. Redman, R. Rodriguez, and R. Stout. 2005. Fungi in Yellowstone's geothermal soils and plants. *Yellowstone Science* 13:25–30.

Hughes, K.W. and R.H. Peterson. 2007. Collections from Great Smoky Mountains National Park. University of Tennessee Herbarium, http://www.bio.utk.edu/mycology/atbi/ATBIhome.htm. Accessed 02/08/2012.

Marquez, L., R. Redman, R. Rodriquez and M. Roossinck. 2007. A virus in a fungus in a plant: Three–way symbiosis required for thermal tolerance. *Science* 315: 513–515.

McKnight, K.H. 1982. *Checklist of mushrooms and other fungi of Grand Teton and Yellowstone National Parks.* WY: Grand Teton Library and Museum Association.

McKnight, K. 1986. Macrofungi of Yellowstone National Park, Report of Collections. Heritage and Research Center, Yellowstone National Park.

Mohatt, K., C.L. Cripps and M. Lavin. 2008. Ectomycorrhizal fungi of whitebark pine revealed by sporocarps and molecular analysis of mycorrhizae from treeline forests in the greater Yellowstone ecosystem. *Botany* 86:14–25.

Moser, M. 2004. Subalpine conifer forests in the Alps, the Altai, and the Rocky Mountains: A comparison of their fungal populations. In *Fungi in forest ecosystems: Systematics, diversity and ecology.* C.L. Cripps, ed. 151–158. New York, NY:New York Botanical Garden Press.

Moser, M. and K. McKnight. 1984. Fungi (Agaricales, Russulales) from the alpine zone of Yellowstone National Park and the Beartooth Mountains with special emphasis on Cortinarius. In *Arctic and alpine mycology II: Proceedings of the Second International Symposium on Arctic and Alpine Mycology, held August 26–September 2, 1984, in Fetan, Switzerland.* G. Laursen, J. Ammirati, and S. Redhead, eds., 299–318. New York: Plenum Press.

Moser, M., K. McKnight, and J.F. Ammirati. 1999. Studies in North American Cortinarii. I. New and interesting taxa from the Greater Yellowstone area. *Mycotaxon* 55: 301–346.

Mueller, G., G. Bills and M. Foster. 1994. Biodiversity of fungi: Inventorying and monitoring methods. Burlington, MA:Elsevier Academic Press.

Redman, R., A. Litvintseva, K. Sheehan, J. Henson, and R. Rodriguez, 1999. Fungi from geothermal soils in Yellowstone National Park. *Applied and Environmental Microbiology* 65: 5193–5197.

Redman, R., K. Sheehan, R. Stout, R. Rodriguez, and J. Henson. 2002. Thermotolerance generated by plant/fungal symbiosis. *Science* 298(5598):1581.

Rossman, A.Y. 1994. Strategy for an all-taxa inventory of fungal biodiversity. In *Biodiversity and terrestrial ecosystems: Proceedings of the International Symposium on Biodiversity and Terrestrial Ecosystems, April 17-20, 1994, Taipei.* J. Peng, and C.Zhou, eds., 169–194. Taipei: Institute of Botany, Academia Sinica.

Sheehan, Kathy B. 2005. *Seen and unseen: discovering the microbes of Yellowstone*. Guilford, CT: Falcon.

Tansey, M. and T.D. Brock. 1971. Isolation of thermophilic and thermotolerant fungi from hot spring effluents and thermal soils of Yellowstone National Park. Bacteriological Proceedings 1971, p. 36. American Society for Microbiology, Washington, D.C.

Tansey, M. and T.D. Brock. 1972. The upper temperature limit for eukaryotic organisms. *Proceedings of the National Academy of Sciences* 69(9):2426–2428.

Varley, J. 2005. Molecular approach to biodiversity doubles list of known species in Yellowstone Lake. *Natural Resources Year in Review.* http://www.nature.nps.gov/YearInReview/yir2005/03_B.html

Yafetto, L., L. Carroll, Y. Cui, et al. 2008. The fastest flights in nature: high-speed spore discharge mechanisms among fungi. *PloS One* 3(9):e3237. doi:10.1371/journal.pone.0003237.

Yellowstone Science. 2004. YS Interview: Park botanist Jennifer Whipple and Yellowstone's herbarium. *Yellowstone Science* 12(4):25–34.