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Ecology and Management of Morels Harvested From the Forests of Western North America

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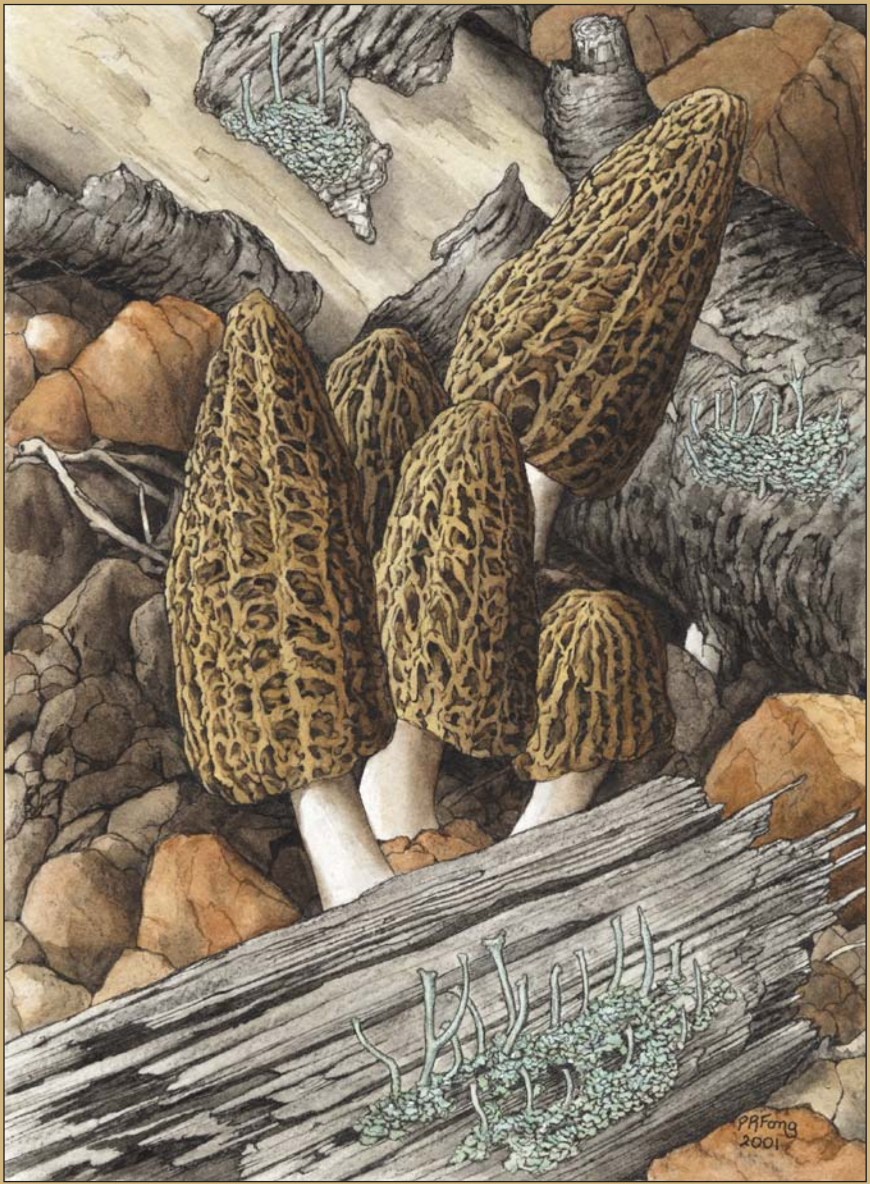

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Cover Art

Peeling bark on the log illustrates the tendency of morels to fruit following tree death. Morels can differ widely in color and shape depending on species, genetic diversity, age, exposure to sunlight, and other environmental conditions. Original painting by Paula Fong (http://www.prfong.com)

Abstract

Pilz, David; McLain, Rebecca; Alexander, Susan; Villarreal-Ruiz, Luis; Berch, Shannon; Wurtz, Tricia L.; Parks, Catherine G.; McFarlane, Erika; Baker, Blaze; Molina, Randy; Smith, Jane E. 2007. Ecology and management of morels harvested from the forests of western North America. Gen. Tech. Rep. PNW-GTR-710. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 161 p.

Morels are prized edible mushrooms that fruit, sometimes prolifically, in many forest types throughout western North America. They are collected for personal consumption and commercially harvested as valuable special (nontimber) forest products. Large gaps remain, however, in our knowledge about their taxonomy, biology, ecology, cultivation, safety, and how to manage forests and harvesting activities to conserve morel populations and ensure sustainable crops. This publication provides forest managers, policymakers, mycologists, and mushroom harvesters with a synthesis of current knowledge regarding these issues, regional summaries of morel harvesting and management, and a comprehensive review of the literature.

Keywords: Morel mushrooms, *Morchella*, forest management, special forest products, nontimber forest products, edible fungi.

Summary

Morels are the fruiting bodies of species in the genus *Morchella*. They are prized edible mushrooms that fruit, sometimes prolifically, in many forest types throughout western North America as well as in temperate forests globally. They are commercially harvested and sold locally, nationally, and internationally. Annual commerce in morels likely ranges in value from $5 million to $10 million in western North America; thus they are one of the more valuable special forest products in the region. Large gaps remain, however, in our knowledge about morels. Their taxonomy is confusing and most North American species lack valid scientific names. Their biology, nutritional sources, life cycle, and modes of reproduction are unusual and complex. Ecologically, we do not yet fully understand how and why some morels fruit prolifically following tree death, wildfire, or other forest disturbances. Efforts to cultivate morels have only been partially successful; thus wild crops remain competitive in the marketplace. Species in genera closely related to morels are sometimes harvested or sold as food, but some of these species can be poisonous and their sale affects regulations regarding morel commerce. Morels also can accumulate toxic heavy metals under certain circumstances. As with morel biology, no comprehensive summary exists about morel harvesters and their culture; about social, economic, and environmental aspects of morel commerce; or about harvest regulations that are specific to morels. Morels fruit from Mexico to Alaska in western North America. Within this range, morel crops, forest habitats, land ownership, forest management goals, laws and regulations, and morel commerce differ by region. This publication provides forest managers, policymakers, mycologists, and mushroom harvesters with a synthesis of current knowledge regarding these issues, regional summaries of morel harvesting and management throughout western North America, a discussion of how forest management and morel crops interact, suggestions for useful research, and a comprehensive review of the literature.

Contents

Introduction

In the late 1980s and early 1990s, commercial mushroom harvesting expanded rapidly on federal lands in the Pacific Northwest. Molina and others (1993) examined the species that were being harvested and the issues involved. Three types of mushrooms constituted the bulk of harvested mushroom crops: the American matsutake or pine mushroom (*Tricholoma magnivelare*), various species of chanterelles (*Cantharellus* and related genera), and morels (*Morchella* species). This publication completes a series of three General Technical Reports (GTRs) focusing in greater detail on the ecology and management of these commercially important fungi. The first (Hosford and others 1997) discussed the American matsutake and the second (Pilz and others 2003) examined chanterelles. All of these publications were written for forest managers, policymakers, and the general public, but contain sufficient detail and references for use by mycologists (people that study fungi) and other scientists.

American matsutake are the most valuable mushrooms harvested in the Pacific Northwest but are not as abundant as chanterelles or morels. Chanterelles are the most abundant, but sell for considerably lower prices than American matsutake or morels. Morels are more valuable than chanterelles and more abundant than American matsutake; hence in combination, the total value of morel crops in the Pacific Northwest is larger than either of the others (Blatner and Alexander 1998, Schlosser and Blatner 1995).

Morels are more valuable than chanterelles and more abundant than American matsutake; hence in combination, the total value of morel crops in the Pacific Northwest is larger than either of the others.

Morels are distinct in a number of other ways. Compared to most other harvested forest fungi, they occur in a wider variety of forested ecosystems and habitats, they appear to be more genetically diverse, they differ widely in appearance, their taxonomy and distinctions among species are poorly defined and in flux, they exhibit heterogeneous and adaptive lifestyles, and their potential interactions with forest management activities are complex and numerous. Additionally, they are among the most avidly sought and highly esteemed mushrooms for culinary use and ease of preservation.

Morels are of global importance, not only because they are widely appreciated wherever they grow, but also because international commerce in morels is extensive. Cultivated morels still have not replaced wild-harvested morels in most markets. We will discuss the reasons why morels are difficult and expensive to grow. Meanwhile, harvesting morels from forests remains profitable and forest management plays an important role in maintaining such crops.

This publication focuses on morel mushrooms that grow from Mexico to Alaska and from the Rocky Mountains westward. We have chosen this geographic region for three reasons. First, morels occur in large crops and are commercially harvested in significant quantities in many places throughout western North America. Second, forest ecosystems throughout this region differ from forests east of the Rocky Mountains in their greater abundance of conifers, sparser summer precipitation, and more frequent wildfires. Lastly, several excellent books address morels of the Eastern United States, but we know of none that specifically address morels in the West.

“Managing” morels is a multifaceted issue. Biologically, it entails understanding their ecological niches, life cycles, nutrient sources, and reproductive strategies. Forest management issues include how the organism persists in ecosystems over time and how it reacts to disturbance, whether natural or produced by humans. Cultivation efforts illustrate the complexity of morel lifestyles and why they will likely remain predominantly wild-harvested for the foreseeable future. Methods that harvesters use to collect morels demonstrate the harvester’s interest in sustainability. Culinary use and concerns about inherent or absorbed toxins will stimulate further debate about regulating commerce in wild mushrooms. The value of morels in national and international markets affects the demand for access to harvesting opportunities and the environmental impacts associated with harvesting. Harvester strategies and transient workers pose challenges and opportunities for local communities and forest managers. Mixed ownership of forest land and varied land management goals create a mosaic of mushroom harvesting regulations that can be confusing to harvesters and difficult for land management agencies to enforce. These considerations overlay regional differences in forest ecosystems, climate, morel productivity, available labor, and transportation networks. This complex matrix of management issues and concerns, and our lack of understanding about essential aspects thereof, provide ample opportunities for continued research. Investigations that involve collaborative participation by individuals and organizations with diverse perspectives and interests will be especially useful for resolving management controversies while supporting economic opportunities (Pilz and others 2006b). By addressing all these issues, we aim to provide readers with a comprehensive synthesis of current knowledge and a thorough compilation of pertinent sources of information.

This publication is intentionally written for readers with diverse interests and backgrounds, so the following comments about format and usage are meant to improve clarity. With the exceptions of spore size and one figure, only English units are used. Conversion factors for metric units are provided in the section immediately preceding the “Literature Cited” section. All Web sites listed in this publication were last accessed and checked for availability on 20 December 2006.

All prices cited in the literature from other countries have been converted to U.S. currency values by using historical exchange rates that existed at the time of the original publication.[1] We use mycological terminology (technical terms about fungi) throughout the document. Each term is explained at first usage and listed in a glossary immediately after the "Closing Remarks" section. Acronyms used in only one section are defined at first usage. Common acronyms found in multiple sections of the document are USFS (U.S. Department of Agriculture, Forest Service) and BLM (U.S. Department of the Interior, Bureau of Land Management). Various terms, acronyms, and definitions are used around the world for wild crafted products. "Special forest products" is used by federal land management agencies in the Pacific Northwest and the states of Oregon and Washington. "Nontimber forest products" is the most common usage in the literature and internationally. We use either according to the context.

We use both scientific and common names interchangeably and in combinations; our intent is to make the text explicit yet readable. Frequently we abbreviate "*Morchella*" to "*M.*" when referring to a species of morel by scientific name. The appendix is a table of common and corresponding scientific names for all the organisms we mention in our text. To facilitate finding names in the appendix, fungi are listed in alphabetical order by scientific name; all other organisms are listed in order by common name.

One of the biggest challenges in preparing this document was the lack of agreement on scientific and common names for Western morels. Scientific names for morels described from other continents should be used for North American morels only provisionally, if at all, until comparison of specimens proves they are identical. Preliminary studies are revealing more diversity and endemism (native to only one place, region, or continent) than many researchers expected to find. As a result, the application of scientific names to North American morels is in a state of flux. Because common (vernacular) names are not applied according to a fixed system, they vary tremendously in their usage. Table 1 provides the names that we will use in this document. It is not meant to be definitive or unchanging; it merely provides consistency to our discussion and is based on our current understanding of Western morel species.

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[1] Prices from other currencies were converted to dollars with historical data corresponding to the year of the cited report by using tables obtained from the Web site of the OANDA Corporation, http://www.oanda.com/convert/fxhistory.

Table 1—Names used in this publication for distinctive western morels occurring in western North America north of Mexico

Our usage[a]	Disturbance[b]	Morel clade[c]	Scientific names[d]	Comments
Natural black morel	None or nonfire	Black	(*M. elata*) (*M. conica*) (*M. angusticeps*)	Putative species A (Pilz and others 2004)
(Pink?)[e] burn morel	Fire	Black	(*M. conica*) (*M. angusticeps*)	Putative species B (Pilz and others 2004)
(Green?)[e] burn morel	Fire	Black	(*M. conica*) (*M. angusticeps*)	Putative species C (Pilz and others 2004)
Gray morel[f]	Fire	Unknown	(“*M. atrotomentosa*”[g] as used by McKnight 1987)	Putative species D (Pilz and others 2004) Also called “fuzzy foot” or “black foot” morel
Mountain blond morel	None or nonfire	Unknown	None yet	Putative species E (Pilz and others 2004)
Yellow morel	None or nonfire	Yellow	(*M. esculenta*) (*M. crassipes*)	Likely several difficult-to-distinguish species (*M. crassipes* is an old-growth *M. esculenta*) (Kuo 2005, 2006)
Red-brown blushing morel	None or nonfire	Blushing (several subtropical species)	*Morchella rufobrunnea* (*M. deliciosa*)	In Xalapa, Mexico (Guzmán and Tapia 1998) and likely California (Kuo 2006) The similar *M. deliciosa* likely does not grow in the West
Half-free morel	None or nonfire	None of the above	*Morchella semilibera* (*Mitrophora semilibera*)	

[a] Common names for morels are so numerous, and used so inconsistently, that we make no effort to cross-reference them. We use “natural black” and “gray” morels, because these terms are common among commercial harvesters. This list is likely not inclusive of all the unique morel species that will eventually be identified in western North America. Kuo (2005) suggested there are other distinct black morels in western North America.

[b] Nonfire disturbances include insect infestations of trees, logging, tree death, floods, landslides, or any disruption or compaction of soil layers. Division of morels into fire and nonfire species reflects current understanding of how particular morels typically respond to disturbance. As species become better delineated and described, we might find that some species have more diverse habitat preferences and fruiting triggers. See “Morel Strategies” section and Kuo (2005).

[c] Two major clades, or groupings of closely-related true morels, are currently recognized in North America, “yellows” and “blacks.” A third clade of subtropical blushing species (*M. rufobrunnea, M. guatemalensis,* and *M. rigidoides*) is postulated by Guzmán and Tapia (1998).

[d] Most scientific names used for morels in North American field guides were given originally to European species, and it is currently unknown which, if any, of these species actually occur in North America. *Morchella rufobrunnea* and *Morchella semilibera* are the only scientific names in our chart that most taxonomists would accept as applicable in North America. We list the other scientific names (abbreviated and in parentheses) because they are widely used in the literature, but the North American morels to which these names have been assigned might be endemic species that require original names.

[e] Co-author Carol Carter (Pilz and others 2004) suggests that burn morels in the black clade are likely two or more species. These species can be difficult to distinguish by field appearance because their shades of color intergrade. Co-author Nancy S. Weber tentatively suggests “pink” and “green” as common names for these putative burn species.

[f] The gray morel can range in color from very dark to almost blond as it matures (see fig. 2 in the “Species Descriptions” section). As with the “natural” black morel, we use a common name for this morel that is widely used among commercial mushroom harvesters. It also reflects this morel’s overall color when it is young, fresh, and prime for harvesting.

[g] “*M. atrotomentosa*” is not a valid scientific name. See comments for the gray morel in the “Species Descriptions” section.

About Morels

Whence Morels

The names for morels in many Germanic languages can be traced to the early German dialect called "Old High German" (Weber 1988). *Webster's Third New International Dictionary* provides this derivation [with abbreviations spelled out]: "French morille, of Germanic origin, akin to Old High German morhila, diminutive of moraha 'carrot'" (Gove and others 1993). Regardless of its English etymology, cultures around the world have bestowed names with local meaning (table 2). These are often descriptive. For instance, the indigenous Nahua of Tlaxcala, Mexico, call morels "olonanácatl," a word derived from the Náhuatl language meaning: olotl = corncob + nanácatl = mushroom (Montoya and others 2003). Other names used by indigenous groups in Mexico include "colmenitas" (little beehives), "mazorquitas" (little tender corn ears), "elotitos" (little ears of green corn), and "pancitas" (little paunches) (Guzmán and Tapia 1998). On the other side of the world, on the Tibetan Plateau, morels are called "gugu shamu" meaning the "cuckoo mushroom," because they fruit when the cuckoo bird returns in spring.[2]

Despite the cultural and linguistic evidence that morels are used and esteemed around the world, little information exists regarding Native American uses of morels north of Mexico.

Moerman (1998) did list the Crow Tribe of southwestern Montana and northern Wyoming as using morels for soap, and Gilmore (1919) reported that the Omaha Tribe esteemed boiled morels as food. The Omaha-Ponca name for morels was Mikai^{h}.thi, which translates literally as "star sore." Even some famous early European-American explorers failed to appreciate our North American morels. "Cruzatte brought me several large morells," writes Meriwether Lewis on June 19, 1806, "which I roasted and eat without salt pepper or grease in this way I had for the first time the true taist of the morell which is truly an insippid taistless food. . ." (Ambrose 1996: 362, Nelsen 2002).

Few chefs would recommend cooking morels without plenty of butter or cream, and indeed, many people disagree with Lewis's opinion of morels. Lonik (2002) estimated that 50 million people worldwide pick morels. Morel harvesting has been described in terms like "morel madness" (Weber 1988), "fungal lust" (Boom 1995), "the sickness" (Kuo 2005), and "screams of delight" (Casey 1995). Companies

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[2] Winkler, Dan. 2005. Personal communication. Conservation consultant, Eco-Montane Consulting, 9725 NE 130 Place, Kirkland, WA 98034.

Table 2—Some non-English common names for morels

Common name	Cited scientific names[a]	Country	Reference[b]
Amigasa-take	*M. conica*	Japan	Kreisel 2005, Rolfe and Rolfe 1925
Bankai yangdujum	*M. semilibera*	China	Hall and others 2003
Cagarria	*Morchella* species	Spain	Kreisel 2005
Colmena	*M. angusticeps, M. esculenta, M. conica*	Mexico	Guzmán 1977
Colmenilla	*Morchella* species	Spain	Kreisel 2005
Colmenita	*Morchella* species	Mexico	Guzmán and Tapia 1998
Cutui yangdujun	*M. crassipes*	China	Hall and others 2003
Ekte morkel	*Morchella* species	Norway	Chandra 1989
Elote	*Morchella* species, *M. esculenta, M. conica*	Mexico	Guzmán 1977
Elotito	*Morchella* species, *M. angusticeps*	Mexico	Guzmán 1977
Funguli	*Morchella* species	Ancient Rome	Rolfe and Rolfe 1925
Gaoyandujun	*M. elata*	China	Hall and others 2003
Guchhii	*Morchella* species	Himachal Pradesh, Kashmir, North India	Prasad and others 2002
Gugu shamu	*Morchella* species	Tibet	Winkler[c]
Halbfrei morchel	*M. semilibera*	Germany	Kreisel 2005
Hättmurkla	*M. semilibera*	Sweden	Korhonen 1986
Höhe morchel or Höhlmorchel	*M. elata*	Germany	Svrček 1983
Huhtasieni	*Morchella* species	Finland	Korhonen 1986
Jianyangdujun	*M. conica*	China	Hall and others 2003
Kabuteng hugis utak	*Morchella* species	Philippines	Chandra 1989
Käppchenmorchel	*M. semilibera*	Germany	Dähncke and Dähncke 1984, Kreisel 2005
Kartiohuhtasieni	*M. elata, M. conica*	Finland	Korhonen 1986
Kellohuhtasieni	*M. semilibera*	Finland	Korhonen 1986
Koestliche morchel	*M. deliciosa*	Germany	Dähncke and Dähncke 1984
Kucsmagomba	*Morchella* species	Hungary	Chandra 1989
Leimai yabgdujun	*M. costata*	China	Hall and others 2003
Mazorca	*M. angusticeps, M. esculenta, M. conica*	Mexico	Guzmán 1977
Mazorquita	*Morchella* species	Mexico	Guzmán and Tapia 1998
Merkel	*Morchella* species	Germany	Weber 1988
Mikai^{h}.thi	*Morchella* species	Omaha-Ponca Tribes, North America	Gilmore 1919

Table 2—Some non-English common names for morels (continued)

Common name	Cited scientific names[a]	Country	Reference[b]
Morchel	*Morchella* species	Germany	Kreisel 2005
Morhila	*Morchella* species	Old High German	Gove and others 1993
Morielje	*Morchella* species	Netherlands	Chandra 1989, Kreisel 2005
Morilla	*M. conica, M. esculenta*	Mexico, Spain	Guzmán 1977, Kreisel 2005, Weber 1988
Morille	*Morchella* species	France	Chandra 1989, Kreisel 2005, Weber 1988
Morille conique	*M. elata*	France	Kreisel 2005
Morille vulgaire	*M. esculenta*	France	Kreisel 2005
Morillon	*M. semilibera*	France	Kreisel 2005
Morkel	*Morchella* species	Denmark, Norway	Chandra 1989, Kreisel 2005
Murkla	*Morchella* species	Sweden	Kreisel 2005
Olonanácatl	*Morchella* species	Mexico	Montoya and others 2003
Olote	*M. conica, M. esculenta*	Mexico	Guzmán 1977
Olotito	*Morchella* species	Mexico	Montoya and others 2003
Pancita	*Morchella* species	Mexico	Guzmán and Tapia 1998
Pallohuhtasieni	*M. esculenta*	Finland	Korhonen 1986
Pique	*M. elata, intermedia,* and *conica*	Chile	Honrubia[d]
Pumpalka	*Morchella* species	Bulgaria	Chandra 1989
Rundmorkel	*M. esculenta*	Norway	Kreisel 2005
Rund toppmurkla	*M. esculenta*	Sweden	Korhonen 1986, Kreisel 2005
Sfonduli	*Morchella* species	Ancient Rome	Rolfe and Rolfe 1925
Smardz	*Morchella* species	Poland	Chandra 1989, Weber 1988
Smardz jadalny	*M. esculenta*	Poland	Chandra 1989
Smardz pólwolny	*M. semilibera*	Poland	Chandra 1989
Smardz wyniosly	*M. elata*	Poland	Chandra 1989
Smorchok	*Morchella* species, *M. esculenta*	Russia	Chandra 1989, Kreisel 2005
Smrž	*Morchella* species	Czech	Chandra 1989, Kreisel 2005, Weber 1988
Smrž obecný	*M. esculenta*	Czech	Kreisel 2005
Smrž polovolný	*M. semilibera*	Czech	Kreisel 2005
Speisemorchel	*M. esculenta*	Germany	Dähncke and Dähncke 1984, Kreisel 2005
Spissmorkel	*M. elata*	Norway	Kreisel 2005
Spitzmorchel	*M. conica*	Germany	Dähncke and Dähncke 1984

Table 2—Some non-English common names for morels (continued)

Common name	Cited scientific names[a]	Country	Reference[b]
Spongiae in humore pratorum nascentes	*Morchella* species	Ancient Rome	Chandra 1989
Spongioli	*Morchella* species	Ancient Greece or Rome	Rolfe and Rolfe 1925
Spugnola	*Morchella* species	Italy	Chandra 1989, Kreisel 2005, Weber 1988
Suéter	*Morchella* species	Mexico	Montoya and others 2003
Toppmurkla	*Morchella* species, *M. conica, M. elata*	Sweden	Kreisel 2005, Korhonen 1986
Yangdujun	*M. esculenta*	China	Hall and others 2003
Zbírciog	*Morchella* species	Romania	Chandra 1989

[a] Scientific names are those used in the cited publications.
[b] Most names listed in this table were compiled and provided by Paul Kroeger. 2005. Personal communication. President, Vancouver Mycological Society, 101 - 1001 West Broadway, Box 181, Vancouver, BC V6H 4E4 Canada.
[c] Winkler, Dan. 2005. Personal communication. Conservation consultant, Eco-Montane Consulting, 9725 NE 130 Place, Kirkland, WA 98034.
[d] Honrubia, Mario. 2005. Personal communication. Professor, Departamento de Biología Vegetal, Área de Botánica, Laboratorio de Micología-Micorrizas, Facultad de Biología, Campus de Espinardo, Universidad de Murcia, 30100 Murcia, Spain.

selling morel products have similarly descriptive names such as “Morel Mania”[3] and “Morel Heaven.”[4] Such is the popularity of morels, that they are commonly a theme in cartoons (Grace 2005), and their harvest in Alaska was used as the setting for a murder mystery novel by Stabenow (1995). In table 2, the global popularity of morels is illustrated by listing various names for morels in languages and countries around the world.

Distribution

Morels grow in all countries of the Northern Hemisphere that have temperate or boreal forests (Arora 1986), that is, forests that experience a distinct cold season, especially with winter snow. They also occur in some Mediterranean or subtropical regions such as coastal California (Arora 1986, Kuo 2005), the highlands of

[3] Morel Mania is a private company specializing in morel-related items. They list twelve 2006 morel festivals in Wisconsin, Michigan, Illinois, Indiana, Kentucky, and Missouri on their Web site. http://www.morelmania.com/4Events/index.html.

[4] “Morel Heaven” is now called “Mazur’s Mushrooms and More” after the founder and morel enthusiast Larry Lonik died and close friends continued the business. The Web site http://www.morelheaven.com/ lists annual festivals in Michigan.

Mexico and Guatemala (Guzmán-Dávalos and Rodríguez-Alcantar 1993, Guzmán and Tapia 1998), and the Middle East (Goldway and others 2000). Many morels in the Southern Hemisphere were likely introduced from the Northern Hemisphere, but endemic species also seem to exist. For instance, preliminary data suggest that although Australia has some introduced morel species (Barnes and Wilson 1998), it also hosts two possible endemic species.[5] This finding is not surprising given that morels in Australia and Tasmania associate with eucalypts and acacias (Faris and others 1996, Stott and others 2002), trees that are very different from those endemic to Northern Hemisphere forests. In Chile, morels growing with blue gum trees (*Eucalyptus globus*) and in Monterey pine (*Pinus radiata*) plantations in the Mediterranean climatic region were likely introduced along with those tree species,[6] but Gamundi and others (2004) also reported native morels in the southern beech (*Nothofagus*) forests of Argentina and of Chile. Both introduced and native morels are being studied. Researchers from the Universidad de Concepción in Casilla, Chile, in conjunction with the national Instituto Forestal, have begun a program of inoculating chestnut trees (*Castanea sativa*) with *Morchella conica* spores in an effort to produce mycorrhizal seedlings for out-planting.[7] In Argentina, research has begun on native morel productivity and enhancement in Chilean cedar (*Austrocedrus chilensis*) forests of the Patagonian Andes in Chubut Province.[8] Supporting commercial opportunities to harvest morels in a sustainable manner is one goal of the project. Research sites include Los Alerces National Park and nearby private lands where commercial morel harvesting can be proscribed and study sites kept secure.

Morels can be found throughout the United States if you look in the right habitats, such as the forested slopes of Hawaiian volcanoes (Hemmes and Desjardin

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[5] O'Donnell, Kerry. 2005. Personal communication. Microbiologist, Microbial Genomics and Bioprocessing Research Unit, National Center for Agricultural Utilization Research, U.S. Department of Agriculture, 1815 N University St., Peoria, IL 61604.

[6] Palfner, Götz. 2005. Personal communication. Biologist, Departamento de Ciencias Químicas, Universidad de La Frontera, Av. Francisco Salazar 01145, Casilla 54-D, Temuco IX Región, Chile.

[7] Reinoso, R.; Cjas, D.; Chung, P. [and others]. 2005. Evaluation of the mycorrhization process on plants of the species *Castanea sativa* (Fagaceae) with mycorrhizal *Tuber aestivum* and *Morchella conica* (Ascomycetes). [Unpublished abstract]. 4th international workshop on edible mycorrhizal mushrooms, 29 November–2 December 2005, Murcia, Spain. Professor, Departmento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Edmundo Larenas S/N, Concepción, Casilla 160-C, Chile.

[8] Barroetaveña, Carolina. 2006. Personal communication. Post-doctoral researcher, Centro de Investigación y Extensión Forestal Andino Patagónico CC. 14, Esquel (9200), Chubut, Argentina. Dr. Mario Rajchenberg is director of the project and Dra. Barroetaveña will be implementing it.

2002). They are rare, however, in hot climates such as inland southern California, the desert regions of the Southwest, the coastal plain of the Gulf of Mexico, and most of Florida. This distribution likely reflects their common association with trees and their tolerance to cold soils or "psychrotolerance" (Schmidt 1983). Morels also exhibit what has been called "broad ecological amplitude" and "environmental plasticity" (Wedin and others 2004). These terms will be further discussed in the "Biology" section.

Habitats

Disturbance—Throughout this publication we will discuss disturbances such as tree death, soil disruption, or fires as habitat factors that can stimulate morels to fruit, often in large quantities. Such triggers for fruiting appear to differ by species to some extent. For instance, we chose to distinguish "burn" from "nonburn" species of morels because frequent observations by the authors and commercial harvesters, as well as currently published information (McFarlane and others 2005, McLain and others 2005, Pilz and others 2004), suggest that some Western species only occur for a year or two after forest fires, whereas other species occur year after year in areas that have not burned. Absence of evidence to the contrary does not constitute proof of fruiting exclusively under certain conditions, however, and what we call burn or nonburn species might fruit occasionally under the reverse conditions. In resolving this issue, it will be especially important for future data to specify if the collected morel was found growing from burned soil or not, rather than simply from within a wildfire perimeter, because nonburned areas frequently remain within the boundary of a forest fire.

Even morels that we call "nonburn" species can respond with large flushes of fruiting in response to disturbances such as soil displacement, soil compaction, tree death, or other stimuli. The following sections illustrate the range of such conditions.

Arora joked that morels "usually grow outdoors."

Range of habitats—Morels have adapted to a wide range of habitats and environmental conditions. Illustrating the wide range of places and conditions where morels fruit, Arora (1986) joked that morels "usually grow outdoors." We will not list all literature reports of the places, conditions, and circumstances where morels fruit, but here are some examples and references for further reading.

- Kuo (2002) and Weber (1988) discussed morel habitats in general, describing habitats they had seen or heard about, including river bottoms and flood plains, burn sites, areas landscaped with wood chips, near old sawmills, near wood piles, and near railroad beds.

- Weber (1988) described unusual habitats such as fields, dunes, landscaped areas, garbage dumps, abandoned coal mines, old mine tailings, cellars and basements, and along railroad tracks, but cautioned against eating morels from some of these habitats.
- Lonik (2002: 31–33) listed 62 places to find morels.
- Thompson (1994) made it clear that even though morels are common in riparian (river and stream) forests, they do not appear after heavy flooding.
- Hallen and others (2001) described morels fruiting away from trees in sand dunes and open meadows.
- Huffman and Tiffany (2001) mentioned road cuts, excavations, deer trails, orchards, and sand bars of rivers.
- Ramsbottom (1953) described morels fruiting in bomb craters, trenches, and the ashes of burned buildings after World War II.
- Kaul (1975) said morels fruit in bomb craters, areas where bonfires have burned, in limed soils, and soils where ashes have been spread.
- Carpenter and others (1987) and Stamets (1993, 2000) described large numbers of morels fruiting in the aftermath of the Mount St. Helens eruption, although the mushrooms were too gritty to clean and eat.
- Obst and Brown (2000) reported that 90 percent of morels found at their boreal forest study site fruited on the better drained hummocks of soil rather than in low-lying swampy areas.
- A construction worker observed morels growing where sheetrock had been allowed to disintegrate outdoors in winter rains.[9]
- Several authors of this publication have observed morels fruiting in the footprints of previous morel hunters.
- Almost any morel hunter will tell you they find some morels where they are unexpected.

Trees—Many morels fruit in nondisturbed forests in association with live trees. Others fruit in great abundance with trees that are declining, dying, or recently dead. Thompson (1994) provided a fascinating tale of the latter situation by recounting his massive morel harvests from 1971 to 1977. As Dutch elm disease (see appendix for scientific names) spread westward across the Midwestern United States, he followed the fungal bounty reliably found around the bases of dying and recently dead elms. The association of particular morel species with either healthy or moribund trees, and sometimes both, will be discussed in greater detail in the "Biology" section. We list a few examples from the literature here.

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[9] Avery, Lydia. 2006. Sheet-rocking contractor, P.O. Box 260, Alsea, OR 97324.

- Weber (1988) reported morels in Michigan as associated with oak-hickory or beech-maple forests, or under sycamore, elm, ash, cottonwood, and apple trees.
- Kuo (2005) listed morels in the Eastern United States as associated with ash, elm, and tulip trees, and often found in old apple orchards.
- Thompson (1994) found morels with senescent or dying apple trees, just-dead cottonwoods, and especially elms.
- Volk and others (1997) described morels fruiting with elm, ash, aspen, tulip poplar, and black cherry.
- Tiffany and others (1998) stated that most morels fruit near elms in Iowa and that black morels are rare and only found in upland oak forests on limestone outcroppings.
- Boom (1995) described morels in the Sierra Nevada range of California as "necrophiles of the alpine forest."
- Stamets (2000) described immense crops of morels after the 1988 Yellowstone forest fires.
- Pilz and others (2004) reported morels fruiting disproportionately in recently burned or insect-infested true fir forests in eastern Oregon.
- McFarlane and others (2005) described morels fruiting most abundantly in burned true fir/spruce forests at higher elevations in Montana.
- Keefer (2005) found morels fruiting close to subalpine fir in forest that burned the previous summer in British Columbia.
- Winder (2006) cited Canadian herbarium data (Natural Resources Canada 2005) that indicate *M. elata* grows in association with domesticated or wild members of the Rosaceae such as apple, cherry laurel, and ocean spray.

Timing

When do morels fruit? Many reports describe vegetative indicators of what Kuo (2005) called "angst relief" for impatient morel hunters. Examples of such signs are "when apple trees are in bloom" and "when oak leaves are the size of mouse ears" (Hammond 1999). Kuo (2005) provided eight examples, including when lilacs are in bloom and trilliums begin to flower. Low (1995) suggested a colorful indicator: "…when the hard, brown galls of cedar-apple rust hang their orange, gelatinous spore bodies on juniper trees." *Geopyxis carbonaria*, another postfire fungus, often fruits before burn morels, but is no guarantee morels will follow (Obst and Brown 2000). Lonik (2002) reported that in the Eastern United States, the morel season moves south to north at about 100 miles per week. Kuo (2005) provided a map that shows the progression of fruiting northward in the United States and southern Canada from the end of February to mid-June. An online progression map can be accessed through subscription to the Morel Mushroom Hunting Club at http://www.morelmushroomhunting.com/.

The bottom line is that morels fruit when winter snow has melted, the soil is beginning to warm, and the air is still humid. In any one location, the season can last from several weeks to several months depending on rainfall, humidity, topography, and the morel species. Warmth and humidity provide the conditions morels need to continue development once they start fruiting. In areas that have hilly or mountainous topography, morels will fruit first at low elevation or on south-facing slopes that warm up early, then at higher elevations and on north-facing slopes that warm up later (Low 1995). Burned soils also warm more quickly than nonburned soils because the black surface absorbs infrared radiation better. As with fruiting locations, the timing and length of morel fruiting can be unexpected. Although morels typically fruit in the spring, Sturgis (1905) reported massive quantities of morels fruiting on the 11th of September at 7,000 feet elevation in southwestern British Columbia in an aspen and spruce forest that burned the previous summer. Equally unusual, Goldway and others (2000) described morels fruiting continuously for 8 months in a nature reserve in northern Israel where they grew near a steady supply of spring water and under dense shade.

Morels fruit when winter snow has melted, the soil is beginning to warm, and the air is still humid.

Taxonomy

Kindred organisms—Both Weber (1988) and Kuo (2005) discussed, in general, the history of morel taxonomy, the frustrating inaccuracies, and the incompleteness of much of the earliest work. We will not expand upon their discussions here, other than to note two important early descriptions (Persoon 1797: 36, Fries 1822: 5) that are referenced by Weber (1988), and a French treatise on morel species by Constantin (1936).

Arora (1986), Kuo (2005, 2006), and Weber (1988) all provided general discussions of morel taxonomy. Descriptions of the genus *Morchella* can be found in Arora (1986: 785), Hanlin and Hahn (1990: 66), Jacquetant (1984), Smith and others (1981: 53), and Weber (1988: 128-129).

O’Donnell and others (1997) applied molecular methods of genetic analysis in order to better understand the evolutionary relations between *Morchella* and other closely related fungi. In many instances, such methods are modifying our understanding of how organisms are related to each other, and taxonomic discussions in older field guides often are outdated. The following classification scheme illustrates the position of *Morchella* and the related "look-alike" genera *Verpa* and *Gyromitra* in taxonomic context by using family and genus arrangements as per O'Donnell and others (1997).

Kingdom Fungi
- Phylum Ascomycota
  - Subphylum Pezizomycotina
    - Class Pezizomycetes
      - Order Pezizales
        - Family Morchellaceae
          - Genus *Morchella* (true morels)
          - Genus *Verpa* (thimble morels)
        - Family Discinaceae
          - Genus *Gyromitra* (false morels, lorchels)

Rather than rigid hierarchical categories of relationships based on observable characters, such as the outlined classification scheme above, the analogy of a "tree of life" is now often used to describe how closely organisms are related (Lutzoni and others 2004) and how long ago they had common ancestors or branching points. For instance, Birren and others (2003) and Galagan and others (2005) suggested morels diverged from related fungal lineages in the Mesozoic era about 100 to 150 million years ago. Discoveries of this nature are occurring at an increasingly rapid pace and redefining taxonomy. In an effort to keep up with the pace of discovery, collaborative Web sites are being used to compile the information. Taylor and others (1996) are coordinating the Ascomycete branch of the Tree of Life Web Project (http://tolweb.org/tree?group=Ascomycota&contgroup=Fungi) where current information can be found.

Calling morel taxonomy "problematic" is an understatement.

Morel species—Morel taxonomy above the level of species is not controversial, but when morel species are discussed, calling the field "problematic" is an understatement (Weber 1995). The Index Fungorum online database (http://www.indexfungorum.org/Names/Names.asp) lists 196 species and subspecies worldwide (CABI and others n.d.). Hallen and others (2001) estimated that more than 100 morel species have been described based on their morphological features. These are features of form (size and shape) or other characteristics (for instance, color or texture) that can be observed either macroscopically (with the naked eye) or microscopically. Examples of morel features that are often described include color of ridges, pits, and stem; configuration of the ridges; spore size and shape; attachment of the head to the stem; texture of head and stem; discoloration and bruising; stem wall thickness or layering; and changes in such features as a morel ages. The problem is that morels are extremely polymorphic (able to exhibit a wide variety of forms), and such observable features often intergrade among described or presumed species.

Such polymorphism undoubtedly has a genetic component, but environmental conditions such as moisture and sunlight also can affect the growth, development, form, size, and color of morel fruiting bodies. For instance, Jung and others (1993) asserted that the tan, gray, and large forms of the eastern yellow morel are actually all one polymorphic species in the clade of yellow morels.[10] Morels can change color in response to ultraviolet radiation (Jacobs 1982) and grow quite large if conditions of warmth and humidity are favorable. Thompson (1994), in his autobiography of a lifetime of picking morels, claimed that variations in morel appearance seemed to be consistently related to the type of trees growing where he found the morels, so perhaps such food sources also play a role in determining morphology. Royse and May (1990) also found little correspondence between variation in allozyme patterns (an enzymatic analysis of genetic variation) and morphological characters. The interplay between genetic variation, morel nutrition, and the environmental conditions influencing development of the fruiting body are likely quite complex.

In addition to morphology, fungal species can be delineated based on the ability to interbreed, long-term isolation of populations (for instance, geographic isolation), or consistent differences in the genetic makeup. Unfortunately, mating trials with morels are difficult to conduct. Getting colonies of fungi to grow together (compatible) or to exhibit inhibition zones (not compatible) is an easy, but not always definitive, laboratory procedure. To demonstrate full mating compatibility, the reproductive cycle must be completed with the production of morel fruiting bodies and spores. This process is difficult for reasons that we will discuss under the section on attempts at commercial cultivation. Similarly, just because populations have been geographically isolated for extended periods of time from other populations, does not necessarily mean they have diverged sufficiently to be considered separate species. So how can species of morels be distinguished? There is no one criterion that is ideal for all circumstances, but molecular techniques of genetic analysis are gaining broader acceptance (Taylor and others 2000).

Studies of genetic differentiation and speciation among morels have yielded some interesting results. For instance, Jung and others (1993), Bunyard and others (1994, 1995), and Wipf and others (1996a) reported more genetic variation between

[10] Because many North American morels might not yet have valid scientific names, their use by the authors we cite must be considered the equivalent of using imprecise common names. We default in our discussion to the common names listed in table 1.

distant populations of morels within the same species than between different morel species (although these results might in some cases reflect inaccurate species delineations). Similarly, Wipf and others (1999) reported that the genetic differences between black and yellow morel clades approach the magnitude of the differences between the genera *Morchella* and *Verpa*.

Molecular methods of genetic analysis are being applied with increasing sophistication to the question of how many species of morels actually exist in North America and whether they deserve different scientific names than species previously described in Europe. The literature on this topic is technical, sometimes contradictory, often narrowly focused, and potentially compromised by the lack of valid scientific names. Unless one is a specialist and familiar with all the publications, the implications of such research can be confusing. For readers who wish to explore the progress of such studies, they are listed here in chronological order: Gessner and others (1987), Yoon and others (1990), Royse and May (1990), Jung and others (1993), O'Donnell and others (1993), Bunyard and others (1994 1995), Gessner (1995), Buscot and others (1996), Wipf and others (1996a, 1996b, 1999), and O'Donnell and others (2003). Although Gessner (1995) preceded some of the other papers, it is a review paper that can help the reader put this field of research in perspective.

We summarize some of the conclusions that have been derived from these studies. Bunyard and others (1994, 1995) asserted that there are probably only three major groups of morels (black, yellow, and half-free morels) and speculated that there were probably only a few polymorphic species based on their samples. O'Donnell and others (1993) discerned 12 distinct morel species or species complexes from 150 morel collections in North America and Europe, although this was only a conference abstract with no indication of how representative the samples were. In a second abstract, O'Donnell and others (2003) described analyzing a global collection of 600 morel specimens. Twenty-eight species were identified, and they fit into two clades (groups of similar species). Thirteen species fell into the yellow-tan-gray "esculenta" clade, and 15 into the black "elata" clade. Twenty-four of the 28 species were found on only one continent. North America appeared to be the ancestral home of *Morchella* and had the greatest diversity of morels with 13 endemic species—4 yellow and 9 black.

Kuo (2006) has summarized recent unpublished evidence about morel species on his Web site entitled The Morel Data Collection Project http://www.mushroomexpert.com/morels/mordat.html and in his book (Kuo 2005). Kuo concluded that there are likely more than a dozen North American species. He asserted that yellow morels are actually two look-alike species in the east, but that neither occurs in California; rather, the similar species growing in coastal California is the same as *M. rufobrunnea* in Mexico. He also affirms that what has been called *M. crassipes* in the Eastern United States is simply a very large form of the yellow morel. In the Western United States, results published by Pilz and others (2004) differ from recent species descriptions posted on The Morel Data Collection Project Web pages (Kuo 2006), especially concerning green and pink morels as putative burn species. Readers interested in the evolving field of morel taxonomy will have plenty of interesting new developments to contemplate in the years to come.

It is important to note, however, that simply discerning distinct species is only the first step in resolving their taxonomic status. To be recognized as a species with an acceptable scientific name, appropriate collections must be accessioned to a public herbarium and a taxonomist must publish a thorough description of the vouchered collection specimens. Naming and publishing must be in accordance with the International Code of Botanical Nomenclature (Greuter and others 2000). Ideally, a sufficient number of specimens will have documented collection information so that a tentative range for the species, as well as its typical habitat and fruiting conditions, can be described. Once a species has been validly named, then that scientific name is available for use. Most morels in North America lack scientific names that meet the standards of the International Code of Botanical Nomenclature.

Most morels in North America lack scientific names that meet the standards of the International Code of Botanical Nomenclature.

Given the preceding discussion, readers are advised to treat the names in table 1 and the following species descriptions as subject to change in the near future. This information is presented here as a synopsis of our current understanding of morels in western North America.

Species Descriptions

Publications like this often include a key before species descriptions; the reader can use such keys to determine the species of a specimen by choosing among series of alternate choices about morphological characters or habitat preferences. We have chosen not to include such a key because the taxonomy of western morels is still in flux and the identity of some of the putative species described below is tentative. The names “natural black,” “green,” “pink,” “gray,” and “mountain blond” morels derive from the 2004 publication by Pilz and others, which provides a field key to these putative species (the only species that were found on the sites in the study). Alternative common names that we list are those we have encountered in harvester vernacular and other sources of information. All such names are problematic and, as noted elsewhere, valid scientific names would be much preferable if they were available.

None of the following descriptions constitute formal, complete, or technical species descriptions. Instead, they are intended to provide readers with some relevant details concerning the appearance of the morels that we discuss. Adequate descriptions for the pink, green, and mountain blond morels will require systematic assessment of fresh and dried features of specimens that have been confirmed to be genetically distinct. It is likely that some western morel species have not yet been identified, let alone described. Readers who wish to assist with collections for such analyses should refer to pertinent publications (Mueller and others 2004, Weber and others 1997) and contact interested taxonomists regarding their preferred collecting and description procedures.

Descriptions for the natural black, pink, green, gray, and mountain blond morels are excerpted and modified from Pilz and others (2004). Descriptions for the yellow and half-free morel are adapted with minor modification from Weber (1988). Guzmán and Tapia's *The Known Morels in Mexico, a Description of a New Blushing Species,* Morchella rufobrunnea, *and New Data on* M. guatemalensis (1998) was consulted for the description of the red-brown blushing morel.

Natural black morel—also called black morel, conica, and angusticep (fig. 1).

Description—**Head:** in profile broadly rounded, conic to irregularly ellipsoid when young, often broadening especially near the stalk as it matures. **Ribs:** minutely and inconspicuously velvety when young, becoming dry and smooth with age; shades of dull grayish tan, steely gray, or dark brownish gray when young, becoming black by maturity; edges typically remain intact and sterile. **Pits:** dull grayish tan to steely gray when young, grayish tan or light brown in age. **Stalk:** ivory to light tan or washed with dusky rose when young, varying to tan or rosy tan in age; surface smooth at first, appearing grainy in age; never brown to black. **Spore size:** (23-)[11] 26–33 x 15–16 (-18) µm.[12]

Ecology—This common morel fruits on nonburned soils, litter, and duff including nonburned islands in burned areas. When found on burned soils, they apparently fruit no sooner than the second spring after an intense wildfire.

[11] Extreme values listed in parentheses.

[12] Fungal spores are often measured in micrometers (µm). A micrometer is one millionth of a meter in length or 1/25,000th of an inch. This unit of measure is also called a micron.

David Pilz

Figure 1—
Natural black morel.

Comments—The name “natural” for this black morel derives from commercial harvesters who collect them from nonburned or nondisturbed forests, hence fruiting under what they referred to as “natural” conditions. Arora (1986) diplomatically circumvents the controversy surrounding an appropriate scientific name for this species or group of species by referring to it as “the so-called ‘*M. elata-M. angusticeps-M. conica*’ complex.” It appears to be widespread, common, and is routinely harvested from nonburned forests in the Pacific Northwest. Black morels, that we believe were this species, fruited prolifically in nonburned but insect-killed, grand fir stands on the Lakeview Ranger District of the Fremont National Forest, Oregon, in 1994 (Weber and others 1996). Pilz and others (2004) reported this morel as the most abundant on their nonburned plots (both healthy and insect-killed forests) and it also fruited the second year (but not the first) following a fire on burned plots.

Pink morel—previously lumped with those referred to as angusticeps, conicas, burn, fire, or black morels

(No definitive image available)

Description—**Head:** at first elongate conic with rounded conic apex, sometimes expanding to broadly conic in age. **Ribs:** not conspicuously velvety when young, becoming dry and smooth in age; cream-colored to pale shell pink when young, typically black well before maturity; edges typically remain intact, sometimes with a fertile strip down the center. **Pits** cream-colored to dusky pink or pinkish tan when young, becoming pinkish tan to light pinkish brown at maturity. **Stalk:** white or nearly so at all ages; smooth at first becoming slightly grainy in age; never brown to black. **Spore size:** 21–24 x 13–16 µm.

Ecology—Fruiting likely restricted to burned soils the first spring or early summer after an autumn fire, but in very small quantities, if at all, thereafter.

Comments—Although genetically distinct (Pilz and others 2004) from the natural black morel, and fruiting under different ecological circumstances (burned versus nonburned forests), this species has not been differentiated in current field guides. Additional work will be necessary to describe reliable differences in appearance from the green morel, and possibly other species, that fruit in the same habitat and ecological conditions (burned soils).

Green morel—also previously lumped with those referred to as angusticeps, conicas, burn, fire, or black morels

(No definitive image available)

Description—**Head:** at first elongate-conic with rounded conic apex, sometimes expanding to broadly conic in age. **Ribs:** not conspicuously velvety when young, becoming dry and smooth in age; gray when young, becoming black well before maturity; edges typically remain intact, sometimes with a fertile strip down the center. **Pits:** dark gray to dark olive gray when young, olive gray to olive brownish gray in age. **Stalk:** white or nearly so at all ages; smooth at first becoming slightly grainy in age, never brown to black. **Spore size:** 20–24 x 13–16 µm.

Ecology—Fruiting likely restricted to burned soils the first spring or early summer after a fall fire, but in very small quantities, if at all, thereafter.

Comments—The natural black, pink, and green morels we describe all key out to *Morchella elata* complex, *M. conica*, or *M. angusticeps*, depending on the reference used. Kuo (2006) suggested that what we call pink and green morels actually are part of a complex of more than two species and that morphological differences remain inadequately described to distinguish among them without DNA analysis. From an observational perspective, commercial harvesters see more morels than scientists do, and although their methods of drawing conclusions might not be as systematic or precise, harvesters invariably recognize differences in the mushrooms they collect. For instance, one experienced harvester states:

> Some harvesters already distinguish the green species of black fire morel, calling them "pickles." They assert that compared to other black fire morels, green morels dry and re-hydrate differently, are more robust, bruise reddish or brown, and fruit later in the season when gray morels begin to appear.[13]

Gray morels—also called fuzzy foot morel, black stocking morel, or black foot morel (fig. 2).

Description—**Head:** elongate-ovoid to nearly columnar when young, expanding variously in age. **Ribs:** conspicuously velvety/hairy when young, the hairs collapsing with age; silvery gray to charcoal gray when young; gray to black at maturity where intact; edges extremely fragile, soon cracking and breaking away to expose the white to ivory underlying tissue; lacking fertile tissue. **Pits:** deep gray to nearly black when young, varying from gray to tan to dark ivory in age. **Stalk:** charcoal gray to nearly black when young, becoming pale gray to tan to ivory at

Karl Olson

Figure 2—A series of photographs illustrating color changes in a maturing gray morel. Photographs taken June 25, July 2, and July 9, 2003, at the Livengood Fire (78 miles NW of Fairbanks, AK). Note varied scales (spruce needle size) and lighting in each photograph.

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[13] Evans, Larry. 2005. Personal communication. President, Western Montana Mycological Association, P.O. Box 7306, Missoula, MT 59807.

maturity; densely velvety from projecting hyphae when young; the velvety layer stretched apart leaving tufts of brown hyphal tips on an ivory, off-white, or pale tan background in age. **Spore size:** 19–25 x 13–16 µm.

Ecology—The gray morel fruits in conifer forests and is found abundantly the first spring or summer after a wildfire and in reduced numbers the second postfire year. It is found in greatest abundance at high elevations and northern latitudes. Its fruiting season of late spring into summer (McFarlane and others 2005) follows, but overlaps, the fruiting of the pink and green burn morels.

Comments—McFarlane and others (2005) described the gray morel as being large, heavy, and durable, and as having a "double wall," a feature that refers to alternating darker and lighter layers of flesh seen when the stem is cut in cross section during harvesting. The gray morel is a good match for what McKnight (1987) called the "burn site morel" or *Morchella atrotomentosa* (Moser) Bride. Because Moser (1949) described *M. esculenta* var. *atrotomentosa* as a "*nov. var. ad.*[*sic*] *int.*" or "temporary new variety," not as an unqualified new variety, it is not considered to have been published in accordance with the International Code of Botanical Nomenclature (Greuter and others 2000). Thus neither that name nor combinations based on that name are available for valid scientific use. This morel would not currently be considered a close relative of *M. esculenta* anyway. Although the common name of "gray" morel is widely used for this species in the Pacific Northwest; in eastern North America, young specimens of some yellow morels also are called "gray" morels (Weber 1988:103). Kuo (2006) called this morel the "fuzzy foot" morel to avoid using color attributions, because the color of the fruiting body changes as it matures.

Mountain blond morel—also called western blond morel (fig. 3).

Description—**Head:** columnar to narrowly obtusely conic when young, variously expanding with maturity but typically remaining relatively narrow in relation to height. **Ribs:** essentially glabrous when young, becoming dry and waxy in age; pale grayish tan when young, ivory to pale tan in age and then often with rusty ochre stains; edges typically remain intact and are sterile. **Pits:** light smoky gray when young, near straw yellow or the color of a manila folder in age. **Stalk:** ivory to cream-colored, sometimes with rust-colored or amber discolorations; smooth. **Spore size:** 23–26 (-28) x 14.3–16 (-18) µm.

Ecology—Both the mountain blond and yellow morels occur in western North America, but the mountain blond morel appears to be more commonly found in conifer forests (especially true fir, lodgepole, or ponderosa pine forests), whereas yellow morels are found more often in riparian hardwood forests that are sometimes mixed with conifers (Pilz and others 2004). Kuo (2006) called this putative species the "western blond" morel, and suggested that it also can be found among hardwoods at lower elevations and that it is primarily distinguished from the yellow morel by the morphological features described in the next paragraph.

Comments—The mountain blond morel closely resembles yellow morels (*M. esculenta* in the broad sense). In parts of Oregon, these two morels are often lumped together as "esculentas." However, a close comparison of specimens with most descriptions of *M. esculenta* from Europe or elsewhere in North America reveals differences. Unlike members of the yellow morel complex centered on *M. esculenta*, the head is relatively narrow rather than oval or rounded, especially in young specimens. Also, the primary ribs are strongly vertical and relatively straight, thus producing elongated pits rather than the rounded to somewhat irregular pits generally attributed to *M. esculenta*.

David Pilz

Figure 3—The mountain blond morel (center), compared to two natural black morels (either side). All specimens found on the Sisters Ranger District, Deschutes National Forest, in a pine forest that had been thinned the year before, but not burned.

Yellow morel—Also called esculentas, common morel, and many other common names (fig. 4).

Description— **Head:** oval to subcylindrical or slightly tapered toward the apex, but seldom strongly conic. **Ribs:** at first similar in color to pits and close together, gradually spreading as the head expands and becoming paler than the pits; usually white to creamy white, then stained rusty yellow or dingy brown; more waxy than velvety; collapsing or flaking away in old age. **Pits:** generally more round than elongate in maturity; pale dingy gray to tan when young, becoming tan, dull ochraceous, or golden tan as spores mature. **Stalk:** off-white to ivory or pale cream color; appearing covered with fine meal in youth; surface layer stretched apart in age; base often enlarged, appearing pleated or gathered. **Spore size:** 21–25 (-28) x 12–16 µm.

Ecology—This species is usually found in riparian forest of willow, cottonwood, alder, or ash, or sometimes in oak forests or fruit orchards, In the west, black morels are more abundant at high elevations than yellow morels, although their ranges overlap (Arora 1986).

Comments—Yellow morels are less common in western than in eastern North America. In western montane forests that consist solely of conifer tree species, light-colored morels might more likely be the mountain blond morel. Along coastal California, yellow morels are likely the red-brown blushing morel, *Morchella rufobrunnea*.

Pamela Kaminski, http://www.pamelasmushrooms.com/

Figure 4—
Yellow morel.

click here to continue

Red-brown blushing morel—*Morchella rufobrunnea* (fig. 5).

Description—**Head:** conical to subconical to ovoid when mature. **Ribs:** whitish to grayish when young, becoming yellowish, brownish, or brownish-yellow with age. **Pits:** vertically elongate when young, becoming irregularly shaped with age. **Stalk:** irregularly wrinkled near base with minute dark granules toward the top; whitish to cream, pale gray, darker grayish brown, yellowish toward base, blushing in irregular spots brown, brownish orange, or pinkish red to ferruginous when injured or maturing (both head and stalk), sometimes almost completely reddish brown. **Spore size:** (19-) 20–24 (-25.5) x (13-) 14–16 (-17) µm.

Ecology—Growing in moist subtropical oak, sweetgum, white-alder (*Clethra*), and alder forests in the Xalapa region of Mexico. Perhaps also along coastal California in landscaping mulch.

Comments—Kuo (2005, 2006) suggested that what has been identified as *M. deliciosa* in California is actually *M. rufobrunnea*. He also suggested that *M. rufobrunnea* was the morel that Ower described cultivating in his first patent (Ower and others 1986), rather than *M. esculenta*. At the time of the patent, *M. rufobrunnea* had not yet been described and was not yet suspected as a separate species along coastal California. *M. guatemalensis* and *M. herediana* are other morel species that occur in subtropical regions of Mexico and Central America, but do not range further into North America (Guzmán and Tapia 1998).

Hugh E. Smith, http://www.hughsmith.org/

Figure 5—Red-brown blushing morel.

Half-free morel—*Morchella semilibera* (fig. 6).

Description— **Head:** often taller than broad, subcylindric to broadly conic with a rounded to truncated apex when young; often broader than tall in age; up to one-half of the lower part of the head and margin free of the stalk and forming a skirt, otherwise attached to stalk in the same manner as other morels. **Ribs:** often running from the top to the bottom of the head with irregular cross-ribs; ribs broad, flat, moist to velvety in youth, and collapsing and darkening to dark grayish brown or black in age. **Pits:** grayish tan when young, grayish tan to tan at maturity. **Stalk:** ivory white to dull creamy yellow, surface scurfy as if dusted with fine cornmeal or bran, elongating to 2.5 to 3 times the length of the head with age; tapering toward the apex, swelling especially at the base, and becoming fragile. **Spore size:** (19.5-) 22.5–26 (-30) x (12-) 14–17 (-21) µm.

Ecology—Occurring under conifers, cottonwoods, and alder. Fruiting is erratic.

Comments—The half-free morel in the western North America might be a different species than that in the east. Kuo (2005) mentioned a half-free morel from Oregon that differs genetically from the eastern half-free morel. He also suggested that both are different from the European *M. semilibera*. If so, new scientific names might be forthcoming, but the half-free morel is morphologically distinctive and for now we chose to retain the use of the scientific name *M. semilibera*. The habitat of this morel is similar to both the edible yellow morel and the potentially poisonous *Verpa bohemica* or “early morel.” Be sure to check whether the head is attached to the stem part way down. This is best discerned by cutting the specimen in half lengthwise from top to bottom for a longitudinal-section view. If the head is attached to the stem halfway down, it is an edible half-free morel; if the head is attached only at the top of the stem, it is a potentially poisonous *Verpa*.

Pamela Kaminski, http://www.pamelasmushrooms.com/

Figure 6—Half-free morel (*Morchella semilibera*).

Potentially harmful look-alikes—Two closely related genera of mushrooms have potentially harmful species that could be mistaken for morels by the inexperienced harvester. These are *Verpa* (the thimble morels) and *Gyromitra* (the false morels or lorchels). Some people consume some species in these genera, and *Verpa bohemica* is sometimes sold commercially. However, some species in these genera are potentially toxic, especially if improperly cooked, and are best avoided. Arora (1986), Kuo (2005), and Weber (1988) provide good descriptions of these genera and species, as do most mushroom field guides. Figure 7 illustrates key differences in appearance between *Morchella* species and representative *Verpa* and *Gyromitra* species. Species in the related genera *Helvella* (elfin saddles), *Disciotis* (veined brown cup fungus), and *Discina* (pig's ears) are not shown because their features are easily distinguished from the pitted and ridged heads of morels. Readers are encouraged to familiarize themselves with the differences among all these genera before collecting true morels. This publication is not an identification guide. The reader is responsible for her or his own health. For further information about the risk of eating these mushrooms, see the section on "Toxins and Contaminants."

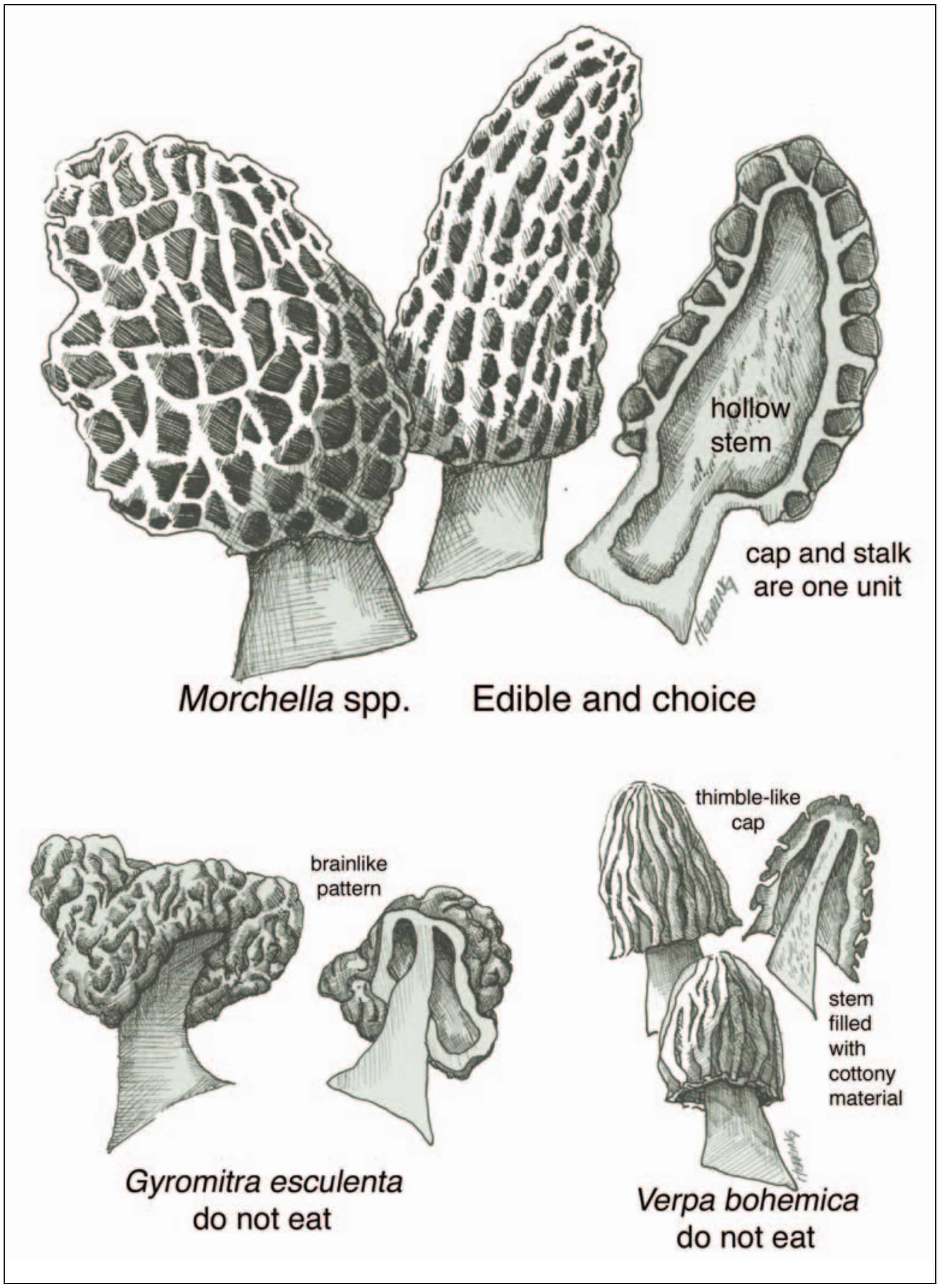

Figure 7—Comparison of three genera sometimes referred to as "morels": *Morchella, Gyromitra,* and *Verpa.* Some species in the genera *Gyromitra* and *Verpa* contain poisonous compounds and should be avoided. Illustrations by Margaret Herring. Reprinted from Wurtz and others (2005: 8).

Biology

To understand how morels seem unique among edible forest fungi in their adaptations, it is necessary to understand their life cycle, modes of nutrition, and reproductive strategies.

Overview—The broad ecological amplitude and environmental plasticity discussed by Wedin and others (2004) were considered adaptations to environments that experience unpredictable periods of rapid change. These strategies could prove useful to morels because they live in forests that experience episodic and catastrophic events such as wildfires, insect infestations, windstorms, volcanism, earthquakes, floods and, more recently, human-caused disturbances such as logging. To understand how morels seem unique among edible forest fungi in their adaptations, it is necessary to understand their life cycle, modes of nutrition, and reproductive strategies.[14] We begin with a brief overview of how fungi live and reproduce in order to clarify how morels differ from most other harvested forest mushrooms. Then we describe the sequential stages of a morel life cycle.

Mushrooms are the reproductive structure of some types of fungi. They generally are fleshy and have a stem and a cap or (in the case of morels) a head. Mushrooms are one type of "sporocarp" meaning "spore-bearing fruit or structure." Conks and truffles are examples of others. Sporocarps are also commonly called "fruit bodies" or "fruiting bodies" (American usage), although they are not technically "fruits" like those formed by plants.

Fungi are an entire branch on the tree of life, and actually shared a common ancestor with animals more recently than either did with plants. Many types of fungi, for instance yeasts, live as single cells. Others, such as the fungi that produce mushrooms, form filamentous multicellular structures that can be quite large. They do this by producing one-cell-wide strings of cells called hyphae (hypha singular). These threadlike hyphae often form dense interconnecting webs. Such webs of hyphae are called mycelia or mycelial colonies. A mycelium (singular) would typically represent a colony formed by a genetically distinct individual, and a collection of separate genetically distinct mycelial colonies would be called mycelia (plural). As we will see, morel mycelial colonies cannot simply be considered genetically distinct individuals as are the mycelia of many other mushroom-producing fungi.

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[14] Technical mycological and genetic terminology is necessary to clearly explain these topics. Potentially unfamiliar concepts are explained and the glossary contains definitions for some of the less common terms we use. Ulloa and Hanlin (2000) and Kirk and others (2001) also provided definitions of mycological terms. King and Stansfield (2002) and Rédei (2003) can be consulted for genetic terminology, although a good, recent, standard dictionary is likely adequate. For the sake of brevity, many topics are incompletely explained, some scientific terminology is avoided, and exceptions to generalizations are sometimes not mentioned. Our intent is to provide a wide range of readers with a basic understanding of how morels differ from other important wild edible mushrooms; the implications that these differences have for understanding morel biology, ecology, and reproduction; and how the differences relate to managing forests for sustainable morel harvesting opportunities.

The mycelia of multicellular fungi live and grow inside their food sources. Because fungi do not have chlorophyll, they cannot produce their own food and must obtain it elsewhere. Fungi absorb nutrients directly through their cell walls from the nutritional substrate in which they grow. They also can excrete enzymes that break down resistant compounds (such as lignin in wood) into simpler molecules that can then be absorbed. Among fungi as a group, almost any other organism can serve as a source of food, even other fungi. Each species of fungus, however, usually concentrates on just a few types or sources of nutrition. These can be living or dead organisms. Fungi that eat (decompose) dead organisms are called saprobes. Fungi that kill or harm the live organisms they are consuming are called parasites. But many fungi have evolved mutually beneficial (symbiotic) relations with photosynthetic organisms such as plants, algae, and cyanobacteria. In these cases, the host organism derives some benefit from the fungus in return for providing the fungus with food. Perhaps the most important such symbiosis is mycorrhizal. The term mycorrhiza (mycorrhizae or mycorrhizas plural) literally means “fungus-root.” Mycorrhizae are dual organs of absorption common to almost all land plants. The fungal hyphae actually grow among, and in some cases into, the outer cells of the plant’s root tips. This is the zone where nutrients are exchanged between the fungus and the plant. The hyphae of mycorrhizal fungi also grow out into the soil, where their mycelial web creates what is functionally a vastly larger fine root system for the plant than it could produce itself. The fungus absorbs water and mineral nutrients with its mycelial network and shares them with the host plant, and in return the fungus absorbs carbohydrates from the plant’s roots. This symbiotic relationship between fungi and plant roots likely played a key role in the successful colonization of land by formerly aquatic plants. For years, morels were considered saprobes, decomposing organic matter in the soil, but as we will see, some are now believed to have the ability to form mycorrhizae and other unique fungus-root structures.

Fungi that produce mushrooms can reproduce both sexually and asexually (without sex). In effect, when most fungal cells divide, they are cloning themselves (producing a genetically identical copy). For instance, a hyphal cell from a mycelial colony might get stuck to the leg of an insect and deposited elsewhere. If that cell continues to divide, it would produce another genetically identical mycelial colony in the new location. Multicellular fungi primarily reproduce with spores; these are the fungal equivalent of seeds, although spores are single-celled and much smaller than seeds. Spores can be either sexual or asexual. Morels produce a type of asexual spore called a conidium (conidia plural, also called a conidiospore). These are the equivalent of a hyphal segment creating a new clonal colony, but the fungus does it intentionally by producing a spore, designed for dispersal, on a special hyphal structure called a conidiophore. Asexual spores typically have the entire genetic complement of the mycelium that produces them. Whether asexual spores produced by morels have the entire genetic complement of the mycelium is not yet known.

One difference between sexual and asexual spores is that sexual spores typically have half the genetic material (haploid) of the mycelial colony that produced the sporocarp. Such haploid spores are produced by a process called meiosis, the same process that produces sperm or eggs in mammals. Most edible mushrooms are the fruiting bodies of fungi classified as Basidiomycetes. Morels and most culinary truffles (such as those in the genus *Tuber*) are members of the Ascomycetes, however. These two major branches of fungi are named after the type of structure (basidia or asci) where meiosis occurs and the sexual spores are formed. For instance, with matsutake, chanterelles, and boletes, basidia are found on the sides of the gills, covering the ridges under the cap, or inside the pores under the cap, respectively. In morels, asci are found on the surface of the pits in the heads.

Understanding how morel (Ascomycete) reproduction differs from that of most other edible (Basidiomycete) fungi requires a cursory explanation of fungal genetics. Genetic information in the nucleus of each cell resides on DNA molecules called chromosomes. Complex organisms have sets of a certain number of chromosomes; the particular number of chromosomes in the set is usually a trait that is common to members of a shared taxonomic grouping. It has not yet been determined how many different chromosomes *Morchella* has. Each chromosome in the set is different, that is, it has different genes coded along its length than the other chromosomes in the set. In a haploid condition (for instance a sexual spore), each cell nucleus has only one copy of each chromosome in the set. These nuclei are referred to as haploid nuclei. Diploid nuclei have two copies of each chromosome.

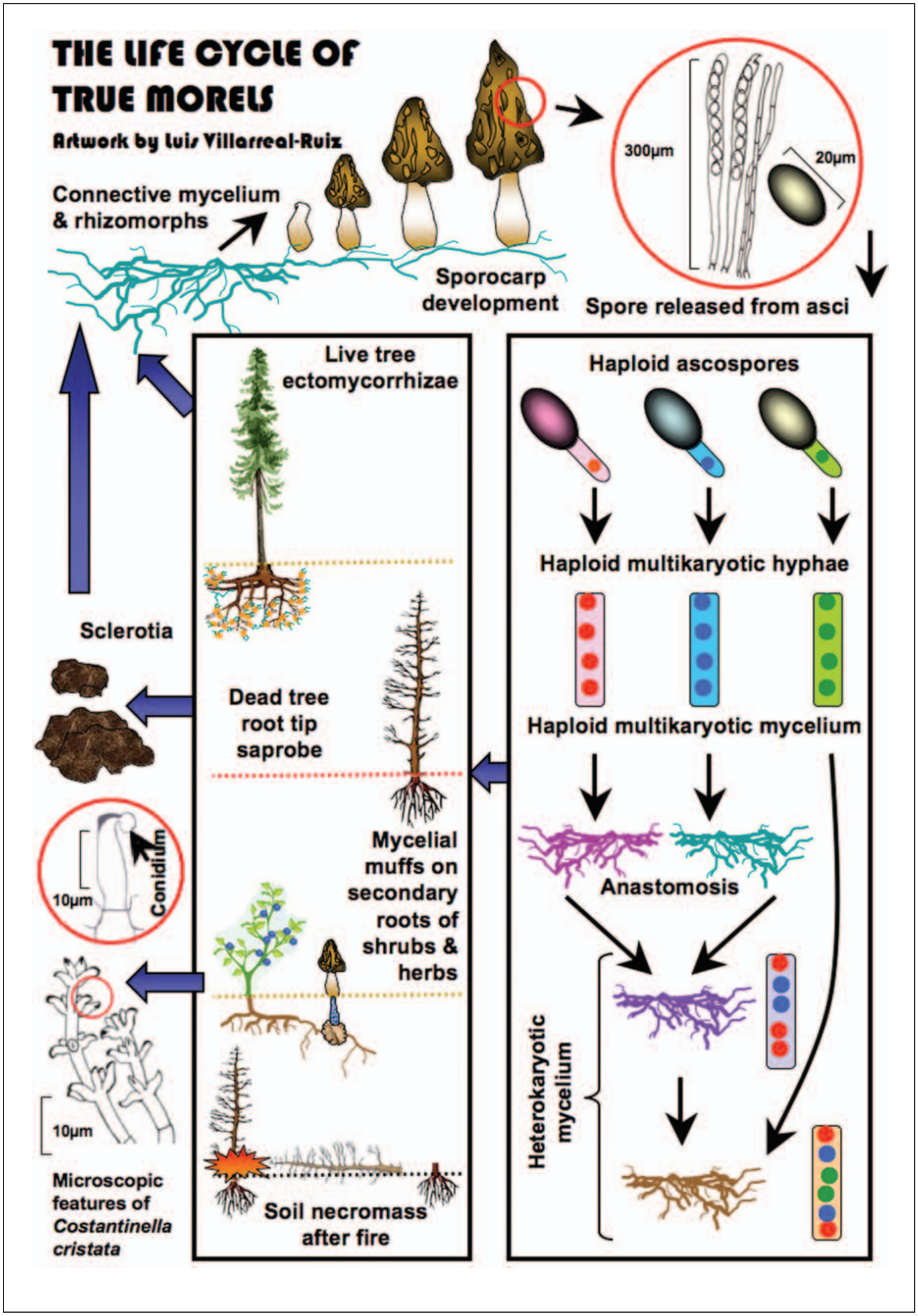
In a diploid nucleus, the paired copies of each chromosome are called homologous chromosomes. Homologous means that each of the paired chromosomes has the same genes at the same places along their lengths, but because the genes on each chromosome can differ slightly, the chromosomes are not identical. These slight variations in the genes on homologous chromosomes are called alleles. An example of allelic variation of a gene would be different alleles of the gene that codes for hair color. A useful analogy is to think of the two chromosomes in a pair as two libraries of books (genes). Both libraries contain the same books in the same order on their shelves but the individual libraries (chromosomes) might contain different editions (alleles) of any one book. During meiosis, the diploid nuclear state of the fungus individual is reduced to a haploid state in the sexual spore. In the process, the allele for a particular gene can be derived from either of the paired homologous chromosomes in the parent. Continuing the analogy above, this would be like creating a new library by photocopying each book, but selecting only one edition from either, but not both, of the original libraries. This reorganization of parental alleles on the chromosomes of the haploid sexual propagules ensures no two offspring receive the same set of alleles on their chromosomes, even if they have the same parents.

Animals and plants are diploid throughout their entire lives because two sets of homologous chromosomes pair up into a diploid nucleus during fertilization. Many fungi, by contrast, can grow for periods of time with only one haploid nucleus (or multiple copies of the same haploid nucleus) per cell. This situation is common when sexual spores germinate and grow for a while in search of other haploid hyphae that are compatible for mating. Fungi do not have genders in the sense of different male and female features, but they do have mating types that must be compatible.

Among Basidiomycetes, a haploid hypha of one mating type typically finds and fuses (anastomoses) with another haploid hypha with compatible mating-type genes. The two compatible haploid nuclei from these fused hyphae just pair up in each cell of the newly formed mycelium without combining to form the single diploid nucleus usually observed in plants and animals. These fungal hyphae are called dikaryotic (Chang and Miles 2004: 58). A karyon is a nucleus containing DNA, so a dikaryon is an organism having two nuclei per cell. In this case, however, the nuclei are haploid, consist of compatible mating types, and are paired. Such cells have the full genetic complement needed to sexually reproduce through the DNA-swapping and chromosome-halving process called meiosis, but the paired haploid nuclei in each cell do not actually fuse for this process until immediately before meiosis begins in the sporocarp.

The nuclear state of a typical morel mycelium, however, is different than many of the mushroom-producing fungi in the Basidiomycetes. Morel hyphal cells have long been observed to have many nuclei per cell. This is called a multikaryotic or multinucleate condition. Recent genetic analysis suggests that, like many Ascomycetes, these are not just multiple copies of the same haploid nuclei, but that many different haploid nuclei co-exist unpaired in the typical morel mycelium. Because the nuclei differ, this is called a hetero-karyotic condition. Morels might also be capable of the highly unusual feat of haploid meiosis. In mammals, the equivalent would be a haploid female growing from an unfertilized egg and then mating with herself to produce offspring. We will discuss the implications of these features for morel reproduction and management later in this section. Morel hyphae also can coalesce to form a number of other interesting structures that we discuss as we come to them (fig. 8).

Morels might be capable of the highly unusual feat of haploid meiosis.


THE LIFE CYCLE OF TRUE MORELS
Artwork by Luis Villarreal-Ruiz
Connective mycelium & rhizomorphs
Sporocarp development
300µm
20µm
Spore released from asci
Live tree ectomycorrhizae
Haploid ascospores
Haploid multikaryotic hyphae
Sclerotia
Dead tree root tip saprobe
Haploid multikaryotic mycelium
Conidium
10µm
Mycelial muffs on secondary roots of shrubs & herbs
Anastomosis
Heterokaryotic mycelium
10µm
Microscopic features of *Costantinella cristata*
Soil necromass after fire

Mycelia—Let us start our examination of the morel life cycle with a germinating sexual spore. Such spores are released from one of the microscopic asci lining the pits in the morel head. Asci are specialized, elongated sac-like cells where sexual spores develop; hence these spores are called ascospores. Morel ascospores have 15 to 30 or more haploid nuclei per spore at maturity (Weber 1988). Thus when an ascospore germinates, the resulting hyphae are already multinucleate or multikaryotic, that is, each cell has multiple copies of the unique haploid nucleus that was formed during meiosis. The linearly arranged cells that form morel hyphae are separated by walls called septa that have pores (Hervey and others 1978, Kendrick 2001). Physiological processes control the passage of cytoplasm (cell contents), nutrients, moisture, and nuclei through these pores. These septa allow researchers to determine how many nuclei exist in each cell. Morel mycelia are almost always multinucleate. They average 10 to 15 nuclei per cell but can range up to 65 (Hervey and others 1978, Volk and Leonard 1990).

The initial haploid hyphae of all sexually reproducing multicellular fungi must fuse with other hyphae (or propagules) containing different haploid nuclei (with compatible mating types) in order to complete a sexual life cycle. Morel hyphae anastomose readily and frequently (Volk and Leonard 1989a, 1990). The result of these frequent fusions among morel hyphae is a heterokaryotic mycelium; that is, many different haploid nuclei coexist in the same hyphae and mycelium (Arkan 1992, Volk and Leonard 1989a). Although heterokaryosis is common in some groups of fungi, it is not common among the fungi that produce most edible mushrooms such as chanterelles, matsutake, or boletes. Stott and Mohammed (2004) stated that heterokaryotic cells are found in the vegetative hyphae, sclerotia, and sporocarps of morels. Volk and Leonard (1990) suggested that there might be pairing of haploid nuclei with compatible mating types within the heterokaryotic mycelium of morels, but such pairing is not as prominent as in fungi that typically

Figure 8 (opposite)—The life cycle of true morels. Ascospores are the sexual spores of morels, resulting from the process of meiosis. They are produced in asci, which are found lining the pits of a morel head. Ascospores are often ejected forcefully from the tip of the asci. They typically contain multiple copies of the same unique haploid nucleus and when they germinate, they form haploid hyphae, also with multiple copies of the same nucleus. The right box illustrates the formation of heterokaryotic mycelia. Among many edible forest fungi, the hyphae from only two haploid spores fuse to form a dikaryotic mycelium. Among morels, additional ascospores (illustrated by green) also can fuse with pre-existing mycelia contributing their unique haploid nuclei to a mix of nuclei in what is then called a heterokaryotic mycelium. We do not know what, if any, limits or constraints there might be to the number of ascospores that can contribute unique haploid nuclei to an existing mycelium, nor whether the types of nuclei present in the hyphae differ among segments of a mycelial network. The left box illustrates the range of potential nutritional substrates that morels seem capable of using. Nutritional preferences could vary by species or environmental circumstances. *Costantinella cristata* is an asexual stage of morel reproduction wherein the hyphae of the morel mycelium form unique structures (conidiophores) to bud off spores (conidia) that include at least one, and possibly more, nuclei from the mycelium. Field and cultivation evidence suggests that sclerotia (tight masses of hyphae thought to store nutrients) can often be an intermediate stage between mycelial growth and fruiting. When morels fruit, the needed nutrients often appear to be translocated by strands of hyphae called rhizomorphs (because they resemble roots).

form paired dikaryons and, significantly, other haploid nuclei continue to co-exist in the same cells. Patterns of anastomosis and heterokaryogamy within and between morel species have not yet been fully investigated, but mycelia of some morel isolates, from putatively different species, appear not to anastomose (Volk and Leonard 1990).

Heterokaryosis in morels has several significant implications, even though the actual expression of these possibilities in nature is not well understood (Kaul 1997). For instance, the haploid hypha from a germinating ascospore does not necessarily have to search for another haploid hypha of a compatible mating type to form a dikaryotic mycelium. It might be able to simply fuse with an established heterokaryotic morel mycelium and contribute its own genetically unique nucleus to the mix of heterokaryons already in the mycelium. The heterokaryotic nature of morel mycelia might also confer adaptation to a broader range of ecological and environmental conditions (Buscot 1992b) because such mycelia have more genetic diversity than those with only two paired haploid nuclei. If hyphae from germinating ascospores can and do indeed fuse with existing mycelium, this could confer the potential for continuous variation and adaptability (Kaul 1997) in response to environmental fluctuations (for instance, episodic droughts) or trends (such as changes in soil chemistry as a forest matures). Additionally, having a variety of alleles of each gene (on the various haploid nuclei) might mask the effect of deleterious mutations because there is a greater probability that a good copy of the gene exists than if the mycelium were only dikaryotic.

Defining a morel “individual” and its spatial extent in the soil is problematic.

Additionally, defining a morel “individual” and its spatial extent in the soil is problematic. For instance, many mushrooms that are classified as Basidiomycetes (such as chanterelles, matsutake, and boletes) form distinct dikaryotic mycelial colonies that can be considered individuals. The structural tissues of all the mushrooms arising from such discrete colonies are genetically identical, so the spatial extent of the colonies can be roughly mapped by analyzing the DNA of their sporocarps. Because morels are formed by heterokaryotic mycelia, no two sporocarps need be alike. Indeed, the mycelium that produces the morel is more like a diverse genetic colony than an individual. Even morels fruiting side by side often appear genetically distinct,[15] and thus are likely composed of different combinations of the multiple haploid nuclei that exist in the mycelium from which they fruit. Therefore the extent of mycelial colonies can only be very roughly mapped by the presence of

[15] Dunham, Susie. 2005. Personal communication. Technical editor, Department of Forest Science, Oregon State University, Corvallis, OR 97331. Preliminary results from analysis of morels collected by Tricia Wurtz in her morel studies near Fairbanks, Alaska.

morels, and if such "patches" of fruiting bodies are in close proximity, it would be difficult to discern whether they are connected and share some nuclei.

The psychrotolerance (Schmidt 1983) of morel mycelia refers to their ability to grow and compete in cold soils. This trait appears to be a common feature among many genera and species in the phylum Ascomycota. For example, Schadt and others (2003) sampled fungal DNA from tundra soils under snow, and of the 125 sampled clonal sequences they extracted, at least one-third were members of the Pezizomycotina, the subphylum of fungi that includes morels. This suggests early adaptation of this fungal lineage to cold environments. In the section "Reproductive Strategies" we will discuss the potential implications of this adaptation to the mass fruiting of fire morels.

The mycelia of some species of morels can produce asexual conidia (Alexopoulos and others 1996). These are produced on and released by simple hyphal structures (conidiphores) and represent a means of clonal propagation. In effect, the mycelium "buds" into spores. No information exists about whether the full range of different nuclei found in a heterokaryotic morel mycelium is transferred into each conidium as it is formed. Individual morel conidia might or might not represent clonal propagation depending on whether all the genetic information in the parent mycelium is replicated in that particular spore. In morels, this conidial stage looks similar to powdery mildew. Because no sporocarps (mushrooms in this case) are produced by such asexual means of reproduction, mycologists working before the advent of genetic analysis often did not know the identity of fungi exhibiting a conidial stage and gave them separate names. In the case of morels, this stage was given the name *Costantinella cristata* by Matruchot (1892), but Molliard (1904a, 1904b) and Constantin (1936) confirmed it to be an asexual reproductive feature of *Morchella* mycelium. Although commonly reported in artificial cultivation, few reports exist of this stage in natural settings. Stamets (2000) reported that in outdoor settings, he only sees it on inoculated sawdust.

Morel hyphae can form a variety of other structures, including sclerotia, mycorrhizae, mycelial muffs, and sporocarps. We discuss each in the following sections. Multiple hyphae can also grow in thick root-like strands called rhizomorphs (literally "root forms"). Rhizomorphs are efficient structures for rapidly transporting large quantities of nutrients or cytoplasm from one location to another and might play an essential role in the rapid formation of fruiting bodies. For instance, morels are sometimes described as emerging from long subterranean stems or various aggregates of hyphae (Philippoussis and Balis 1995, Stamets 2005). These subterranean stems can be connected via rhizomorphs to other structures such as nutrient storage organs (called "sclerotia") (Philippoussis and Balis 1995) or to mycelial

click here to continue

aggregations (called "muffs") that form around some roots (Buscot and Roux 1987). Buscot (1989) noted that this tapered underground stem quickly disappears as morels mature.

Mycorrhizae—Morels were originally thought to be saprobic (decomposing dead organic matter) because tested cultures grow rapidly in pure culture on simple nutrients such as starches, sugars, and nitrates (Robbins and Hervey 1959) and can be induced to fruit without association with plant hosts. Mycorrhizal fungi, by contrast, grow more slowly in pure culture and do not fruit without forming a symbiosis with their host plants.

Moser (1949) suggested that some morels might have the ability to form mycorrhizal symbioses with trees or at least to form mycorrhiza-like structures. Assuming that this relationship is optional for morels that also have saprobic abilities, this form of symbiosis has been called a "facultatively mycorrhizal" nutritional strategy. Trappe (1996) discussed the nature of mycorrhizal symbioses and noted that both the structure and function of mycorrhizae are important characteristics. Each can vary with such factors as the species involved, their developmental stage, the nutrient status of each partner, seasonal shifts in their nutrient allocation patterns, and the specific soil environment. These factors create a shifting spectrum of relative advantages and disadvantages to the fungus and plant symbionts. Johnson and others (1997) provided a chart of relative benefits and costs to both fungus and host along a spectrum from mutualism to parasitism, but recognized that net benefits and costs can change over time as circumstances change for each symbiont. Not only is it inappropriate to assume that both partners benefit equally, but the observable structure of a mycorrhiza does not necessarily correspond to its functions. We note these caveats because most tested morels have the saprobic abilities noted above, morel mycorrhizae sometimes exhibit weakly developed structural features,[16] few studies have examined benefits to the trees, and some morels form a different type of association with the larger roots of some plants (see the following section on muffs).

Buscot and Kottke (1990) and Buscot (1992a, 1992c) described ectomycorrhizae[17] on Norway spruce associated with *M. rotunda*, *M. esculenta*, and *M. elata*. Subsequently, Buscot (1994) described seven types of morel mycorrhizae with

[16] Many types of mycorrhizal associations have been described. The interested reader can find recent information in Peterson and others (2004) and Smith and Read (1997).

[17] Ectomycorrhizae are a common type of mycorrhiza formed on many forest trees in the Pinaceae, Fagaceae, and Betulaceae. Many prized edible mushrooms such as chanterelles, boletes, and matsutake are ectomycorrhizal fungi.

Norway spruce. In these descriptions, Buscot noted that *M. esculenta* mycorrhizae featured minimal development of a Hartig net[18] and suggested that other bacteria and fungi might be involved in facilitating the symbiosis (Buscot 1992c). With *M. elata*, Buscot (1992a) reported that morel mycorrhizae only formed as a "secondary" mycorrhizae after replacing previous mycorrhizae formed by other fungi. Harbin and Volk (1999) reported that *M. esculenta* and *M. elata* were facultatively mycorrhizal with apples, elms, and black spruces. They reported formation of typical ectomycorrhizae and noted that inoculated seedlings grew more than noninoculated control seedlings. Although apples and elms are not common hosts of ectomycorrhizal fungi, they can be (Molina and others 1992), and morels certainly fruit in proximity to these trees. Dahlstrom and others (2000) reported that mountain blond morels and natural black morels from the Pacific Northwest formed several typical mycorrhizal structures (ecto- and ectendomycorrhizal) with ponderosa pine, Douglas-fir, western larch, and lodgepole pine. To date, we know of no reports of fire morels being tested for their ability to form mycorrhizae.

Hobbie and others (2001) provided additional circumstantial evidence that morels might use both saprobic and mycorrhizal nutritional strategies. They studied isotope ratios in a variety of fungi noting that: "In general mycorrhizal fungi are enriched in ^{15}N and depleted in ^{13}C relative to saprobic fungi." The *Morchella* specimens they sampled yielded intermediate values.

A not-yet-tested hypothesis is that morels, by forming mycorrhizae, might also be positioning themselves to rapidly decompose the fine root tips of trees when these roots senesce or the tree dies. Abundant morel fruiting following tree death could be facilitated by such a flush of nutrients (Dahlstrom and others 2000, Pilz and others 2004, Vrålstad and others 1998).

Muffs—Whereas mycorrhizae generally form only on the terminal root tips where water and nutrients are absorbed, some morel species also appear capable of forming distinctive associations with the conducting root sections of several plants. Buscot and Roux (1987) first used the term "mycelial muffs" to describe a "fragile downy mass of relatively diffuse [morel] mycelium" surrounding conductive roots. The mycelium penetrated the phloem (living tissues just under the bark) of the root, suggesting absorption of nutrients. Although this might be considered a parasitic relationship, the root continues to function and the association appears to be short lived. The muffs seem to be connected to morel fruiting bodies and disappear

[18] The Hartig net is a structure typically formed by ectomycorrhizal fungi that consists of a network of fungal hyphae growing between the epidermal and cortical cells of a root tip.

rapidly as the morels mature. Buscot (1989) speculated that such muffs function similarly to sclerotia (see next section) by supporting fruiting body growth through rapid transfer of nutrients.

Lakhanpal and others (1991) traced rhizomorphs from morel fruiting bodies to mycelial muffs on strawberries, grasses, and ferns. Philippoussis and Balis (1995) described a morel mycelial sheath around the small roots (but not root tips) of European alder (*Alnus glutinosa*), wooly blackberry (*Rubus tomentosus*), and locust (*Robinia pseudoacacia*) in Greece. Shad and others (1990) traced rhizomorph connections between morels and the absorbing roots of strawberry and grasses, and the rhizomes of ferns, although in this case the mycelium did not form the "muffs" described by Buscot and Roux (1987). In all these reports, the morel mycelium was observed to penetrate all the tissues and cells of the root section where it grows except the water-conducting xylem.

Sclerotia—Morel sclerotia are nodules of tightly woven hyphae (fig. 9). True sclerotia, as defined by structures formed by the species *Sclerotina sclerotiorum*, have a differentiated structure including a rind, whereas the sclerotia of morels is an undifferentiated dense mass of mycelium (Volk and Leonard 1989b). Hence morel sclerotia are more appropriately called pseudosclerotia (false sclerotia). For simplicity, however, we also will use the term "sclerotia" as defined by Willetts (1972) as any "macroscopic fungal resting structure." Morel sclerotia have been described as 1 to 5 cm in diameter (Leonard and Volk 1992) and having the texture of slippery walnut meat (Volk 1991). Miller and others (1994) described sclerotia associated with morels in nature as pale brown, smooth, irregular in shape, and clustered in small to large aggregates. Philippoussis and Balis (1995) noted they often incorporate soil particles and that their form varies by species. They can have thick walls and are cold tolerant (Volk and Leonard 1990). Morel sclerotia are commonly formed in pure culture and are used in artificial cultivation as a step toward producing fruiting bodies (see the section "Cultivation"). Buscot (1993) noted that the types of sclerotia formed in pure culture differ by the genetic strain that is grown and whether the strain is produced from single or multiple spores. Stamets (1993) noted that black morels produce numerous small golden-yellow to orange sclerotia, whereas yellow morels produce fewer, larger, walnut-brown sclerotia. It is widely speculated that morel sclerotia are nutrient storage organs that are resistant to desiccation and cold temperatures. In culture, sclerotia can "germinate" to produce either fruiting bodies or new mycelium (Volk and Leonard 1990). When they produce fruiting bodies, mycelia and rhizomorphs often are an intermediate stage for translocating the stored nutrients. Such translocation takes place by differential concentrations

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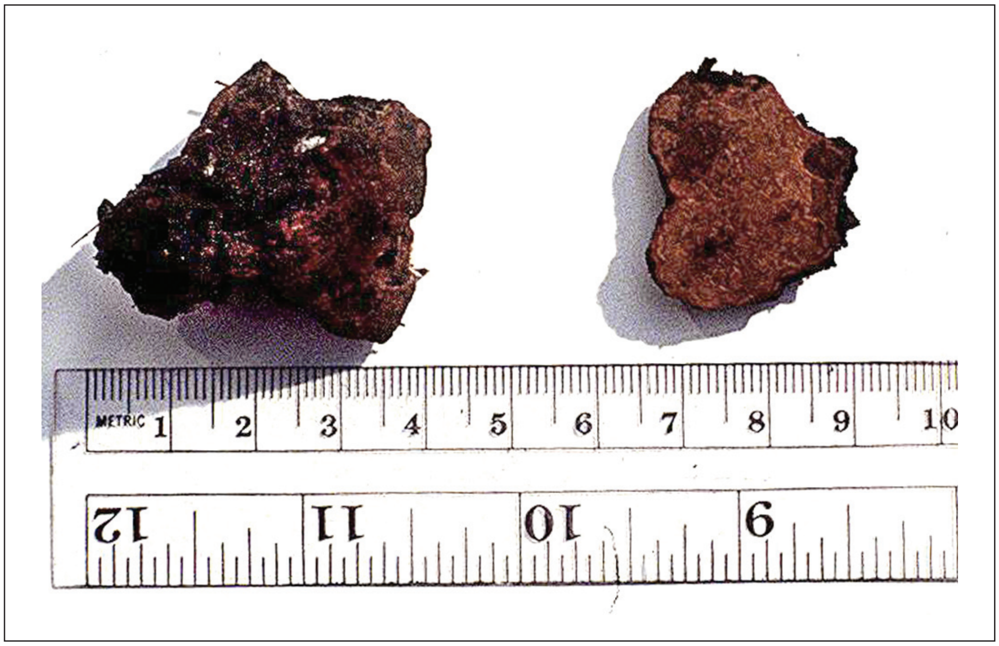

Figure 9—*Morchella* sclerotia.

of dissolved chemicals, thus producing turgor pressure that causes mass flow of cytoplasm (cell contents) through the pores in the septa that connect adjacent cells (Amir and others 1992). It has been postulated that the nutrients stored in sclerotia are translocated and depleted to produce mass fruiting following wildfires. The first year after a fire in the Grand Tetons, Miller and others (1994) found that what they believed to be morel sclerotia were more abundant in burned soils where many morels had fruited than in the nonburned soils of adjacent forest stands. The described sclerotia were still found the second year after the fire, but their numbers had declined.

Fruiting—As noted in the introduction, various factors have been associated with morel fruiting. Conceptually, these factors can be grouped into (1) conditions that facilitate mass fruiting such as loss of food supply, changes in soil pH and chemistry, loss of competition from other soil micro-organisms, or flushes of readily available nutrients; (2) environmental triggers that initiate fruiting such as changes in soil temperature or moisture; and (3) persistent conditions that support morel growth such as warmth, rainfall, and humidity.

Such fruiting may represent a last-ditch effort to reproduce when the morel's food source disappears.

Factors that facilitate fruiting—Tree death (without fire) has been noted as a factor in massive morel fruiting by many observers. Well-documented examples are provided by Pilz and others (2004) and Thompson (1994). Volk and others (1997) theorized that such mass fruiting represents a last-ditch effort to reproduce when the morel's food source disappears. In the case of morel species that fruit annually without wildfire as a trigger (such as the yellow, natural black, and mountain blond morels), the fungus might be deriving important nutrients from mycorrhizal relations with host trees and reacting to a loss of regular nutrition by fruiting more abundantly when the host tree dies. Similarly, the mass fruiting of fire morels also could be a strategy to colonize new habitats in response to loss of food resources destroyed in the fire. If fire morels can form mycorrhizae, heat-killed trees could be a lost food resource, as could incinerated duff on the forest floor or burned organic matter in the upper soil horizons. Vrålstad and others (1998) provided a good discussion of the ecological and reproductive strategies of the postfire fungus *Geopyxis carbonaria* and its adaptations to stand-replacement fires in boreal forests. They showed that *G. carbonaria* forms mycorrhiza-like structures and noted that it fruits abundantly after fires. They also speculated that the fungus derives nutrition from live trees through mycorrhizal relations, but that when the tree becomes moribund, the fungus decomposes the root tips as they die. Consequently, they regard mass fruiting as a strategy for escaping from postfire habitat rather than colonizing it. Why natural black morels do not seem to fruit the first year after a fire, even when the trees were killed, remains a puzzle because they appear to fruit abundantly when insects kill the trees in the absence of fire (Pilz and others 2004, Weber and others 1996).

Changes in soil pH and mineral chemistry following fires or other soil disturbances have also been advanced as reasons for mass morel fruiting. A variety of studies (Brock 1951, Ghosh and Majumdar 1986, Güler 2000, Kaul 1975, Singh and others 2004, Winder 2006) have examined the effects of pH and mineral nutrition on mycelial growth in pure culture and fruiting in the field. Winder (2006) cultured and tested isolates from vouchered sporocarps that were tentatively identified as *M. elata*. The best pH for growth of mycelium in culture varied by the relative concentration of calcium and other inorganic ions commonly found in wood ash, but neutral pH values were generally optimal. In northern India, Singh and others (2004) provided the most detailed description of soil properties where morels fruit. These soils are typically sandy loam with humus, good aeration, and pH from 6.5 to 7.0. Compared to soils where morels were not fruiting, they had higher levels of carbon, nitrogen, calcium, nitrates, and sodium, and lower levels of phosphates, chlorides, and potassium.

Carpenter and others (1987) made the point that phoenicoid fungi[19] (fungi that fruit in burned areas) are not just associated with fires, but also with soils heated by volcanism. Their study of areas affected by the 1980 eruption of Mount St. Helens in Washington state found that the explosive blast blended organic debris and pH-neutral tephra into a heat-sterilized mix that buried live mycelium under snow. As the snow melted, surviving fungal mycelium in the buried soil had the opportunity to grow into this deposit, presumably without significant competition from other soil microbes. Morels fruited abundantly in such heat-sterilized mixed deposits on north-facing slopes and in heat-killed but standing forests that received an 8- to 15-inch ash deposit, but not in areas with deeper deposits or no admixed organic matter.

None of the aforementioned studies, however, postulates a mechanism that would explain how pH or mineral changes could nurture abundant fruiting, although a higher rate of nitrification as a result of increased soil pH after a fire does facilitate decomposition of soil organic matter (Pietikäinen 1999). Likely what is most important for abundant fruiting is a readily available source of carbohydrate nutrition to support the energy-intensive production of numerous ephemeral sporocarps. Reduced competition from other soil microbes and flushes of easily decomposable organic matter following soil heating are plausible contributors to such nutrition.

González-Pérez and others (2004), Hart and others (2005), Pietikäinen (1999), Pietikäinen and others (2000), and Treseder and others (2004) provided recent reviews and discussions about how forest fires affect soil microbial communities and organic matter. In all cases, these effects depend on a large variety of factors such as fire intensity and duration, soil moisture, soil type, and the thickness of various soil layers. Fritze and others (1994) noted that forest fires, depending on intensity, can reduce microbial (fungal and bacterial) biomass in the humus layer of the soil by 30 to 85 percent, and this can last for 5 or more years. Pietikäinen (1999) noted that bacteria are generally more tolerant of heat than fungi are, so fungal competitors could be disproportionately affected by heating the upper layers of the soil. A flush of easily decomposable organic matter could come from heat-induced changes to existing organic matter in the soil, or from newly formed "necromass," that is, all the forest soil organisms killed by the fire. Such necromass could consist of plant roots, arthropods (insects), annelids (earthworms), mollusks (slugs and snails), fungi, and bacteria. González-Pérez and others (2004) noted that necromass

A flush of easily decomposable organic matter could come from forest soil organisms killed by the fire.

[19] Named after the mythological bird called the Phoenix, which arose from the ashes of its own pyre.

from moderate burns can provide a large input of readily decomposable substances. Lipids derived from recently dead plants and microbes in the upper layers of moderately burned soils can constitute 2 to 6 percent of the organic matter in the soil humus. Fritze and others (1994) estimated that microbial biomass alone constitutes approximately 2 percent of soil carbon in coniferous forests. Pietikäinen and others (2000) reported that when forest soil is sterilized at 285 to 320 ºF and reinoculated with native microbes, there is a peak of microbe respiration about a month later, indicating the presence of easily decomposed necromass, readily available soluble organic matter, or both.

Although high temperatures (greater than 450 ºF) can alter existing organic matter to create organic compounds that are toxic (Fritze and others 1998) or more resistant to decay (Czimczik and others 2003, González-Pérez and others 2004, Pietikäinen 1999), other organic compounds become more soluble (Moser 1949, Pietikäinen 1999) or easily decomposed, especially at moderate temperatures (around 300 ºF). González-Pérez and others (2004) noted that hemicelluloses and lignin begin to degrade into simpler (hence more digestible) compounds at 265 to 375 ºF. Egger (1986) tested the enzymatic abilities of a variety of postfire ascomycetes. He tested one morel isolate that he identified as *M. elata* that was collected from the ashes of a burned wood pile in a gravel pit. That isolate did not associate with roots, nor did it show any ability to decompose oils or lignin, but it did exhibit strong cellulase activity. Based on this evidence, Egger classified his isolate as belonging to a litter/fine root decomposer group.

The availability of readily utilized organic matter in burned soils is consistent with claims by Stamets (2005) that artificial morel patches can be established by inoculating recently burned areas. Circumstantial evidence also supports the notion that ideal conditions for morel growth might result from moderate soil heating. Commercial harvesters report fire morels fruiting in the "red needle zone," that is, areas where the fire was hot enough to kill the trees, but not so hot that the canopy was consumed. The next spring, dead reddish needles fall in these areas (McFarlane and others 2005). Keefer (2005) likewise reported that fire morels fruited in areas where 20 to 100 percent of the duff layer was consumed by a fire, but occurred most abundantly in areas where a moderate 60 to 80 percent of the duff layer was consumed. Morels do fruit in intensely burned areas also. Perhaps such morels have sufficient nutrients for fruiting already stored in their sclerotia or maybe they obtain a flush of carbohydrate nutrition from necromass formed in deeper, less-heated layers of the soil.

Factors that trigger fruiting—Temperature and moisture are thought to act as stimulants to initiate fruiting and as requirements for continued fruiting. Buscot

(1989) noted that *Morchella rotunda* begins fruiting when soil temperatures exceed the minimum of 43 ºF and the speed at which morels mature thereafter is related to the time-integrative measure of degree-days above that baseline temperature.[20] Similarly, the initiation of morel fruiting in Missouri is related to degree-days above 36 ºF.[21]

Stamets (2000) observed that air temperature fluctuations between 40 to 60 ºF during spring initiate the formation of the morel primordia (miniature "buttons" that have the potential to grow into full-sized morels). He stated that temperatures above 60 ºF encourage the primordia to grow but halt the formation of new primordia. Thompson (1994) claimed that soil moisture is only important for morel fruiting after the soil has warmed, whereas Goldway and others (2000) suggested that slowly drying soil stimulates morel fruiting.

Factors that support fruiting—Once morels begin to fruit, total seasonal productivity might be related to the amount of rainfall during a short period of optimal temperatures. For instance, during the years 2001 to 2005 in north-central Missouri, the first day of morel fruiting reliably fell between the 104th and 110th days of the calendar year (mid-April) and total seasonal production was closely correlated with the number of rainfall events of greater than 10 mm during the next 2 weeks (see footnote 21). Such rainfall not only hydrates the morel mycelium that is nourishing the growing fruiting body, but likely also maintains high humidity levels near the soil surface so the growing morel does not dry out and shrivel.

Fruiting body—A morel mushroom (fruiting body or sporocarp) is the reproductive structure that *Morchella* species use to produce and disseminate their spores. Morel fruiting bodies seem able to arise directly from diffuse mycelia, from dense muffs of mycelia in the soil, or via rhizomorphs or hyphae that transport nutrients from sclerotia or mycelial muffs surrounding plant roots (Buscot 1989, Buscot and Bernillon 1991, Volk and Leonard 1990). Morel mycelia and muffs appear to shrink as the fruiting bodies develop (Buscot 1989) so it is probable that water, cytoplasm, and nutrients are being translocated to the sporocarp as it develops.

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[20] Degree-days are calculated by summing, across all of the days within the period measured, the difference between a selected baseline temperature and the daily mean temperature. For instance, if the mean temperature on day one was 2 degrees above the chosen baseline temperature, and on day two it was 3 degrees above the baseline temperature, the cumulative degree days for that 2-day period would be 5.

[21] Bruhn, Johann[a] and Mihail, Jeanne[b]. 2005. Morchella fruiting patterns relative to climate and associated vegetation. [[a]oral presentation, [b,a]unpublished abstract and poster]. 4th international workshop on edible mycorrhizal mushrooms, 29 November–2 December, Murcia, Spain. [a]Forest Mycologist, 108 Waters Hall, and [b]Professor, Department of Plant Pathology, 109 Waters Hall, University of Missouri, Columbia, MO 65211.

When conditions are optimal, these primordia can grow, in 1 day, into morel fruiting bodies that are two-thirds their final size.

Buscot (1989) described three stages of morel growth. The initial "pre-emergence" phase lasts about 3 to 4 weeks and consists of producing the initial primordia. When conditions are optimal, these primordia can grow, in 1 day, into morel fruiting bodies that are two-thirds their final size. Final growth in size and maturation can take 1 to 10 more days. Likely the length and timing of these phases differ by morel species, native habitat, local environmental conditions on the forest floor, general climate patterns, and specific weather events. Masaphy (2005) presented a detailed description of the development of morel fruiting bodies and their microscopic structures illustrated with a scanning electron microscope. Ower (1982) provided a series of six photographs of morel development from a primordium to a young sporocarp over a period of 21 days. Weber (1988) also included a series of four photographs taken over 16 days showing the growth of a fruiting body of a yellow morel.[22]

Morels form their spores in a structure called an ascus (asci plural). An ascus is an elongated tube that typically holds eight sexual spores produced by meiosis. In morels, asci line the pits in the head of the morel but not the ridges (Alexopoulos and others 1996). The fertile layer where asci are formed is called the hymenium.

If sexual spores are to be produced, at some point two compatible haploid nuclei must pair up to engage in the genetic mixing process of meiosis. In many mushrooms, such pairing occurs before the fruiting body is formed, so all of the hyphae that fuse to form the fruiting body have the same dikaryotic cells. The situation appears more complex in morels. Greis (1940) first described the early steps of meiosis occurring in the morel sporocarp immediately underneath the hymenium, but the nuclear condition of the hyphae was not described (Volk and Leonard 1990). Ower and others (1986) claimed in their patent for growing morels commercially that morel mushrooms can be formed from monokaryotic (haploid) "primary" mycelium derived from a single spore. Gessner and others (1987) found parental genes from more than one set of parents when they compared the genetic makeup of offspring from single *M. delicious* or *M. esculenta* sporocarps, but they also found the sporocarp tissue to be haploid. Kendrick (2001) described how dikaryotic hyphae often proliferate in ascomycete sporocarps formed mostly by haploid hyphae. Volk and Leonard (1990) described the ascus mother cell (where meiosis occurs) as multinucleate. At least by this point in the development of the sporocarp and its microscopic structures, compatible haploid nuclei must pair up if meiosis is to occur. Perhaps each morel is composed of a variable mixture of mono-, di-, multi, or heterokaryotic hyphae and the pairing of haploid nuclei can occur anywhere

[22] Photographs taken by Jim Weber.

from the mycelium (Volk and Leonard 1990) to the ascus mother cell immediately preceding meiosis. If the hyphae that form morel sporocarps contain a variety of different haploid nuclei, then the ascospores produced by that fruiting body could derive from equally varied genetic lineages. Whatever the case, laboratory and genetic techniques have advanced sufficiently so that common patterns of nuclear condition and nuclear pairing in morel sporocarps could be characterized and whether these patterns differ by species or other factors also could be determined. The nuclear condition of the hyphae that form morel mushrooms and the location where compatible haploid nuclei pair up in preparation for meiosis require greater clarification if genetic population studies based on analyzing sporocarp tissues are to be correctly interpreted. Similarly, until more is known, researchers comparing growth characteristics in pure culture, or breeders selecting strains for cultivation, run a risk of being incorrect if they assume that two tissue cultures from the same sporocarp are genetically identical or that all spore cultures from a given sporocarp derive from copies of the same two paired haploid nuclei as in dikaryotic fungi.

Experienced morel hunters and morel taxonomists know that morels differ widely in their appearance. Their polymorphism might reflect genetic variability, but likely some of the variation is also environmentally induced. For instance, Stamets (2000) has noted environmentally-induced variation in appearance of morels grown from a single clonal culture (or strain) of genetically identical mycelium. Tiffany and others (1998) noted, in a summary of the morel collection project conducted by the Prairie States Mushroom Club during 1984-95, that morel collections differed widely in appearance. Sometimes specimens seemed to change species as they aged, while at other times they retained characters they typically displayed when they were young. Morels are known to produce beta-alanine and similar compounds that in combination with various biochemical pathways can produce a range of colors and shades from green to black (Jacobs 1982). These pigments are thought to be produced in response to sunlight and provide protection from ultraviolet radiation. Darker pigments could also warm the sporocarp during cool spring weather by more effectively trapping infrared radiation.

Although mammals and birds rarely consume morels (Lonik 2002), certain insects love them, creating competition that recreational and commercial morel harvesters sometimes face. For instance, Wurtz and others (2005) reported that one year 50 percent of the morels collected on research plots in Alaska were infected by insects from either the insect family of Mycetophilidae (fungus gnats) or Sciaridae (black fungus gnats). In other years, none had insects. Cobanoglu and Bayram (1998) found 13 species of mites and 2 species of flies associated with *M. conica* and *M. esculenta* in Turkey. Werner (2002) described morels in California being infected by *Aradus debilis* (and possibly other *Aradus* species), an interesting beetle-like true bug (order Hemiptera) called flat bugs (family Aradidae). For feeding, these bugs have a "long, thin, tube-like stylet" (rostrum) instead of chewing mandibles. They insert this stylet into individual hyphae of the morel and suck out the cell contents. This feeding stylet can be longer than the bug's body length and is strong enough that the bug can hang by it. However, when a morel is picked, the bug drops off, presumably because it detects a loss of turgor pressure as the mushroom is severed from its mycelium. Werner (2002) also found wireworms (larvae of click-beetle family Elateridae), rove beetles (family Staphylinidae), and millipedes (class Diplopoda) on or in morels. Because millipedes generally feed on detritus (dead organisms), perhaps they found shelter in the morels and ate them as they decayed.

Spores—As previously noted, the ascus mother cells are multinucleate, but only one pair of two compatible haploid nuclei migrates into each developing ascus, goes through the process of meiosis, and contributes new haploid nuclei to the ascospores. After meiosis, the newly recombinant haploid nucleus in each spore repeatedly replicates itself so that by the time spores have matured and are ready for release, each has 15 to 30 copies of the same haploid nucleus (Weber 1988). The large number of nuclei in each spore might facilitate the rapid production of enzymes and proteins, thus allowing more rapid early growth than would be possible for spores with fewer nuclei. Whether the number of nuclei limit or influence the speed of morel spore germination and early hyphal growth remains to be tested, but new morel mycelia do grow very rapidly in pure culture.

Only toward the end of the 10- to 14-day development of a morel sporocarp do their spores become mature, and only then are they released (Pilz and others 2004, Weber 1988, Winder 2006). Like many Ascomycete fungi, morel spores are forcibly ejected from their asci. If the morel is not disturbed in any way, spores can simply be released over time as the sporocarp dries. Often however, when the spores are ready to be released, disturbances such as puffs of wind, raindrops, bumps by animals, or even harvesting can trigger simultaneous ejection of spores in large numbers. So many spores can be released so rapidly and forcibly, that this phenomenon can be both visible and audible (Weber 1988) even though each individual spore is tiny (about 8/1000th of an inch in length). Schmidt (1979) described a hiss that can last 2 to 4 seconds. Weber (1988) estimated that, depending on size, each morel mushroom can produce from hundreds of thousands to millions of spores.

Morel spores germinate readily without any special requirements other than moisture (Hervey and others 1978, Schmidt 1983, Volk and others 1997, Weber 1988). Thus morel spores are not likely to persist in soils (Schmidt 1983) in the manner that basidiospores can (Miller and others 1994). Because morel spores are so small, wind currents easily lift them. The open landscape following a fire increases the likelihood that more and stronger breezes will reach the ground without being blocked by vegetation than would be the case in a nonburned forest. Thus fire morels might have better opportunities to spread a greater portion of their spores over long distances than nonfire morels. However, when rainfall stimulates the release of morel spores, most are likely washed into the nearby soil.

Population genetics—If morel mycelial colonies in nature typically do contain a heterogeneous mixture of different haploid nuclei, then such colonies cannot be understood as unique or distinct dikaryotic individuals that always produce genetically identical mushrooms. Rather, they should be considered populations of nuclei or genes. For instance, Aegerter (1995) quoted geneticist Dr. Carol Carter that no two morels she has analyzed are identical, even if they are growing in a cluster (fig. 10). Even though the boundaries of a morel mycelial colony cannot be determined by mapping identical dikaryotic sporocarps (as can be done with many other edible mushrooms in the Basidiomycetes), studies of breeding and population genetics can still be conducted because these rely on similarities in gene ratios among samples, not on unique dikaryotic individuals.

David Pilz

Figure 10—A cluster of natural black morels. Likely no two are genetically identical although they are connected at the base and arise from a common mycelium.

For instance, Dalgleish and Jacobson (2005) used molecular methods of genetic analysis to determine that yellow morel colonies were effectively outbreeding (with ascospores) over distances of at least 300 to 3,000 feet in a hardwood forest in central Iowa. An unpublished genetic analysis (see footnote 15), conducted on burn morel specimens mapped and collected by Tricia Wurtz near Fairbanks, Alaska, showed that (over a distance of 450 feet) morels nearer to each other were more closely related than morels more distant from each other. Yoon (1990) reported that yellow morel populations separated by tens of miles were quite similar and might be derived from the same population, whereas gene flow was minimal between populations separated by hundreds of miles.

Inbreeding and haploid meiosis—Inbreeding occurs when closely related individuals mate or when individuals mate with themselves (self-fertilization). Inbreeding is generally disadvantageous because deleterious mutations in the organism's genome are concentrated and expressed more often as maladaptations for living and breeding in a given environment. Under certain circumstances, however, inbreeding can be useful. As an example, imagine an isolated tree that had no potential mating partner nearby. If the tree is monoecious (having both female and male sex organs), then the tree can self-fertilize, produce seeds, and establish a new population of its species. Otherwise, it would eventually die leaving no offspring. Self-fertilization still produces some genetic recombination, however. During meiosis, alleles are shuffled between the paired chromosomes, hence the resultant sexual propagules have different combinations of alleles on their chromosomes than the parent (singular in this case). Although genetically very similar, offspring resulting from self-fertilization do differ from their parent and from each other.

Dalgleish and Jacobson (2005) suggested morels likely are capable of substantial inbreeding because most spores from a single sporocarp are capable of forming a heterokaryotic mycelium with each other under laboratory conditions (Hervey and others 1978, Volk and Leonard 1989a). Such inbreeding might occur if ascospores are deposited and germinate near the mycelial colony that gave rise to the sporocarp where they were produced. If such spores are capable of joining this progenitor mycelium through anastomosis, then the nuclei they contribute would be closely related to at least some of the other nuclei in the heterokaryotic mycelium, namely the ones that paired up to undergo meiosis to produce that ascospore.

But morels might be able to take the process of inbreeding one step further. As noted in the introduction, morels might also be capable of the unusual feat of haploid meiosis. This would involve two identical copies of the same haploid nucleus pairing and undergoing the process of meiosis even though none of the alleles on their paired chromosomes differed. Even though segments of these chromosomes could be swapped in the process of meiosis, little or no difference would exist in the resulting sexual spores because the original paired haploid nuclei were identical. In effect, the haploid ascospores would then function in the same manner as a clonal conidium, but the ascospore would only have one haploid nucleus inside, whereas a conidium could potentially have many if the parent mycelium is heterokaryotic. Ower and others (1986) provided the evidence that cultivated morels are capable of haploid meiosis in their patent for growing morels. They described haploid sclerotia-forming sporocarps that produce sexual spores. Zickler and others (1995) discussed haploid meiosis in filamentous ascomycetes concluding that different mating-type alleles are not necessary for haploid nuclei to pair and go through meiosis, but that in wild strains of the fungus they studied (*Podospora anserina*) compatible mating alleles almost always ensured that meiosis involved different haploid nuclei. Whether any species of morel actually conducts haploid meiosis in nature is not known, but it might be a useful strategy for colonizing new habitats (Dalgleish and Jacobson 2005). If a spore lands where no other morel spores or hyphae are available for anastomosing into a di- or heterokaryotic mycelium, then this haploid mycelium would still be capable of forming fruiting bodies and disseminating more spores elsewhere. Such ascospores would have the same genetic identity as haploid conidia formed by the same mycelium. Both would be clonal propagules. Nevertheless, such ascospores might be more effectively distributed than conidia because the latter are formed on short hyphae near the soil surface, whereas ascospores are produced by the much taller sporocarp and are forcibly ejected into the wind.

Whether any species of morel actually conducts haploid meiosis in nature is not known, but it might be a useful strategy for colonizing new habitats.

Reproductive strategies—Morels grow in a wide variety of habitats. They appear able to use a variety of food sources opportunistically as the need and circumstances dictate. They are genetically diverse and have mechanisms, such as frequent anastomosis and heterokaryogamy, for maintaining high genetic diversity in their mycelial colonies. Such genetic diversity likely allows colonies to adapt to changing environmental conditions and shields the expression of harmful mutations. They appear capable of both inbreeding and outbreeding depending on where their spores land and on the relatedness of nearby hyphae or mycelia that are available for anastomosis. They even appear capable (at least in cultivation) of producing sporocarps and sexual spores from mycelial colonies established from a single haploid spore (haploid meiosis).

Wedin and others (2004) noted that several Ascomycete groups are capable of either forming lichens, or living without photosynthetic partners, depending on ecological conditions. They speculated that such broad ecological amplitude and environmental plasticity are useful strategies for fungi that are adapted to ecosystems where the mix of resident species, and their organization into an ecological community, can change abruptly and unpredictably. Insect infestations, wildfires, floods, landslides, blow-down from windstorms, and volcanism are all examples of episodic catastrophic events that can destroy a forest and produce large morel crops. In their discussion of fungus lifestyle strategies, Pugh and Boddy (1988) noted the following characteristics of fungi that are adapted to rapid colonization of new environments: effective dispersal, rapid uptake of nutrients, rapid mycelial extension, ability to use easily assimilable resources, and a rapid and total commitment to reproduction as the ephemeral nutrient flush is depleted and significant competition from other micro-organisms resumes. The characteristics of morel biology and ecology appear to match many of these criteria.

Large crops of fire morels in western forests remain somewhat of an ecological mystery.

Nevertheless, large crops of fire morels in western forests remain somewhat of an ecological mystery. Why do only fire morels fruit, and in such large quantities, for only a year or two after fires in areas where nonburn morels are otherwise found (Pilz and others 2004)? Do mycelial colonies of fire morel species persist in forest soils (without fruiting) for the decades or centuries between forest fires? Although forest fires and morel fruiting can sometimes overlap in boreal and alpine environments where the morel fruiting season is relatively late, most forest fires in western North America occur in the dry summer months later than the morel fruiting season in the moist spring or early summer. So any morel spores that land in an area that burns later that summer would be destroyed if they had not already germinated and grown down into the soil at sufficient depth to escape heat-induced mortality. Hence it seems that the mycelia of burn morels must be present in the soil before a fire in order to grow during the following winter and fruit in the spring. If fire morels persist in forest soils as sclerotia, and if these are formed at soil depths where fire-induced soil heating is not lethal, then such sclerotia would be ideally suited to recolonize the upper soil horizons where other micro-organisms were killed. The nutrients stored in such sclerotia could be used to rapidly form new invading mycelia during the cold winter months (Schadt and others 2003) when other fungi are at a competitive disadvantage. Thus fire morels could quickly capture the flush of readily decomposable organic matter (including necromass) released by the heat from the fire before other microorganisms do so. As logical as this theory might sound, to date, DNA analyses of nonburned forest soils have not found morel mycelium or mycorrhizae where they would be expected under this hypothesis. For instance, 9 months after a prescribed fire in a ponderosa pine forest in eastern Oregon, Fujimura and others (2005) found no morel mycorrhizae in soil cores 15 cm deep under morel mushrooms, even though most trees were not killed in the burn. If the morels were forming mycorrhizae, perhaps the soil samples were too shallow or taken at the wrong time of year.

Also, why do nonfire morels seem to skip fruiting the first year following a fire, whereas they do fruit in abundance following insect infestations? In both cases the trees were killed, so if losing a mycorrhizal partner as food source is a signal to fruit, why do they do so in one case and not the other? The truth is no doubt out there, but to find it, we still have some digging to do.

Cultivation

Context—If morels can be grown artificially, why would harvesting them from the wild remain economically competitive? Indeed most edible saprobic mushrooms, such as button (*Agaricus* species), shiitake (*Lentinula edodes*), or oyster (*Pleurotus* species) mushrooms, are cultivated. Only a very small fraction of the commercial supplies of these mushrooms are collected from the wild. Sometimes markets that specialize in wild foods will sell wild-collected saprobic mushrooms, but most people who collect them do so for personal use. Cultivated mushrooms are comparable in cost to wild-collected mushrooms, but cultivated mushrooms can be produced in any quantity needed to meet demand, and production is much more reliable and consistent throughout the year compared to the seasonal and weather-dependent crops of wild mushrooms. However, edible ectomycorrhizal mushroom species (such as chanterelles, boletes, or matsutake) cannot yet be profitably cultivated. These fungi do not fruit in the absence of their hosts, so researchers and agronomists have had little success cultivating them, even in plantations of trees whose roots are inoculated with the fungus. The one exception is truffles, some of which are easy to inoculate on trees and yield very high economic returns to balance the expense, time, and risk required to establish plantations. Even with truffles, it can take 10 years or more to recoup investments and yield net profits.

Although harvesting morels in the wild costs as much as collecting other mushrooms, morels have the advantage that they can be dried quickly and easily, and when they are rehydrated, they are as flavorful (if not more so) than the fresh product. Therefore, wild harvested morels can be sold year-around, thus reducing the fluctuations in supply and prices. Dried mushrooms are light weight and inexpensive to ship. Some other wild-collected mushrooms, such as boletes, also have favorable drying and rehydration characteristics, but many wild-collected edible mushroom species lose desirable flavor or texture in the process.

Morels fall in between saprobic and mycorrhizal mushrooms in relative difficulty of cultivation. We discuss the history of, current status of, and prospects for growing them because cultivated morels might eventually compete with wild morels.

History—Brock (1951) and Leonard and Volk (1992) discussed early claims of successful morel cultivation beginning in the 1880s. Leonard and Volk (1992) also described the early circumstances surrounding the first U.S. patent for growing morels and early efforts to commercialize the process. Briefly, Ower (1982) published a short description of how to artificially grow morels before applying for a patent. To patent the process, he joined with Dr. Gary Mills and Jim Malachowski, researchers at Neogen Corporation, a biotechnology firm associated with Michigan State University (Volk 1990). The first U.S. patent issued for cultivation of morel mushrooms (Ower and others 1986) drew immediate attention in the mycological community (Coombs 1986). Ower was robbed and murdered in a park in San Francisco before the 1986 patent was issued, but Gary Mills and Jim Malachowski continued to develop the process and received two additional patents (Ower and others 1988, 1989). Malachowski subsequently left Neogen, but Mills continued the process of commercializing morel cultivation (Volk 1990). The patents were based on "*M. esculenta*" cultures derived from sporocarps collected on the campus of San Francisco State University. Kuo (2006) speculated these morels were actually *Morchella rufobrunnea*. Although the cultivation technique was based on one species, the patents claim the methods apply to all *Morchella* species. The texts of the patents were sufficiently detailed to claim rights, but sufficiently vague to stymie efforts by others to replicate the process. The methods centered around techniques and nutrient regimes to grow and prepare sclerotia for controlled germination into sporocarps. Growing sclerotia is an intermediate step that is not required to cultivate most other saprobic mushrooms.

In 1990, Neogen Corporation partnered with Domino's Pizza to operate a test plant under the corporate name of "Morel Mountain" in Mason, Michigan (Barnes and Wilson 1998; Haugen 1994, 1998). Illinois-based Terry Farms bought the rights to the cultivation process in 1993, and in 1995 constructed a growing facility at their Auburn Technology Park in Auburn, Alabama. Increasing sclerotial mass and lipid content, inducing more reliable and simultaneous fruiting, and increasing yields, bed densities, and growth rates of morels were all foci of efforts to improve the economics of morel cultivation (Haugen 1998). Interestingly, an annual report by the Thermal Storage Applications Research Center of the College of Engineering at the University of Wisconsin–Madison describes an "80 ton falling film ice slurry system" (EPRI 1998) developed for the morel mushroom facility of Terry Farms. This device suggests Terry Farms was experimenting with a period of cold wet conditions to trigger reliable or well-timed fruiting. Hammond (1999) said that the plant was shipping 3,000 pounds per week from coast to coast by the end of the decade. One of the early complaints about these cultivated morels was that they lacked the aroma and taste of wild morels, but this was disputed by Perry Mulleavy, director of the Terry Farms project, who claimed their "white" morels were preferred by chefs over the wild collected black morels (Coombs 1994).

After several more transfers of cultivation rights and associated corporate mergers, morel cultivation has resurfaced at "Diversified Natural Products," Scottville, Mason County, Michigan, where the original patent coauthor Gary Mills is vice president for the Gourmet and Functional Foods Division (Miller 2004a, 2004b). As of 2005, the company started selling fresh mixes of morel, shiitake, oyster, black poplar (*Agrocybe aegerita*), and cinnamon nameko (*Pholiota nameko*) mushrooms called "Midsummer Exotics Gourmet Mix "(Diversified Natural Products 2005). To date, we know of no one else who has been successful at large-scale indoor cultivation of morels by using the methods pioneered by Ower and refined by Mills and associates.

Constraints and opportunities—Leonard and Volk (1992) and Stott and Mohammed (2004) provided good discussions of morel cultivation, and the latter provided the most recent review of accumulated knowledge about morel life cycles, sexuality, and sclerotial development in culture. Kaul (1997) also reviewed recent advances in the reproductive biology and ecophysiology of morels that pertain to attempts at artificial cultivation. As Volk (1991) clearly indicated, morels have a complex life cycle that complicates the process of scaling up cultivation methods to efficient commercial procedures.

Morels have a complex life cycle that complicates the process of scaling up cultivation methods to efficient commercial procedures.

For instance, morels appear to need the intermediate stage of sclerotia formation (Ower and others 1986, 1988, 1989; Volk 1991) before they will fruit. Some evidence suggests that this stage occurs when the mycelium runs out of food within its growth substrate (Amir and others 1992, 1993, 1994, 1995a, 1995b), whereas others conclude that nutritional deficits are not necessary for sclerotia formation (Singh and Verma 2000, Volk and Leonard 1989b). Although Kaul (1997) concluded that the nutritional needs of morels are simple and similar among species; Aegerter (1995), Barnes and Wilson (1998), Güler (2000), Stamets (2000), Stott and Mohammed (2004), and Winder (2006) asserted that growth substrates and their nutritional composition affect mycelial characteristics and sclerotia formation. For instance, Arkan and Güler (1991), Sharma and others (1997b), and Singh and others (1999) provided specific substrate and nutritional formulations for sclerotia production without nutrient deficits. Arranging nutritional deficits in a commercial morel cultivation operation might result in delayed or decreased production, hence selecting morel strains that do not require nutritional scarcity to induce sclerotia formation might enhance profitability. Singh and others (1999), Stamets (2000), Stott and others (2002), Stott and Mohammed (2004), and Volk and Leonard (1989a) discussed the importance of strain selection for enhancing sclerotial development. In fact, Stamets (2000) speculated that strain selection has been critical to the success of the cultivation methods pioneered by Ower, Malachowski, and Mills because no one else has been able to successfully replicate their methods. Volk and Leonard (1989b) also noted that darkness is required for sclerotia to develop, and that once formed, they likely also need specific environmental clues to germinate and form fruiting bodies (Volk 1991). Perhaps the "falling film ice slurry system" (EPRI 1998) noted in the previous section is a means to break sclerotial dormancy.

Strain selection also is important for desirable aroma and taste.[23] As Coombs (1994) noted, some disagreement existed regarding the flavor of morels cultivated by Morel Mountain in the early 1990s. Bensoussan and others (1995) contended that the aroma of morels differs by strain, and Leonard and Volk (1992) concluded that there is ample potential for selecting strains of morels with good flavor and optimal growth characteristics for cultivation. Doing so will require some research, however. Each additional criterion that is added to strain selection trials can exponentially increase the number of strains that need to be tested for an optimal mix of desirable characteristics. For instance, if only the best 1 out of 10 strains is selected for flavor, and the same selection criterion is applied to strains for best speed of growth, sclerotia formation, ease of triggering sclerotia to fruit, and high productivity, then the number of strains that would need to be tested for these five characteristics would be 10^5 or 100,000 strains. If more strains are tested for any one of these characteristics, or other criteria were added, the number would be even higher. Although methods likely exist to simplify and streamline such selection processes, there are clear limits to how cost-effectively strain selection can be applied to enhance morel production because testing some of these characteristics can be time-consuming and expensive. Although strain selection and breeding are integral components of all mushroom cultivation (Chang and Miles 2004), the complexity of the morel life cycle significantly increases the number of characteristics that must be tested and thus the expense.

[23] Cultivated fungal strains are typically either haploid (derived from a single spore) or dikaryotic (from two germinating spores with compatible mating types that are allowed to anastomose). Even if a cultivated *Morchella* strain is haploid, it is likely to be multikaryotic (many copies of the same haploid nucleus per cell). Likely, it is possible to cultivate heterokaryotic *Morchella* mycelia in pure culture, but doing so could complicate selection for particular traits because expression of those traits might be controlled by competition among dissimilar genes on the different nuclei.

Another factor complicates and increases the expense of strain selection for morel cultivation. A morel mycelium grows quickly in culture, but not for long. Cultured morel strains quickly senesce, losing their vigor and viability, so strains must be repeatedly reselected from spore cultures (Barnes and Wilson 1998, Stamets 2000). Such spore cultures can be obtained from morel strains that have already been screened for desirable characteristics; however, additional screening could be needed because some of the genetically different offspring might no longer retain an optimal mix of cultivation characteristics. Lastly, Stott and Mohammed (2004) made the point that resolving issues of morel taxonomy and species identification would greatly enhance comparative studies of morel growth characteristics. Such knowledge would be especially relevant to cultivation efforts if there are differences among morel species in how they preferentially obtain nutrition and what triggers them to fruit.

Prospects—While cultivation of morels on large commercial scales is being refined, other approaches also exist. For instance, a quick search of the World Wide Web reveals several companies in the United States that sell morel-growing kits for outdoor cultivation. We know of no trials that evaluate the efficacy of such kits. Because the inoculum is introduced into ideal habitat for morels, wild morels might already have colonized the habitat and fruited anyway. On the other hand, there is no obvious reason why introducing morel mycelium to ideal habitat would not work. How many morels fruit, how reliably they fruit, and how long a patch fruits likely all depend on local circumstances and the strain that is being sold. The buyer will just have to experiment to determine whether this method is worth their while.

If it is so difficult to induce morels to fruit in culture, why not simply grow and sell the mycelium as food or flavoring? This would be very easy to do because morel mycelium grows fast, needs only simple nutrients, and would not require strain selection for sclerotia or fruiting characteristics. Patents for producing mushroom concentrates, essences, and extracts by growing mycelium in liquid culture were filed by Szuecs (1950), and edible mushroom products were added to the list in a subsequent patent (Szuecs 1958). Gilbert (1961) reported that Szuecs included *M. hortensis* isolates in his trials of various edible mushrooms and it worked well. Gilbert subsequently expanded on this submerged culture work by conducting trials with a selection of 10 *Morchella* strains representing what he considered several morel species. He found they all were easy to cultivate and grew as uniform spheres of mycelium. He reported the harvested mycelium tasted as good as the sporocarps, although the strains he grew differed in flavor. He reported that frozen, dried, and powdered mycelium, as well as extracts, all retained flavor. By contrast, Bensoussan and others (1995) used chromatographic profiles to compare the concentrations of odor-causing molecules in fresh and rehydrated morels and morel mycelium. They concluded that rehydrated morels retain more odor molecules compared to rehydrated mycelium. How this finding relates to the taste of rehydrated morel mushrooms versus rehydrated mycelium, especially in cooked products, is not clear.

Although inexpensive to produce, mycelial products lack the visual allure and cooking characteristics of an actual morel mushroom, therefore they are unlikely to command the same prices. Nevertheless, these products might very well obtain some market share as food additives, for instance in powdered sauce mixes.

Wild-collected morels likely will have a value premium in markets for many years to come.

Lastly, genetic modification of cultivated foods is a rapidly advancing field that could easily be applied to morels. *The Handbook of Fungal Technology* (Arora and others 2004) describes already developed techniques for modifying fungi. *Morchella* strains could be modified to improve flavor, enhance nutritional value, facilitate cultivation, or remove allergens or toxic compounds. If, however, propagules from genetically modified morels escaped into natural settings, wild populations of the same species of morel might more rapidly incorporate such altered genes than would wild populations of plants from the release of pollen or seeds from genetically modified members of their species. As micro-organisms, morels have the potential to grow and reproduce more rapidly than many plants do, and the apparent ability of morel mycelium to incorporate new nuclei into an already established heterokaryotic mycelia might hasten the spread of such altered genetic material. Whether modified genomes would negatively affect wild populations is hard to predict. Regardless, many consumers remain cautious about potential health risks from consuming genetically modified organisms. Wild-collected morels likely will have a value premium in markets for many years to come.

Collecting to Cooking

Harvesting—Mushroom chef Jack Czarnecki has described morels as “infuriatingly elusive” (Apple 1998) and, indeed, they are often well camouflaged. Most collectors in western forests have espied a morel that was actually a pine cone, or vice versa. Others describe the experience of having difficulty finding morels at the beginning of the season until they find the first one and fix the mental search image in their minds. Tales about the similarity of morel and Easter egg hunts abound. Kuo (2005), Lonik (2002), Thompson (1994), and Weber (1988) all provide thorough and enjoyable discussions of morel hunting. Whereas recreational morel harvesting can be a relaxing adventure, commercial morel harvesting is often very hard work (Brown and Marin-Hernandez 2000, LeVaux 2005). Not only must harvesters frequently walk long distances to find patches that have yet to be visited, but cutting morels from their bases involves a lot of bending over. Harvesting in burned areas is often gritty and dirty, and without a forest canopy for protection, workers are directly exposed to rainstorms and intense late spring sunlight. Mosquitoes can be fearsome in the spring.

Commercial harvesters use a couple of strategies that they believe will maintain or enhance the productivity of morel patches. All mushroom buyers stipulate that the dirty bases of morels be cut off. Most buyers and harvesters recommend simply cutting morels off their stem rather than plucking them first and then trimming off the base. Cutting them in place does not disrupt the mycelium like plucking does. Especially when morel bases are attached to long tapered mycelial masses, such as those described by Buscot and Roux (1987) and Stamets (2005), leaving this mass in place is likely a good idea. How harmful such mycelial disruption truly is to morel colonies is simply not known, but it makes sense to err on the cautious side because cutting has other benefits. Cutting morels in place prevents additional handling and keeps the morels cleaner. Additionally, morels can have primordia (not-yet-expanded morel "buttons") attached to their base. Left in place, these primordia have the potential to grow into harvestable morels if fruiting conditions remain favorable. In any case, there is no reason to believe that cutting morels does more harm than pulling, so given the practical reasons for cutting, the practice might as well be encouraged.

There is no reason to believe that cutting morels does more harm than pulling.

In areas where harvesters experience little or no competition, they often practice a technique known among themselves as "farming." It consists of harvesting only large morels and returning in a few days to harvest the others after they have grown more. Less effort is required to harvest a pound of 3-inch-tall morels than to harvest a pound of 1-inch-tall morels, so this practice is economically effective if the patch is not too distant to revisit and if others don't find and harvest the patch in the interim. Some harvesters also believe this allows morels to spread more spores, but this is only likely if the remaining morels are allowed to mature. In areas with open access and significant competition from other harvesters, revisiting partially harvested patches becomes less practical because others are likely to collect the smaller morels that were left behind.

Commercial mushroom hunters frequently use containers that are well ventilated. Morels can dry, become lighter, and lose fresh-weight value in such containers, but solid containers retain too much humidity and heat, thus providing a favorable environment for insects, mold, and bacteria that can quickly degrade morel quality. Another rationale for the aerated containers is that the morels might spread their spores through the holes or gaps in such containers while in transit from the field to the buying stations. Given that morel spores mature only when the morel itself approaches maximum size, collections of fresh and young morels likely do not distribute viable spores from ventilated containers. As morels do near maturity, they become dry and can release large quantities of spores. Therefore, the efficacy of this method likely depends on the maturity of the morels being collected. Even if large numbers of spores are spread from such containers, we do not know if supplemental spore distribution helps to maintain morel populations or enhance their productivity. As with cutting morels from their bases, however, ventilated containers and potential spore distribution are unlikely to do any harm and might as well be encouraged because such containers keep the collected mushrooms in better condition anyway. Moore and others (2005) recommended that only food-grade containers be used for collecting to prevent collected morels from contamination by other substances. They also provided several recommendations for hygienic handling, temporary storage, and transportation to buyers. Anyone wishing to collect commercially can obtain a quick education in handling procedures from mushroom buyers because it is in their interest to purchase quality mushrooms. Old, dirty, crushed, moldy, crumbling, or insect-ridden morels have little value.

Processing—Kuo (2005), Lonik (2002), and Weber (1988) provided good general discussions of how individuals can process and preserve morels. Mushrooms are perishable and invariably deteriorate and dry in transit, thus morels intended for markets that sell fresh mushrooms are sorted for young specimens that are in good condition.

Drying morels is the preferred method of preservation. Morels should not be canned, as they have a low acid content necessitating high temperatures and pressure to avoid bacterial contamination (Weber 1988). Morels can certainly be frozen, but as with many other mushrooms, their texture is better preserved if they are sautéed briefly before freezing. Morels are easily and quickly dried because their flesh is thin and air can flow inside the hollow stem and head. They rehydrate quickly for the same reasons. Many connoisseurs of morels believe their flavor is concentrated and enhanced by drying and rehydration, so dried morels lose little value compared to fresh ones. Morels lose about 90 percent of their weight during the drying process (Crisan and Sands 1978, Pilz and others 2004). They gain 5 to 6 times their weight in water during rehydration (Kenney 1996). Although some heat can be used for drying morels, temperatures above 120 ºF should be avoided. Dry, circulating air is much more effective than heat alone (Weber and others 1996). Home food driers with a fan and temperature control are very effective for small-scale use. If outdoor temperatures are warm and dry, morels can be dried on screens, strung up on fishing line threaded through them, or if no other means are available, spread out in a single layer on tarps. Depending on humidity, warmth, and breezes, morels drying on tarps might need turning to prevent spoilage from lack of airflow. In remote locations without electricity or warm dry weather, harvesters and buyers improvise with wood stoves, propane heaters, and generators to run fans (Kenney 1996). The same principles of warm, dry, circulating air apply.

Spores are often released in great abundance as morels dry, leaving easily visible yellow deposits. For both commercial and recreational harvesters, heavy spore loads in the air can be a health concern (Weber 1988, Weber and others 1996). Ventilation can be essential in commercial drying sheds. Recreational harvesters can also experience ill effects when drying morels at home, especially if food driers with fans blow the spores around indoors. Bronchial asthma, allergic conjunctivitis (inflamed eyelids), and rhinitis (inflamed nasal passages) are potential consequences (Benjamin 1995).

Marketing—Local, national, and international marketing of commercially collected morels is considered in greater detail in our section on "Morel Commerce." Suffice it to say here that morels are marketed about every way conceivable. They are sold fresh and dried, in quantities and locations ranging from a few pounds at local restaurants to shipments of tons overseas. A given seller will often market morels in many different ways as prices fluctuate with supply and demand. Value-added products, such as attractively packaged dried morels with a sauce mix and a story about the source of the morels, complement the shelves of many stores specializing in natural products. Kenney (1996) noted that so far there are no markets for morel powder, but there is for the morel chips that are left over from drying large batches of morels.

Culinary use—

> "….they resembled dried-up brains"
>
> Famous cook James Beard, remarking on how repulsive dried morels looked when he first saw them in a store (Apple 1998).

Iqbal (1993) noted morels are quite nutritious. Dried morels are 42 percent high-quality protein, low in calories, and rich in minerals. Although similar claims can be made for other mushrooms, most people do not eat morels solely for their nutrition. People eat morels because they taste so good.

Morels can cause digestive upset in some people (Beug 2004). Weber (1988) noted that such intestinal discomfort is more common with black morels than with yellow morels and that reactions are accentuated by the consumption of alcohol. Weber (1988) also noted that yellow morels have a milder taste but longer shelf

The cardinal rule is to always cook morels thoroughly and start with modest quantities until you become confident of no ill effects.

life than black morels. The cardinal rule is to always cook morels thoroughly[24] and start with modest quantities until you become confident of no ill effects. Likewise with drinking alcohol before, during, or after a meal with morels; experimenting with small amounts is prudent, but most people can enjoy wine or other alcoholic beverages with morels. Some genera of fungi that are related to morels have toxins that are volatile (see next section), so it might not hurt to cook morels in a ventilated area (Arora 1986).

Morel recipes go as far back as Roman times when they were cooked with wine (Vehling 1977). Weber (1988) described yellow morels as having a delicate flavor that can be overwhelmed with spices but is suitable for simple to elaborate dishes. Wheeler (1996) said the strong flavor of morels pairs well with strongly flavored dishes such as beef goulash, French onion soup, or roasted duck with Madeira sauce. Everyone agrees they go well with butter and cream, but for those who eschew dairy products, olive oil works wonders too.

Many mushroom cookbooks include morel recipes and how to handle and prepare morels. Weber (1988) provided a thorough discussion of morel preparation and cooking. Ferndock and others (1986) offered a complete cookbook of morel recipes from Minnesota. Suggestions for handling and cooking morels, as well as recipes, also can be found in other books about morels such as those by Kuo (2005), Lonik (2002), Thompson (1994), and Weber (1988); and in mushroom cookbooks such as those by Czarnecki (1986), Fischer and Bessette (1992), and Wheeler (1996). This list of books that discuss morel cooking is by no means exhaustive.

Toxins and Contaminants

Toxins in look-alike mushrooms—Morels are related to similar mushrooms in the order Pezizales, especially some species in the genera *Gyromitra* and *Verpa*, that can cause digestive upset or worse. Some of these related fungi are traditionally eaten and even sold, but they can be risky and none are recommended. See figure 7 for illustrations of *Gyromitra* and *Verpa*, the two related genera most often confused with morels. We recommend consulting field guides with good color photographs to improve familiarity with the species that grow in your area, but we urge caution and skepticism concerning comments in older guides about edibility. Both Weber (1988) and Kuo (2005) thoroughly discussed these related species and provided excellent photographs.

[24] All wild mushrooms should be cooked before consumption. Cooking destroys bacterial contaminants that might cause illness. For that matter all mushrooms, wild or cultivated, should be cooked to release their full nutritional value because chitin in their cell walls otherwise inhibits digestion.

Benjamin (1995) and Weber (1988) likewise provided thorough discussions of the toxins found in these mushrooms and their effects on health. Because the literature they cite is extensive, we refer to their summaries for this section. Ethylidene gyromitrin is the most important initial poisonous compound. It breaks down during digestion into a variety of toxic hydrazines including monomethylhydrazine (MMH), a component of rocket fuel. Because it has a boiling point of 189.5 ºF, cooking usually volatilizes the toxin. Although this might explain why some individuals eat these species with seeming impunity, it also means that the cook or others in a poorly ventilated room can be exposed to the inhaled vapors. The toxin also can persist in cooking water and be absorbed through broken skin.

Concentrations of gyromitrin differ by species. Concentrations even differ by the strain of a given species, so mushrooms collected in one area might be relatively safe, whereas the same species collected elsewhere could have high concentrations of toxic compounds. Additionally, people exhibit a range of tolerance and sensitivity to the toxins; children can be especially vulnerable to such poisoning. The toxins can accumulate in the body over time, and, as they accumulate with further consumption, there is a narrow threshold between no symptoms and a harmful or fatal reaction. One meal could thus trigger severe symptoms even though the person had eaten them previously with no perceived problems. In addition to the nasty symptoms of gyromitrin poisoning, the compound has been found to be mutagenic (inducing genetic mutations), teratogenic (causing malformed fetuses), and carcinogenic (causing cancer) in microbial and animal exposure trials.

Benjamin (1995) listed symptoms of acute poisoning that appear within 6 to 12 hours and last up to 2 days as fullness and bloating, abdominal pain, vomiting with or without diarrhea, severe headache, and possibly fever. In severe poisoning, the damage can progress to jaundice, breakdown and disorders in red blood cells, fever, delirium, convulsions, and coma. Treatments include such procedures as management of severe hepatitis or liver failure, blood transfusions, medication for seizures, and dialysis for kidney failure.

In the Western United States, the two types of false morels most commonly eaten are the *Gyromitra gigas* complex of related species (the snowbank false morels) and *Verpa bohemica* (the early morel). In the United States, *Gyromitra* is rarely sold, but *Verpa bohemica* is sold in some locations (Benjamin 1995). Consumers of these fungi are gambling with their health and lives. Sellers of these fungi are gambling with fines, stricter regulations, or lawsuits. With so many delicious, safe, edible mushrooms available, why bother gambling?

Morel toxins—Morels are more likely to cause intestinal distress if eaten raw, although even raw, they can be tolerated by some people (Beug 2004). Weber (1988) listed only one example of a morel (*M. esculenta*) being tested for MMH; it had none. Benjamin (1995) cited no such studies, but noted that many people have experienced intestinal distress from uncooked or inadequately cooked morels. As an example, Benjamin (1995) and Kenney (1996) told the story of a retirement banquet in Vancouver, British Columbia, for a chief of police. A pasta salad with raw morel, shiitake, and button mushrooms was served, followed by 77 of the 483 attendees experiencing distress, many vomiting dramatically.

Morels also can absorb toxic minerals and compounds from the soil where they grow. They are similar to many other wild mushrooms in this ability. The scientific literature on wild mushrooms absorbing heavy metals and radioactive nucleotides is especially voluminous in eastern Europe where polluting industries and the Chernobyl nuclear plant meltdown have spread toxic compounds across large regions whose inhabitants have mushroom-collecting traditions (Kalač 2001).

Obst and others (2001) examined concentrations of 27 heavy metals in 16 species of edible mushrooms and the soil where they grew. Samples were taken from polluted and presumably nonpolluted remote areas in the Canadian Northwest Territories near Yellowknife. In general, concentrations of toxic minerals were higher near pollution sources, such as the city of Yellowknife, roads, and especially mines, than farther away. Mushroom species also differed in their tendency to concentrate each of the sampled heavy metals. In a few cases, morels exhibited elevated levels of arsenic, cadmium, and lead compared to other sampled morels, although the concentrations were not sufficiently high to be considered a health concern. Four morels collected from one site, however, did have concentrations of lead that could cause concern if a person ate a few pounds of them. They were burn morels collected 1,500 feet from a highway, but more than 40 miles from any other known pollution source. A second, more comprehensive report on this research will be available from Obst and others in 2007.

Another concern is whether morels can absorb toxic compounds from fire retardant slurries.

In addition to potential heavy metal absorption from pollution sources, in western North America, many acres are being treated with herbicides to control invasive weeds. Trappe and others (1984) reviewed the effect of pesticides on mycorrhizal fungi and concluded that different types of herbicides differed widely in their influence on mycorrhizal fungi and that host plant responses to the herbicides complicated interpretation of published data. Blanco-Dios (2002) reported the only research we found that examined the effect of herbicides on morels. The article described an area treated for 10 years with herbicides near Galicia in northwestern Spain where malformed sporocarps of *M. conica* appeared in 3 of the 4 years that morels fruited.

Another potential concern is whether morels that fruit after fires can absorb toxic minerals or compounds from the chemical fire retardant slurries dropped by tanker planes to control forest wildfires. Such slurries consist primarily of fertilizer (ammonium polyphosphate), thickeners (clay), and in some cases, rust inhibitors (sodium ferrocyanide) (Fire-Trol Holdings, L.L.C. 1999). Toxicity is considered a minor concern for fish, plants, and wildlife, but none of these organisms adsorb and concentrate heavy metals from the soil as well as fungi. Even plants that absorb such compounds likely do so through the assistance of their mycorrhizal fungi. Most fertilizers have small levels of heavy metal contaminants, but natural soils have these compounds too. To date, no one has investigated whether heavy metals are present in retardant slurries in sufficient quantities to increase concentrations in morels that fruit where slurries were applied to fires the previous summer. Nor has there been any analysis of how likely it is that potential increases in concentration would pose a health risk to individuals who consumed morels collected from areas where retardants were applied. Retardant slurries are usually dyed orange so the aerial observers can tell if the load was dropped in the correct location. Colored slurry might remain stuck to tree trunks until the following spring if rainfall is light in the interim, so if harvesters note it, they might wish to hunt morels elsewhere until more is known about possible risks. The ground area targeted by slurry drops is typically a small percentage of the ground area of the fire, but pickers sometimes preferentially search for morels on the peripheries of fires (Keefer 2005) where slurry drops usually are targeted. If the fire kept burning, slurry drops might be anywhere within the perimeter of the burned area.

Public health regulations—Since the advent of wild mushroom commerce, concerns about the potential health risks of an unregulated wild mushroom industry have periodically surfaced. The major concern is that wild mushroom harvesters or buyers might inadvertently include toxic mushrooms such as *Gyromitra* or *Verpa* in with the edible varieties such as morels. Gecan and Cichowicz (1993) reported that in a 2-year survey by the U.S. Department of Health and Human Services, Food and Drug Administration (FDA), they found that 21 percent of imported morel shipments (seven from France and two from India) contained potentially toxic look-alike species, specifically *Gyromitra esculenta* and *Verpa bohemica*. They cited several FDA reports that document instances of domestic poisoning by these two species found in batches of imported morels. During the period 1980-87, 13 shipments of imported morels were refused entry because they were found to include *Gyromitra esculenta, Verpa bohemica,* and *Helvella* species. In 1996, The FDA issued an alert proscribing all importation without inspection, of all morels from two French companies that had repeatedly shipped morels admixed with *Gyromitra esculenta* and *Verpa bohemica* (FDA 1996).

Although it is highly unlikely that commercial harvesters or buyers in western North America would confuse other genera of mushrooms with morels, some consider *Verpa bohemica* safe and sell it. State and federal food safety agencies have long pressed for tighter controls on the sales of wild edible mushrooms, including morels. Many states, including Montana and Idaho, have provisions in their food safety codes requiring restaurants and other food purveyors to purchase wild mushrooms only from approved sources (Gadbow 2001a). Most states, however, have chosen not to enforce this regulation because it would be a prodigious task to set up a system for independently verifying the correct identification of all wild mushrooms that are collected and sold.

In winter 2005, the Los Angeles County Department of Health Services shut down wild mushroom vendors at farmers' markets in Los Angeles County (Brown 2005). The official who made the decision to enforce the rule stated that the county had the duty to proactively prevent people from getting sick or dying from unsafe foods (Brown 2005). The director of one such market noted, "If the current process for harvesting wild mushrooms is not recognized by the Department of Health Services as an approved source, then all wild mushrooms will have to be eliminated from the hundreds of menus and thousands of tables of Los Angeles restaurateurs and consumers (Tumlin 2005)." He also pointed out the lack of any incidents where people have become ill or died from wild mushrooms purchased in farmers' markets in the United States (Tumlin 2005). Under pressure from wild mushroom consumers and vendors, the Los Angeles County Department of Health Services opted to cease enforcing the approved source provision of the food safety code for wild mushrooms.

We know of no documented instances of consumers being seriously poisoned by wild mushrooms that were commercially collected in western North America.

Given the potential for morel toxicity discussed in this section, further investigation into sources of concern is warranted. On the other hand, with the exception of morels that were not properly cooked, we know of no documented instances of consumers being seriously poisoned by wild mushrooms that were commercially collected in western North America.

Morel Harvesters

Personal Use

Morel harvesting for home use is not only widespread in the Eastern United States, but has an organized tradition. Michigan's competitive morel-hunting festivals are among the most famous. With slogans like "May is Morel Month in Michigan" (Hallen and others 2001), a variety of festivals are held, especially in the upper part of the lower peninsula (Weber 1988). Individuals often compete to collect the most or largest morels from a given area in a set time. Some such festivals like the Boyne City Mushroom Festival (http://morelfest.com/) and the Mesick Mushroom Festival (http://www.mesick-mushroomfest.org/) have occurred annually for nearly 50 years. Similar events are held in Mansfield, Indiana (http://www.mansfieldcoveredbridge.com/other_festivals.php), Irvine, Kentucky (http://kaht.net/events/mmfest_1.htm), Richmond, Missouri (http://home.mchsi.com/~cofcommerce/MushFest2004.htm), Magnolia, Illinois (http://morelmania.com/ismmhc.html), Lewiston, Michigan, and Red Wing, Minnesota. The morel enthusiast Web site called "Morel.com" (http://morels.com/) provides a recent listing of morel festivals in the Midwest and a bulletin board where people can post information about the progress of the season. Kuo (2005) described the competitive and social scenes at several of these festivals. Minnesota has even made the morel its state mushroom (Minnesota Statutes 1998).

Mushroom clubs and mycological societies also frequently sponsor morel hunts (called "forays") in the spring. These provide the opportunity for inexperienced mushroom hunters to learn from those who are more experienced and from professional mycologists. Such forays allow participants to become familiar with appropriate habitat and fruiting clues. Fine (1998) wrote an entire book on the sociology and psychology of morel hunters, especially examining the relationships between amateurs and experts in mycological societies.

Mushroom clubs in the Western United States also sponsor morel forays. These often consist of weekend trips because people frequently must drive long distances between cities and prime morel habitat. Clubs that sponsor such forays include the Western Montana Mycological Association (http://fungaljungal.org/), the Puget Sound Mycological Society (http://psms.org/), the Oregon Mycological Society (http://www.wildmushrooms.org/), the Cascade Mycological Society (http://cascademyco.org/), the North American Truffling Society (http://www.natruffling.org/), and the Mycological Society of San Francisco (http://www.mssf.org/). To find information about such forays, one sometimes has to log onto the member's section of the Web site with a password. Boom (1995) described the enthusiasm that can accompany such outings.

Many morel hunters, however, simply search for morels individually or in small groups of family members or friends. If you know what you are doing, neither festival competitions nor organized forays are necessary to quash a case of spring fever with a good tromp through the woods in search of culinary prizes that result in a succulent dinner.

Commercial

> "In the East, most people report the number of specimens they found. In the West, where people are collecting in burns, they talk about the number of *pounds* they got."
>
> Nancy Smith Weber (O'Driscoll 2001)

Number of harvesters—Data from sales of permits for commercial mushroom harvesting allow us to estimate the number of morel harvesters, field buyers, processors, and brokers in some areas. For instance, national forests in Montana issued 3,642 commercial permits during the 2001 morel season (McLain and others 2005), although the correspondence between the number of harvesters and the number of permits issued is not one-to-one. Some harvesters obtain several less-expensive short-term permits, rather than one seasonal permit. Moreover, some harvesters obtain permits for several forests. Consequently, the number of individuals obtaining permits likely was lower than the number of permits issued. Two to three thousand would be a reasonable guess for the number of commercial morel harvesters working in western Montana in 2001. The number of morel harvesters working in western North America that year would be somewhat higher because not all commercial morel harvesters opted to work the Montana burns. According to McLain (2000), some circuit harvesters deliberately avoid hot spots, preferring to make their money on the margins where they experience less competition. In addition, some morel harvesters do not like the working conditions in the burns, preferring to work in areas where the forest canopy is thicker and where they don't have to breathe in ash as they collect.

Ethnic diversity—People from a variety of ethnic groups and races participate in the morel harvest. Caucasians, members of First Nations or American Indian tribes, Southeast Asians (predominately from Laos and Cambodia), and Latinos (predominantly from Mexico, Guatemala, and El Salvador) are the most common. An unknown, but likely significant percentage of the Latino harvester population in the United States consists of undocumented workers from Mexico and Central American countries. The relative percentage of different ethnic groups is difficult to estimate and likely varies by location and from year to year. As a very rough approximation of ethnic background, Parks and Schmitt (1997) analyzed 1994 permit data from national forests in eastern Oregon for broad categories of surnames. They found that 51.3 percent of the harvesters obtaining permits had Southeast Asian surnames, 44.2 percent had European surnames, and 4.5 percent had Latino surnames. Permit data for 1996 to 1998 for the Sisters Ranger District on the Deschutes National Forest in central Oregon indicated that out of 271 harvesters who had obtained permits, 62 percent of the harvesters had European surnames, 28 percent had Southeast Asian surnames, and 10 percent had Latino surnames (McLain 2000).

Residence—Most commercial morel harvesters do not live near the places where they harvest morels. For example, Parks and Schmitt (1997) found that 73 percent of the permits issued to harvesters in eastern Oregon national forests went to people who came from other locations, and only 27 percent went to people who lived nearby. McLain (2000) found that 59 percent of the 271 harvesters who obtained permits on the Sisters Ranger District from 1996 to 1998 lived in western Oregon, 27 percent lived in other states (generally Washington or California), and only 14 percent lived in nearby central Oregon. Wills and Lipsey (1999) found that most morel harvesters and buyers working in the Yukon came from British Columbia. Likewise, the majority of the harvesters on the 1991 Tok River Fire in central Alaska came from elsewhere (Wurtz and others 2005).

Income strategies—Although no one mushroom harvesting site in the Pacific Northwest produces commercial quantities of wild mushrooms all year long, harvesters and buyers can make a full-time living with wild mushroom crops by moving around various circuits to collect different types of mushrooms (Arora 1999). Subsequent sections describe strategies that harvesters and buyers use to extend their harvest seasons and secure year-round income. McLain (2000) and McLain and others (2005) provided more detailed descriptions of how harvesters and buyers participating in the central Oregon and western Montana morel harvest use these adaptive strategies.

Mobility—The ability to move from place to place to take advantage of the flushes of wild morels is extremely important to commercial harvesters. Mobility is important at two spatial scales–within a harvest area (such as the perimeter of a wildfire) and among multiple harvest locations (some might be in different states or regions). Over time, harvesters accumulate knowledge and experience about mushroom fruiting patterns at both scales. Within a harvest location, morels might fruit at different times in response to features such as tree stands, swales, hillocks, or drainages. Elevation or snow packs could be the determinants of different fruiting times among widely spaced harvest locations. Using their knowledge of fruiting patterns at these two scales, harvesters tend to develop “patch-lines” within harvest locations and “harvest site portfolios” across broader geographic areas.

Patch-lines—Many harvesters develop "patch-lines" when harvesting natural black or other nondisturbance morels. A morel patch is a small area where a concentrated group of morels is fruiting or has been known to fruit. Patch-lines consist of a series of morel patches visited sequentially within a larger area that a harvester roams on a regular basis. Such repeated visits allows harvesters to keep track of what is happening in multiple locations, while keeping their patches picked down thereby reducing the chance that other harvesters will find their patches.

Morel patches can range in size from 1 to 100 square feet or more. Patch-lines that are revisited can, for instance, be spread over miles of walking or scattered among multiple spots that can be conveniently visited with vehicles from a base camp. Patch-lines might be visited every several days or weekly. Morels often put on a spurt of simultaneous growth called a flush (noun) or flushing (verb). Harvesters who have worked in an area for a long time begin to develop a sense of when a patch or even portions of a patch will flush. Using this knowledge, they are able to work the area very efficiently. Developing and working patch-lines is particularly important when commercial harvesters are focusing on natural black or mountain blond morels because they tend to fruit in the same location each year. Other ectomycorrhizal mushroom species also fruit in nearly the same location each year, so this characteristic of natural black and mountain blond morels might reflect mycorrhizal relations with specific host trees. Although patch-lines are less important for harvesting ephemeral burn morels, even these morels can produce multiple flushes within the first year following a fire, and knowledgeable harvesters can often predict where to search next. Patch-lines are integral to the practice of "farming" described previously in the "Harvesting" subsection of the "Collecting to Cooking" section.

Harvest site portfolios—Mobility at the subregional, regional, and occasionally international scales is also an important aspect of most commercial morel harvesters' and buyers' lives. Many mushroom harvesters develop harvest site portfolios by becoming familiar with a variety of locations where morels fruit. When the crop is poor in one area, they have alternatives. Such portfolios differ in their geographic extent. For example, McLain's (2000) study of wild mushroom harvesters in central Oregon identified three major categories of harvesters–local harvesters who tended to collect morels only in the central Oregon Cascades and Ochoco Mountains, another group that shifted back and forth between the Willamette Valley and the east side of the Oregon Cascades, and a third that followed mushroom circuits ranging from northern California to Alaska, and from the Pacific coast to the Rocky

Mountains. In Canada, harvesters from British Columbia travel to the Yukon, Northwest Territories, or Saskatchewan to harvest morels during late spring and summer; back to British Columbia to harvest chanterelles and American matsutake in late summer and fall; and some then travel south to the United States to harvest American matsutake and other late fall and winter mushrooms (de Geus 1995). A recent study of morel harvesters in southeastern British Columbia indicated a similar pattern; full-time commercial harvesters of nontimber forest products began the work year with morels in the spring, shifted to berries and boletes in the summer, collected American matsutake in the fall, and harvested salal and boughs in the winter (Natural Resources Canada 2004).

Morel harvest site portfolios, however, must be more flexible than portfolios for wild edible ectomycorrhizal mushrooms, such as boletes, American matsutake, and chanterelles. These types of mushrooms, as well as some populations of natural black and mountain blond morels, tend to fruit in the same locations each year, so harvesters develop portfolios consisting of collecting spots where they have previously harvested commercial quantities. By contrast, the large flushes of burn and gray morels that follow fires, and the substantial flushes of natural black and mountain blond morels that often follow tree death or soil disturbance, are typically scattered across the landscape in patterns that are unpredictable more than a year or so in advance. Both harvesters and buyers evaluate the location, timing, and intensity of the previous year's fires to plan their upcoming season's itinerary (Rommelmann 2005). Knowledge of how regional differences in topography, elevation, forest types, and weather patterns affect morel fruiting helps harvesters refine their travel plans to harvest the most morels with the least time, cost, and effort.

Large flushes of morels that follow fires and tree death are scattered and unpredictable.

Morels can be harvested 6 to 8 months a year if harvesters are willing to travel extensively. Such a large morel circuit typically begins in late February to early March in the Sierra Nevada Range, near Mount Shasta in northern California, and in the Siskiyou Mountains of southwestern Oregon. Circuit harvesters then move north and east between mid-March to mid-May to the east side of the Cascade Range in Washington and Oregon. Depending on the weather and the location of large fires in the previous years, such harvesters might then shift around mid to late May to the Blue Mountains of eastern Oregon, higher elevations of the Cascade Range in southern Oregon, and to low-elevation sites in Idaho and Montana. Some harvesters move into British Columbia, the Yukon, and Alaska during July and August. Others remain in the Rocky Mountains, Cascade Range, and the northern Sierra Nevada mountains, moving upward in elevation as the summer advances. Although gray morels can fruit as late as October in parts of the northern Rockies, most morel circuit harvesters shift into harvesting other mushrooms by September at the latest.

Diversification—People unwilling or unable to follow such geographically large harvesting circuits often combine money earned from mushroom harvesting or buying with income from other occupations such as working in forestry, logging, collecting other nontimber forest products, farming, gold panning, jewelry making, woodworking, construction work, or caring for young, infirm, or elderly individuals. Disability or retirement plans also supplement some of the income of some individuals (Arora 2000, Hansis 1998, Love and others 1998, McLain 2000, McLain and others 2005, Natural Resources Canada 2004). Nontimber forest products commonly harvested by morel harvesters when they are not hunting mushrooms include (but are not limited to) salal, beargrass, huckleberries, fiddlehead ferns, moss, ornamental cones, and tree seed. The strategy of harvesting diverse types of mushrooms and other forest products allows some harvesters and buyers to make a reasonably good living (Arora 1999), but others struggle financially (Hansis 1998, Love and others 1998). Buyers are more likely to specialize in purchasing a particular product (such as morels) or type of product (such as wild edible mushrooms), whereas harvesters are more likely to harvest a diverse array of forest products (McLain and others 2005), although considerable overlap exists between the harvest strategies of these groups, as well as the individuals involved.

Information is a particularly important form of social currency, and buying stations constitute one of the most important sites of information exchange.

Cooperation—Despite the sometimes-fierce competition in the morel industry, relationships between harvesters and buyers are typically characterized by mutual interdependence (McLain 2000). Harvesters depend on buyers to purchase their products, but buyers are also dependent on harvesters for bringing in a sufficient quantity of morels of adequate quality to meet the demands of their business sponsors or customers. Information is a particularly important form of social currency, and buying stations constitute one of the most important sites of information exchange. Buyers attract harvesters primarily by establishing prices and grading systems that harvesters perceive as better than those offered by competing buyers. But the information a harvester can learn from a buyer, or at a buying station, also has value. Buyers generally interact with numerous harvesters working in various parts of the forest. Through the banter that takes place in the buying station, buyers pick up valuable information on ground conditions and fruiting patterns over a wider area than one individual, family, or crew alone can cover. Buyers often pass this information on to other harvesters, usually in the form of general hints about elevations and habitat types where morels are fruiting best, rather than in the form of specific locations. Over time, many harvesters establish close ties with specific buyers, and will often preferentially sell to them. The power dynamics of these mutually interdependent relationships, however, are often skewed in favor of the buyer.

Besides exchanging information, mushroom harvesters and buyers help each other out in other ways, such as lodging, hauling water, camping, getting firewood, or transportation. Buyers regularly front gas money to harvesters who run out of money. Harvesters with working vehicles often link up with other harvesters whose vehicles have broken down, or cannot drive for other reasons. For instance, LeVaux (2005) described harvesters negotiating boat rides to access and remove harvested morels from remote areas of 2004 wildfires near Tok, Alaska, during the morel harvest season of 2005. McLain and others (2005) even described buyers helping each other establish new buying stations in unfamiliar territory or to purchase a different type of mushroom.

Most morel harvesters work with at least one other partner. Southeast Asian harvesters usually camp and harvest as large extended family units. Latinos often work in crews. Caucasian harvesters tend to work with one or two partners. Extended families and crewmembers often pool their money. To save gas money, some harvesters can serve as scouts seeking more productive sites. Finding not-yet-harvested areas involves a lot of walking (LeVaux 2005), and hiking with partners, families, or teams is safer.

Motivations—Income is only one of the factors that motivate commercial morel harvesters (McLain 2000). Many seek to avoid, or take breaks from, jobs considered rigid or inflexible even though they supply more reliable income. Mushroom hunting provides an opportunity to leave behind the worries and cares of hectic home lives, to reconnect with nature or one's own spirituality, as well as to share adventures with friends and family in intimate settings. Some consider morel hunting to be stress therapy, an opportunity to kick back, or simply the chance to enjoy spending time in the outdoors. The sense of adventure, the challenge of the hunt, the thrill of discovery, and a feeling of accomplishment are likewise rewarding. In all these respects, commercial morel hunters differ little from recreational harvesters (Love and others 1998). Individuals who derive most of their income from mushroom hunting also value the self-reliant, independent lifestyle (Arora 2000).

Wages—Experienced morel harvesters can earn more than $1,000 per day when they find a combination of abundant high-quality mushrooms, low competition or a superior harvesting strategy, and favorable purchase prices (LeVaux 2005). Most harvesters, however, earn modest wages for hard work. Acker (1986) said that an average wage for a mushroom harvester in the mid-1980s was $830 seasonally, with a few people earning a maximum of $4,000. Obst and Brown (2000) reported an average wage of $15 per hour (all wages converted to U.S. currency) for morel harvesters in the Northwest Territories of Canada. Keefer (2005) reported average daily earnings for morel harvesters in British Columbia of $75, with $125 per day possible for the best harvesters. Other authors, such as Guin (1997), reported that such wages might be standard for experienced harvesters, but the majority of mushroom harvesters earn far less, and many, particularly those with little or no experience, lose money. Harvesters do, however, usually get paid immediately in cash. Alexander and others (2002a) examined how harvester net wages can be calculated. Important variables include minimum wage expectations in a given market and harvester costs. As an example, rising fuel costs reduce the profitability of harvesting mushrooms from remote locations or when traveling between harvest sites in a portfolio of harvest locations.

Opinions about forest management—Morel harvesters have complex and varied opinions about forest management that reflect the complexity of the interactions between morel fruiting, forest conditions, and disturbance events. McLain (2000) provided a few illustrative examples from interviewing harvesters and buyers during the spring season mushroom harvest near Sisters, Oregon.

Harvesters who started collecting around Sisters in the late 1970s and early 1980s appreciated the many gravel or dirt logging roads that provided access to areas that otherwise would have required a long walk. They discovered that natural black morels often grew in the lightly bladed spur roads and cat trails within logging units, where soil had recently been disturbed. Many "old-timers" learned a technique known as "roadhunting," driving slowly along spur roads looking for morels and boletes close to the road. Because such roads were not maintained, harvesters felt frustrated by the gradual decline in convenient access to many harvest areas.

Harvesters at Sisters appreciate light stand disturbances, such as stand thinning, selective logging, and controlled burns; they often target such areas in their search for morels. However, they also criticize practices that remove most of the trees over large areas, such as seed-tree cuts or clearcuts. They maintain that removing most mature trees destroys their natural morel patches for years. Though morels are more likely to be found in thinned or logged areas for a year or two after harvest, experienced harvesters believe that logging large contiguous areas of trees is detrimental to morel mycelia in the long run.

Harvesters also note that widespread insect infestations can produce substantial morel crops. For instance, the Douglas-fir tussock moth killed white fir throughout large areas east of the crest of the Cascade Range during the last two decades. During the height of the die-off in 1987-93, natural black morels fruited abundantly in the dying stands. Harvesters attributed this abundance to the increase in soil organic matter from fallen fir needles. People who had harvested the area prior to the die-off also noted a surge in bolete production as the trees died. They attributed this abundant fruiting to a reproductive strategy on the part of the dying mycelia to spread numerous spores that might start new colonies in healthier stands. Regardless of why abundant fruiting occurred as the trees died, both morels and boletes are now less abundant in these stands. Harvesters have mixed views, however, on the decision by the USFS to forgo intensive cutting or spraying to control the tussock moth. Some felt that the decision was a good one in the long run. By contrast, the adjacent Confederated Tribes of the Warm Springs Indian Reservation chose to control the infestation, and others point to their healthy mixed-conifer stands and productive bolete patches as an example of what could have been done to retain viable mushroom habitat.

Morel Commerce

International

International commerce in morels is extensive and voluminous. Boa (2004) listed morels as considered edible in 28 countries, a conservative figure given that many countries simply have no documentation of their edibility. Excluding Korea, Japan, Taiwan, and western Europe, Boa (2004) found information on morels published in the following countries: Afghanistan, Argentina, Belarus, Botswana, Bulgaria, Canada, Chile, China, Costa Rica, Guatemala, India, Kyrgyzstan, Madagascar, Mexico, Morocco, Nepal, Pakistan, Russia, Slovenia, Spain, Turkey, Ukraine, and the United States. Morels are highly valued as an export commodity, but they are not always eaten in the countries that export them.

Globally, 300,000 pounds of dried morels are traded annually.

Iqbal (1993) provided an overview of global commerce in morels. India, Pakistan, Turkey, Nepal, Bhutan, the United States, Canada, and China, are the largest exporters of dried morels, although many other countries participate. France, Switzerland, and Germany are the main importers, although companies in France sometimes process imported morels and then export them. Globally, 300,000 pounds of dried morels are traded annually. This represents nearly 3 million pounds of fresh morels. One-third of that total originates from India and another third from Pakistan. Prices for dried morels in 1993 averaged around $50 to $60 per dried pound, thus international commerce in morels that year was worth approximately $15 to $18 million. At 90 percent moisture content, prices for fresh morels would be the equivalent of $5 to $6 per pound. Because harvesters only receive a third to a half of final retail prices, their income might be $2 to $3 per pound. Still this represents a lucrative enterprise in rural areas of less developed countries. For instance, Prasad and others (2002) reported that morel harvesting is a vital economic activity for communities in the central Himalayas at 5,900 to 11,800 feet in elevation. Morels are several times more valuable than local medicinal herbs. Almost all families participate in collecting morels and many people set annual fires to stimulate crops. Morel harvesting is also extensive in the northern Indian states of Jammu, Kashmir, and Himachal Pradesh, and in the hilly regions of Uttar Pradesh (Singh and Verma 2000). Sharma and others (1997a) reported that two strains of morels grow in this region, one prewinter (August-October) and one postwinter (March-May). Turkey also exports large quantities of morels, but more of their morels are shipped fresh than morels from India because Turkey is located close to European Union countries, and shipping time is correspondingly reduced.

Morels also are exported to Europe from many other places around the world. For instance, in September 2005 there was a large fruiting of morels in the coastal zone between Santiago and Concepcion in Chile. Local harvesters sold their fresh morels for $4.50 per pound.[25] Exported crops of fresh morels from the Southern Hemisphere might enjoy a price advantage because they are available during the off-season for fresh morels north of the equator.

Iqbal (1993) asserted that the quality of morel exports from some regions is hampered by remote locations, lack of processing facilities and equipment, uneducated harvesters, and unhygienic collecting and processing methods. Global trade in wild mushrooms is still an expanding industry, and most harvesters and buyers are aware of the importance of quality (Boa 2004), so harvest, transport, and processing conditions might have improved since Iqbal's 1993 report.

North America

Large-scale commercial harvesting of morels began in western North America in the 1980s along with the general increase in global demand for wild-harvested mushrooms. In North America, the demand for wild foods increased, and wild mushrooms figured among the newly sought-after delicacies (Burros 1985, Fabricant 1980, Jenkins 1985). European demand for North American mushrooms also grew as nitrogen deposition from power plant air pollution reduced wild mushroom productivity in Europe during the 1980s (Arnolds 1995) and concerns grew about radionucleotide contamination of wild mushrooms as a result of fallout from the 1986 Chernobyl nuclear accident (Kalač 2001).

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[25] Palfner, Götz. 2005. Personal communication. Biologist, Departamento de Ciencias Químicas, Universidad de La Frontera, Av. Francisco Salazar 01145, Casilla 54-D, Temuco IX Región, Chile.

The market for wild morels expanded at a time when the number of people available to harvest wild mushrooms also increased. Growing international demand coincided with an influx of Southeast Asian refugees to both the United States and Canada combined with extensive layoffs in the wood products industry that left many timber and mill workers looking for other forms of forest-based employment. One attraction of harvesting wild mushroom for some Southeast Asian immigrants is that harvesters who speak or write English poorly, or who lack technological workplace skills, can still make a decent living (Hansis 1998).

For more detail about the history of commercial mushroom harvesting in the Pacific Northwest region of North America, consult Amaranthus and Pilz (1996), Hansis (1998), Jones and others (2002), Love and others (1998), McLain and others (1998), Molina and others (1993), Pilz and Molina (2002), or Redhead (1997).

Ecological conditions in the forests of western North America concurrently contributed to large morel crops. Fire suppression, past logging practices, and controversies about appropriate management of public lands combined to produce a landscape of dense young stands prone to wildfires and drought stress. On the east side of the Cascades and in the northern Rockies, the drought years of the 1980s resulted in an unusually large number of extensive forest fires (Parks and Schmitt 1997). The drought also weakened large stands of white fir in the eastern Cascades, making them more susceptible to the tussock moth, spruce budworm, and pine beetle infestations that had gained a foothold in the region in the 1970s. Fire morels fruited abundantly during these years, attracting thousands of new harvesters to the mountains of eastern Oregon, Washington, Idaho, and Montana (Parks and Schmitt 1997). At Sisters, Oregon, and other sites along the eastern Cascades, natural black morels also appeared in unusually large quantities in areas with heavily infected and dying white fir stands (McLain 2000). By the early 1990s, harvesters and buyers had established a tradition of following the burns, or alternatively, harvesting natural morel crops during years when no new burns were available.

Economics

Value—Although data on wild mushroom commerce are rarely collected, in 1985 Jerry Larson, a trade development analyst with the Oregon Department of Agriculture, estimated that the “fledgling wild mushroom industry” contributed $21.5 million to the Northwest economy each year (McRobert 1985). Schlosser and Blatner (1995) estimated the same market at $41.1 million in 1992. Morels constituted 1.3 million pounds of the approximately 3.9 million pounds of wild mushrooms sold in Oregon, Washington, and Idaho that year, and morel harvesters earned about $5.2 million.

Blatner and Alexander (1998) outlined prices for some of the most significant commercially harvested fungi in the Pacific Northwest. It has been estimated that as many as 36 species are traded commercially, but American matsutake, chanterelles, morels, and boletes make up the bulk of the industry. The average price paid to harvesters for morels in the Pacific Northwest United States from 1992 to 1996 was $5.04 per pound. Obst and Brown (2000) reported that the prices paid to harvesters for fresh morels in their study averaged about $3.08 per pound. They found that harvesters could harvest an average of 19.8 pounds per person per day. Actual harvesting time per day was 3 to 4 hours. In their 2001 study of morel markets in Montana, McLain and others (2005) found that prices for fresh morels varied through the season, and Kenney (1996) discussed how global supplies and European demand determine prices. At the beginning of the season around early May, when supplies were low and demand was high, prices began at $8 to $10 per pound. Within 2 weeks, prices dropped to $4.50 per pound and then to an average of about $3 per pound for the remainder of the season.

Obst and Brown (2000) in their 1998 study of morel markets in the Northwest Territories, Canada, reported a seasonal increase in prices for dried morels that had been consistent for the past 10 years. In June, dried morels were sold to international retailers for $32 to $55 per pound. In July, the price increased to $69 to $76 per pound. In August, dried morels sold for $101 per pound, and in September the price increased to $174 per pound. Keefer (2005) reported an average price of $35 per dried pound of morels in the 2004 season in British Columbia. The usefulness of drying and holding morels for sale later in the year depends on the cost of drying and holding the mushrooms and the international supply of dried morels in any given year.

The usefulness of drying and holding morels for sale later in the year depends on the cost of drying and holding the mushrooms and the international supply of dried morels in any given year.

In fiscal year 2000, the BLM issued 773 permits in Washington, Oregon, and California for 52,240 pounds of fungi, with permit sales totaling $15,185. Not all permits stipulated a particular mushroom species, but 11 were specifically for morels. The USFS sold $226,205 worth of commercial permits that year for mushrooms. Although for some species and in some areas, compliance with purchasing permits is relatively high, these figures still represent far less than the total western mushroom trade (Alexander and others 2002b).

More recently, the Pacific Northwest (Region 6) of the USFS (Oregon and Washington) has instituted a program of recording commercial mushroom permit sales and estimated quantities harvested as part of its regionwide Automated Timber Sales Accounting System. This system now tracks the sales of harvesting permits for various special forest products by each national forest for each calendar quarter. Table 3 summarizes the reported value of permits sold and estimated quantities of mushrooms harvested on the various national forests of Region 6 during

Table 3—Estimated quantities of morels harvested[a] and value of commercial mushroom permits sold on national forests in Oregon and Washington during 2004 and 2005

National forest	January-June 2004		January-June 2005	
	Quantity	Permit values	Quantity	Permit values
	Pounds	*Dollars*	*Pounds*	*Dollars*
Colville	5,225	1,045	[b]	
Deschutes	119,544	74,642	67,800	66,088
Fremont-Winema	202,660	202,100	140,240	139,520
Gifford Pinchot	224,657	89,855	328,622	132,469
Malheur	1,200	240	13,800	2,760
Mount Baker-Snoqualmie	13,490	12,400		
Mount Hood	13,460	12,100	16,820	11,260
Ochoco				
Olympic	10,882	4,420	44,400	12,320
Siskiyou-Rogue River	4,558	4,214	6,058	3,902
Siuslaw	15,128	96,470	16,506	99,963
Umatilla	500	100	500	100
Umpqua	104,451	27,150	84,151	24,341
Wallowa-Whitman	2,500	500	2,200	440
Okanogan-Wenatchee	1,020	220	1,192	820
Willamette	50,624	22,764	47,876	28,060
Region 6 totals	769,899	548,220	770,165	522,043

[a] Data derived from sold and removed worksheets, nonconvertible summaries for national forests in Region 6. http://www.fs.fed.us/r6/nr/fp/FPWebPage/FP70104A/FP70104A.htm (20 December 2006).
[b] No data available for blank cells.

the winter and spring quarters of 2004 and 2005. These sales values should predominantly reflect permits sold for morel harvesting because few other mushrooms are commercially harvested at this time of year, most such permits are of limited duration, and most spring permits are only for morels.

It should be noted that the number of people who visit the national forests of the Pacific Northwest United States to harvest morels for personal use far exceeds the number of commercial harvesters. Data are lacking on the total quantities of morels collected by each group, but recreational spending by personal-use harvesters indicates that personal-use harvesting represents a significant local economic activity. The USFS provides more programmatic support for personal-use morel harvesting than for commercial harvesting.[26]

[26] Duran, Frank. 2006. Personal communication. Special Forest Products Coordinator, Region 6, U.S. Department of Agriculture, Forest Service, P.O. Box 3623, Portland, OR 97208-3623.

Markets—Most wild mushrooms that are exported to the European Community from the Pacific Northwest United States are shipped from Seattle (Alexander and others 2002b). In their study of morels of the Blue Mountains region of Oregon, Parks and Schmitt (1997) found that 40 percent of the harvested morels were exported to Europe and Asia, and 42 percent were sold in the Western United States. Tedder and others (2000) reported that from 1994 to 1998, British Columbia and the Pacific Northwest United States shipped an average of approximately 865 tons per year of mushrooms to Europe and 1,148 tons per year to Japan. These figures include all mushroom species, both wild and cultivated, but wild mushrooms likely constitute the vast majority of mushroom exported from northwestern North America. Tedder and others (2000) also noted that some mushroom exports could be classified under other miscellaneous food categories in the U.S. and Canadian export data, so the total likely underrepresents total volumes shipped. They found that the total declared value of these shipments approached $23.8 million (U.S. dollars) per year. Shipments to Japan represent 76 percent of that value, most of which consists of sales of the American matsutake. A consultant interviewed by Wurtz and others (2005) estimated that Oregon, Washington, British Columbia, the Yukon, and Alaska combined supply less than 10 percent of the world's supply of wild mushrooms.

Because northwestern North America supplies so little of the global market, crops elsewhere largely determine prices, and the trade is very competitive. As noted in the international commerce section, large crops of morels are harvested in countries such as China, India, Pakistan, and Turkey. Wage expectations are lower in these countries than in North America, and shipping to European markets is less costly because they are closer (Rommelmann 2005). Profit margins for North American sellers are narrow in both fresh and dried markets, and they must keep costs low to stay in business.

Businesses—With some exceptions, most nontimber forest product businesses are referred to as "very small enterprises," employing fewer than 10 people. Many harvesters, and some small businesses, operate in the "informal economy"; that is, they work and earn money without being tracked through tax payments or business registrations. Although business dealings are correspondingly casual and easy to arrange, workers tend to receive low wages and few benefits. Workers also can experience worse working conditions than they would in the formal economy. Many work in the informal economy because they have few other viable choices (Alexander and others 2002b). As noted earlier, however, harvesters do get paid immediately in cash. Mushroom buyers often handle tens of thousands of dollars in cash each day in high-value, high-volume mushroom harvest areas. Mushroom buying might represent the largest remaining legal cash-based commerce in our society.

For global markets, wild mushrooms must be processed, a complicated process that involves identification, culling, cleaning, sorting, grading, packaging, preserving, storing, shipping, and marketing (Schlosser and Blatner 1997). In 1992, Schlosser and Blatner (1995) reported 520 people employed by mushroom processing firms in Oregon, Washington, and Idaho to handle the crop collected by 10,400 harvesters.

Local Impacts

Several rural locations around the Pacific Northwest are known as "hot spots" for harvesting ectomycorrhizal mushrooms such as American matsutake and chanterelles. Transient harvesters visit these communities annually. Communities such as Crescent Junction and Sisters, Oregon, Shelton and Randle, Washington, Bella Coola and Terrace, British Columbia, have become familiar with this annual influx and have arranged accommodations that are largely of mutual benefit to the community and the harvesters. Transient harvesters of morel mushrooms, by contrast, often visit forests that burned the previous summer; thus the harvest area can only be selected after the previous fire season. The closest local communities and land management agencies are sometimes unfamiliar with the challenges, issues, and impacts that arise from the influx of such visitors.

Social impacts—Much of the regulation associated with the wild mushroom industry seeks to minimize the social tensions that inevitably arise when a large number of people suddenly move into an area. Some of the social tensions occur within the community of morel harvesters, including conflicts over patches, tensions between members of different ethnic groups, domestic disputes, disagreements between harvesters and buyers over prices, conflicts among buyers over location of buying stations, and clashes among buyers over how prices are set and modified. Other social tensions exist between local residents and outside harvesters, such as conflicts over harvest areas or perceptions of transient morel harvesters as invaders that might be armed and dangerous (McLain 2000). Tensions can also arise between harvesters and the land management agencies regarding regulations. For example, local residents are sometimes disgruntled that the agencies are allowing commercial harvest activities or that large numbers of outsiders are allowed to camp in areas that local people customarily use. United States land management agencies have sought to reduce such impacts by creating designated camps for commercial harvesters, setting aside areas for local residents to collect morels for personal use, providing informational materials in a variety of languages and, in at least one case, hiring an interpreter to facilitate communication between agency employees and harvesters who do not speak English (Pilz and others 1999).

Positive social and economic impacts can result from morel harvesters and buyers coming to a community. Harvesters often stay in rental cabins or private campgrounds, purchase food and gas locally, and eat in local restaurants. These activities bring money into communities, many of which would otherwise have few visitors, especially in the spring (Arora 2000, Gadbow 2001a). In addition, some buyers put on workshops for community members on how to harvest morels commercially so that local residents can earn extra money in years when morels are abundant.

Environmental impacts—We discuss elsewhere how the harvest of morel mushrooms influences the persistence and reproduction of *Morchella* as an organism or its productivity as a resource. The impacts of large numbers of harvesters on other resources are a more immediate concern for many managers. For example, in the Blue Mountains, road damage is a problem if harvesters drive on roads that are still wet and soft from snowmelt (Parks and Schmitt 1997). Biologists there have also expressed concerns about how large numbers of morel harvesters walking through the forest would affect elk calving during the spring. If allowed to camp where they choose, harvesters tend to camp next to streams, compacting the soil, trampling riparian vegetation, cutting poles for structures, and gathering up dead wood for campfires. Harvesters sometimes leave behind large amounts of garbage and broken collecting containers, often in areas where cleanup is difficult and costly (Kenney 1996, Penticton Herald 2004, Wurtz and others 2005).

Prior to the 2001 morel season in Montana, federal land managers raised concerns about potential disturbance of endangered species such as grizzlies and gray wolves, possible harvesting of morels and riding of all-terrain vehicles in off-limit wilderness areas, insuring proper sanitation at campsites, arranging adequate waste disposal, limiting the spread of noxious weed seeds on the tires of off-road vehicles, and whether large numbers of people walking through the burns would affect regeneration of lichens, moss, and other plants. The USFS managers discussed these concerns both within the agency and with other interested parties, including locally based mushroom buyers. Drawing on their own experiences with large morel crops in previous years, as well as upon the experiences of forest managers in USFS Region 6, federal land managers in Montana developed a system of permits, camping policies, and outreach efforts that proved quite successful at addressing these concerns (USDA FS 2000).

Policy and Regulation

Land ownership and harvest access—Land ownership is an important determinant of management policies and practices; therefore it also affects morel harvesting opportunities and regulations. In western North America, land ownership can be divided into three main categories, public, private, and tribal. Native Alaskans, First Peoples of Canada, Native Americans of the United States, and the indigenous tribes of Mexico all own or control some communal land or reservations. In many cases, commercial quantities of morels fruit on their forest lands. Because such lands typically are managed for the benefit of the tribe as a whole, managers are in a unique position to restrict access to morel harvesting, control the quantities harvested, and insure that all participants and tribal members share equitably in the benefits of such commercial ventures.

By contrast, large swaths of land in western North America are publicly owned (USDI BLM 1996, USDA FS 2004a). Although some areas are off-limits to commercial activity (Antypas and others 2002), the majority of these national, state, provincial, county, or other public lands are managed by professional foresters for the goal of providing multiple benefits to the public. Typically mushroom harvesting is considered a valid use or a public right on such lands. However, because managers of such lands generally lack the means to enforce harvested quantities or exclusive access rights, the morel harvest is usually regulated with permits and designated harvest areas. The quantities of morels harvested and the number of harvesters collecting in a given area are, with a few exceptions, not limited. Where public land management agencies such as the BLM do specify the quantities of mushrooms to be harvested or stipulate exclusive access, slim budgets often constrain enforcement. Land owned by large timber corporations are increasingly off-limits to morel harvesters (McLain 2000, Parks and Schmitt 1997). Other than public relations, these companies see little benefit in providing access, and dealing with large numbers of harvesters can be costly and potentially litigious. See the regional summaries that follow for more specific information on how land ownership affects morel harvesting in different regions of western North America.

Development of regulations—Although people have harvested wild mushrooms commercially in western North America since at least the 1930s (Redhead 1997), formal regulation of morel harvesting did not emerge in the Western United States until the 1980s. A convergence of market, socioeconomic, cultural, and political changes rendered visible the wild mushroom industry, sparking calls for the development of wild mushroom policies at state, provincial, and federal levels (Arora 1999, Love and others 1998, McLain and others 1998, Redhead 1997). Key factors that contributed to increased regulation of the harvesting of wild mushrooms included expanding market demand, a supply of relatively cheap labor, ecological conditions that favored the production of morels, a shift in North American public land management practices toward ecosystem management (McLain and others 1998), and international emphasis on ascertaining sustainable forestry practices.

In the early 1990s in the United States, pressure from environmental groups and federal court rulings led the USFS and BLM to shift the focus of their forest management from heavy emphasis on timber production toward greater ecosystem restoration and protection. By drawing the attention of land management agencies to the importance of biodiversity and the need to provide adequate protection for a variety of species, including wild fungi, the shift to ecosystem management increased the incentives to regulate the harvest of wild mushrooms. Internationally there has also been a process (Montréal Process Working Group 1999) for ascertaining whether forests are being managed in a sustainable manner. Indicators of sustainability include monitoring the productivity, value, and use of nontimber and nonwood forest products, and these indicators have been used to evaluate how sustainably United States forests are being managed (USDA FS 2004b).

In the Western United States and Canada, arguments in favor of wild mushroom regulation have centered around three primary concerns:

- Difficulties forest managers have experienced or anticipate in controlling large temporary influxes of harvesters.
- Potential negative environmental or resource impacts from large-scale harvesting and associated activities.
- Acquiring some revenue from the commercial sale of products harvested on public lands to help finance management of these resources and needed research regarding sustainable harvesting.

During the last two decades, a variety of policies, regulations, and laws have been implemented to address these issues. Both managers and harvesters have learned much about fair and effective regulation of mushroom harvesting, although controversies have not entirely disappeared and harvesters have often been excluded from participation in development of the regulations. Acker (1986), Love and others (1998), Love and Jones (2001), McLain and others (1998), McLain (2000), Molina and others (1993), Parks and Schmitt (1997), Pilz and Molina (2002), Redhead (1997), Tedder and others (2002), and Wurtz and others (2005) discussed these issues and how mushroom harvesting regulations were developed for various sectors of the industry in different locations.

Current regulations—To comply with regulations, morel harvesters must check with local landowners or local districts of land management agencies because permits, regulations, and fees differ widely and are subject to change. Even where permits are not required for actually harvesting mushrooms, such as in British Columbia, land managers often prescribe other regulations and rules that apply to the activities of harvesters. Many areas are off-limits to commercial morel harvesting, such as parks, wilderness areas, adjacent private property, or areas with sensitive resources, for instance archaeological sites, wildlife, or rare species. Locally available maps are usually needed to avoid these areas. In some cases, adjacent national forests have combined their mushroom permit systems to make it easier for harvesters to obtain widely applicable permits and to facilitate enforcement. Permits are usually required to establish buying stations on public land. Commercial harvesters are sometimes required to camp in specific locations to prevent nearby campgrounds from being filled by harvesters to the exclusion of recreational users.

Public forest management agencies in the Western United States typically define mushroom harvesting as either for personal or commercial use. For instance, if individuals collect just a few mushrooms for use while camping in a national forest, the USFS defines this as "incidental use" and no permits are required. If individuals take larger quantities of mushrooms home for personal use, a free use permit is often required so the USFS can keep track of such activities. Several USFS Regions, including Regions 6 and 10 (Alaska Region) use a special forest products appraisal system to help forest managers calculate fair market prices for commercial permits. The permit prices arrived at through this appraisal system take into account harvesting and processing costs and set fees at roughly 10 percent of the estimated value of the product that an individual can harvest during the season. Harvest quantities, prices, and costs are estimated by interviewing harvesters and surveying buying stations. To encourage compliance, this fee is sometimes modified so permits are more affordable.

To illustrate the range of prices, we provide a few examples. On the Deschutes National Forest in central Oregon, a commercial permit to harvest morels for sale during the spring 2006 harvest season cost $2 per day with a minimum charge of $20. Harvesters could purchase an annual permit for $100. In Montana and Idaho in 2001, the national forests offered commercial harvesters a choice between 7-day, 14-day, 30-day, and seasonal permits, at a cost of $20, $40, $60, and $100, respectively

(DeWolf 2001). The Wallowa-Whitman National Forest in eastern Oregon offers two types of commercial morel permits: $2 per day with a minimum charge of $20, and annual permits that cost $50 (USDA FS 2004c). On the Wenatchee and Okanogan National Forests, spring-season commercial mushroom permits cost $5 per day, with a minimum charge of $20. A seasonal permit, valid only from April 15 to July 31, costs $100. In 2001, the Montana State Department of Natural Resources and Conservation offered commercial harvesters wishing to harvest on state lands a choice of 7-day, 14-day, 21-day, 30-day, and season permits, at a cost of $30, $60, $100, $120, and $150, respectively (Gadbow 2001b). Bureau of Land Management districts calculate the cost of a permit by using the minimum fees established by their state office. In Montana, the minimum price for wild mushrooms was 25 cents a pound in 2003, with a minimum fee of $20 (USDI BLM 2003). The BLM in Fairbanks, Alaska, considered charging 20 cents per pound for permits that would grant the holder exclusive rights to an area (Wurtz and others 2005).

The price for permits to operate buying stations on federal land ranges from $100 on the Deschutes National Forest to $500 on the Wallowa-Whitman National Forest (USDA FS 2004c). Some national forests, such as the Deschutes, only allow buyers to set up stations in designated locations (McLain 2000). Buyers often prefer sites on private land that are more convenient, less expensive, or less subject to surveillance by the USFS.

The States of Montana, Oregon, and Washington have special forest products statutes (MCA 2005, ORS 1995, RCW 1967). These laws require anyone transporting special forest products, including wild mushrooms, to show evidence that they have permission from a landowner to harvest those products. The laws also mandate buyers to keep a record of all special products purchases, including the names, addresses, and permit numbers of harvesters (McLain and others 1998). With the expiration of the 1989 Wild Mushroom Act, Washington no longer requires wild mushroom dealers and buyers to obtain special licenses beyond those required of any business. Alaska, Idaho, and California do not have recordkeeping requirements for wild mushroom buyers.

Challenges—Some harvesters refuse to get permits on principle. Others cannot afford one, especially if mushroom fruiting is poor. In Oregon and Washington, buyers resist state laws requiring them to keep a record of the harvesters from whom they purchase mushrooms. However, harvesters and buyers are not unilaterally against wild mushroom regulations. Regulation has helped address concerns about their own safety, including concerns about excessive use of guns in the woods and the increased risk of wildfire that often accompanies the entry of a larger number of people into the forest. Also, enforcement personnel can help people if they experience injuries, their vehicle breaks down, or they get lost. Reasonable prices, regulations that are sensible, and convenient times, places, and means for obtaining permits all enhance harvester acceptance (Parks and Schmitt 1997, McLain 2000).

Reasonable prices, regulations that are sensible, and convenient times, places, and means for obtaining permits all enhance harvester acceptance.

Current mushroom permit systems on federal lands in the Northwestern United States allow land management agencies to monitor and track who is harvesting mushrooms, and the issued permits fulfill state law requirements in Oregon, Washington, and Montana that harvesters have written permission from landowners to collect mushrooms before they are transported. The permits do little to limit harvesting pressure on the mushrooms themselves, however, unless permitted harvest seasons are shorter than the fruiting season. No restrictions are generally placed on the amount a person can harvest, and in most cases the permits do not grant exclusive access to the permit holder. Anyone who pays for a permit is a potential competitor for all mushroom patches located in the areas where harvesting is allowed. As a result, if competition is intense, each harvester has an incentive to harvest all the mushrooms they find rather than leaving some for later collecting. Harvesting all the mushrooms in a patch reduces the probability that some will mature sufficiently to spread spores. The potential value of mushrooms from a given patch or area also is diminished because small mushrooms are not left to grow larger for subsequent collecting.

Other than the number of permits sold, these regulatory systems provide little monitoring information on the long-term productivity or reproductive viability of harvested mushroom populations. Permit sales are highly dependent on mushroom prices that, in turn, reflect global competition and commerce, so demand for permits provides at best an indirect and imprecise reflection of how the mushroom resource is responding to harvesting pressures.

In regions that do not currently regulate mushroom harvesting, land managers and policymakers can now choose from among many examples of regulatory mechanisms, permit systems, conservation guidelines, monitoring methods, and enforcement practices that have been tried elsewhere. The challenge is to adapt these practices in a manner that is appropriate to the scale and intensity of local harvesting activities, the goals of the landowners, unique aspects of the local forest ecosystem, and the needs of the harvesters, buyers, and local communities.

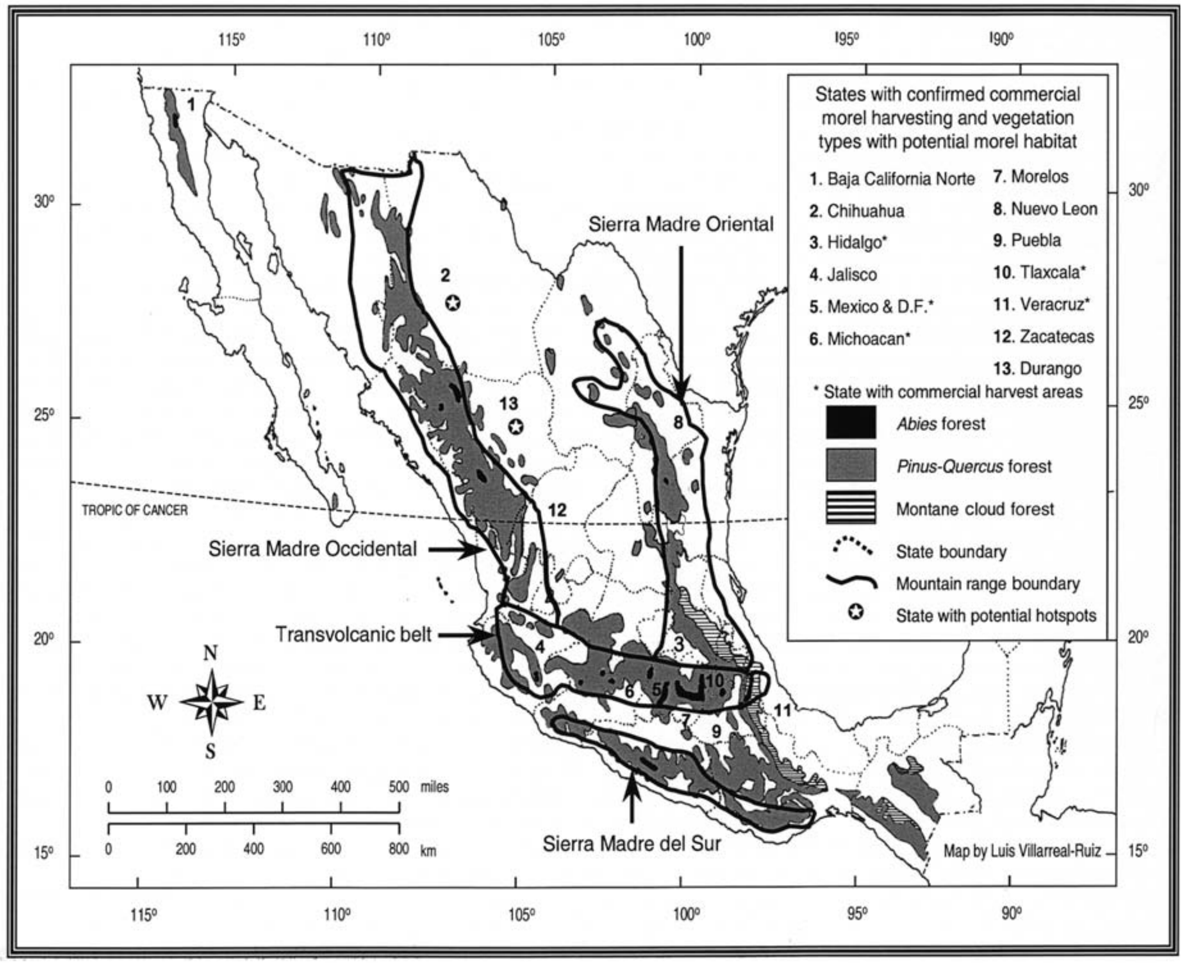

Figure 11—Mexican states with confirmed commercial morel harvesting and vegetation types with potential moral habitat. Map by Luis Villarreal-Ruis, based on Brower (n.d.), Villarreal and Pérez-Moreno (1989), Perry and others (1998), INEGI (n.d.), SEMARNAP and PROCYMAF (n.d.), SEMARNAP (2004).

Regional Summaries

Mountains of Mexico

Mexico is so biologically diverse that it is difficult to generalize about morel habitat; however, morels do fruit in high-elevation forests in most of the mountainous regions of Mexico including the Sierra Madre Occidental, Sierra Madre Oriental, and Sierra Madre del Sur. Morels are especially common in the transvolcanic belt that runs east to west across Mexico at 20 ºN latitude (fig. 11).

The putative specific names reported for Mexican morels are *Morchella angusticeps*, *M. conica, M. costata, M. elata* ("black morel complex"), *M. crassipes,* and *M. esculenta* ("blond morel complex") (Villarreal and Pérez-Moreno 1989). In

Luis Villarreal-Ruiz

Figure 12—Morphological diversity of commercially harvested morels in Mexico.

their recent review and taxonomic article, Guzmán and Tapia (1998) stated, “little is known about the diversity and taxonomy of *Morchella* in Mexico.” Although *Morchella* taxonomy is in flux in Mexico as elsewhere, they concluded that at least seven distinct species have been confirmed. Morels found in North America and northern Mexico (such as the black [*M. elata*] and yellow [*M. esculenta*] clades) also seem to occur in central Mexico. Other Mexican species might or might not be restricted to hardwood forest of subtropical regions. For example, Mexican specimens of *M. guatemalensis* have only been described from montane cloud forests of Veracruz, Michoacán, Morelos, and Jalisco (Guzmán-Dávalos and Rodríguez-Alcantar 1993, Guzmán and Tapia 1998). By contrast, Guzmán and Tapia (1998) described the red-brown blushing morel *M. rufobrunnea* from specimens collected in a montane cloud forest of oak, sweet gum, white-alder (*Clethra*), and alder in a small area around Xalapa, Veracruz. Kuo (2005, 2006) claimed that morels found in landscaped environments of coastal California and originally identified as *M. deliciosa*, also are actually *M. rufobrunnea*. As is also often noted at morel buying stations farther north, commercial morel harvesters in Mexico often bring in morels (from a given locale) that exhibit striking morphological diversity (fig. 12). Whether these differences in size, color, and shape reflect species distinctions remains to be determined.

Ecological studies suggest that Mexican morels occur more commonly with true fir than with pines. Along the transvolcanic belt, yellow morels (*M. esculenta* complex) exhibited low productivity (0.06 lb/ac) in oyamel fir (*Abies religiosa*) forests of Mexico State, but was absent from the pine forests in central Michoacán (Villarreal-Ruiz 1996). No morels were collected from a 5-year mushroom monitoring study in Veracruz in a mixed forest of Mexican weeping pine (*Pinus patula*), other pines, and Hickel's fir (*Abies hickelii*) (Villarreal-Ruiz 1994), but they were found in adjacent oyamel fir forests. Morels can be found in humid oyamel fir forest between 9,200 and 11,000 feet in elevation from August to October, and as late as December in exceptionally wet years. They fruit in nondisturbed soil and on disturbed sites such as side paths or burned areas.

Known areas of commercial morel harvesting include coniferous forests around Mexico City, and the states of Mexico, Hidalgo, Michoacán, Tlaxcala, and Veracruz (INEGI, n.d.; SEMARNAP 2004; SEMARNAP and PROCYMAF, n.d.). Potential morel hotspots might still be discovered in remote and unexplored areas of the northwestern states of Chihuahua and Durango. By contrast, few morels are found in the forests of southeastern Mexico and the Yucatan Peninsula (fig. 11).

Morel harvesting in Mexico is a seasonal and traditional activity of indigenous and mestizo (mixed indigenous and European ancestry) communities.

In Mexico, although the government administers 5 percent of forest land as national forests, fully 80 percent is communally owned or belongs to indigenous communities (World Bank 1997). Only 15 percent of the forests are typically managed for timber or wood products. Until recently, little consideration was given to marketing nontimber forest products (World Bank 1995), but the combined harvest of nontimber forest products from 1995 to 2002 was estimated at 1,172,733 metric tons worth $224 million (Montréal Process Working Group 2003). As such markets grow, communities or indigenous groups that own common land have begun forming federally sanctioned community forest enterprises (CFEs) to manage their forests for sustainable nontimber forest product harvests and optimal economic benefits (Bray and others 2003). In a few cases (Martínez-Carrera and others 2002, Methodus Consultora S.C. 2005) indigenous CFEs monitor mushroom harvests and encourage cooperative marketing. The CFE "Pueblos Mancomunados" in Oaxaca exemplifies a project that encourages sustainable harvesting and commercial marketing of wild mushrooms to national and international markets, although morel productivity is reportedly low (UNEP-WCMC and Methodus Consultora S.C. 2003). Educational mushroom fairs hosted by communities such as the town of San Antonio Cuajimoloyas, Oaxaca, acquaint harvesters with edible mushrooms and marketing opportunities (Mader 2005).

Morel harvesting in Mexico is a seasonal and traditional activity of indigenous and mestizo (mixed indigenous and European ancestry) communities. Because the crops are small and scattered, harvesters often walk several miles to collect mushrooms. Some morel harvesters in central Mexico set fires to encourage subsequent morel fruiting. Traditionally, the harvester's family consumes these morels. More recently, morels are sold fresh in small-town markets or shipped to larger markets in Mexico City.

Boa (2004) referred to the emergent wild edible mushroom industry in Mexico as "small-scale exports of selected species" and morels as one of the most important commercial wild mushrooms (Villarreal and Gomez 1997). In 1997, 33 short tons of morels were exported to USA and Europe (UNEP-WCMC and Methodus Consultora S.C. 2003). In 1996 and 1997, 3.5 and 1.3 short tons, respectively, of *Morchella* species were exported to France (Zamora and others 2001; SEMARNAP and PROCYMAF, n.d.). The future of Mexican morel export to France looks promising. EurocenterNafinMexico, a bureau of economic cooperation co-financed by the European Commission and the Mexican Bank of Development (Nacional Financiera), announced (25 June 2005) on their "Successful Stories" Web page (http://www.eurocentro.org.mx/EN/success.html) that new contracts had been arranged between Mexican and French companies to export $200,000 of fresh morels and $660,000 of dried morels collected from the forests around Mexico City.

Concerns on the part of the Mexican Government about commercial exploitation of mushrooms, animals, and plants led to the normative regulation (NOM-059-ECOL-2001) that includes *M. angusticeps, M. conica, M. costata, M. elata, M. esculenta, M. rufrobrunea*, and *M. umbrina* as protected species (Diario Oficial 2001). Federal law (NOM-110-RECNAT-1996) specifically regulates commercial morel harvesting to control methods of collecting, processing, transporting, and storing (Diario Oficial 1996). Private forest owners, organized as environmental management units (*unidades de manejo ambiental* or UMAs), are required to inform officials and request permission for any commercial harvest. They are also expected to conduct sustainable management studies, estimate expected crops, and institute measures to protect wildlife, manage fires, and control pests. However, the sustainable harvest of morels is rarely ensured because official regulations do not address the unique life history of each protected species, and studies of morel biology in Mexico are lacking. Molecular, taxonomic, and ecological investigations of wild morel populations and their responses to commercial harvesting and forest management are underway by L. Villarreal-Ruiz at the Fungal Resources Lab in the Colegio de Postgraduados, Montecillo Campus. These studies will improve the formulation of practical and effective regulations to promote sustainable harvesting.

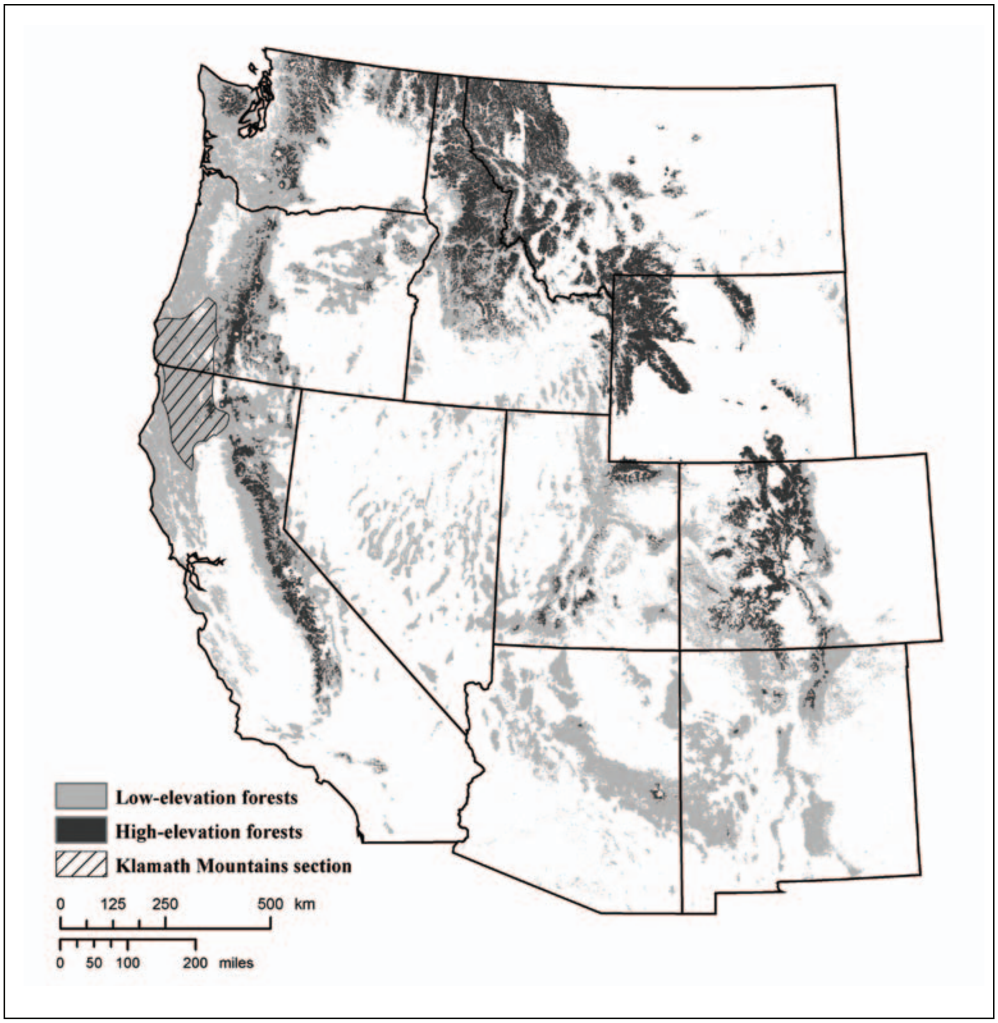

Figure 13—Morel habitat in the Western United States. Commercial morel harvesting occurs predominatly in the high-elevation forests. Map compiled by Bridgett Naylor, geographic information systems analyst, Forestry and Range Sciences Lab, USDA, Forest Service, Pacific Northwest Research Station, La Grande, OR 97850. Data derived from the forest type and ecoregion layers of the National Atlas of the United States, http://nationalatlas.gov.

Overview of the Western United States

Figure 13 provides an overview of commercial morel habitat in the Western United States. Morel habitat predominantly corresponds to the forested areas although they do fruit in irrigated landscape areas of cities located in desert regions. Most commercial collections occur in the higher elevation forests that experience greater snow accumulation and where morels tend to fruit more abundantly, especially in response to wildfires. Although morels do fruit in the Klamath Mountain region of southwest Oregon and northwest California, they occur infrequently on the metamorphic or serpentine soils widely found there. The following sections discuss differences among subregions of the western continental United States, British Columbia, and Alaska.

Interior West and Rocky Mountains

For our purposes, we define the Interior West and Rocky Mountains as west of the Great Plains, north of Mexico, east of the Sierra Nevada range, and south of Oregon, Idaho, and Montana. Morels fruit in forests throughout this area. Much of this landscape is dry relative to the west coast and regions further north, so appropriate forest habitats occur at higher elevations (Miller 2003). Forest habitat for morels is thus patchier and more widely scattered than in regions farther to the west and north. In some cases, such as in Nevada and Utah, morel habitat occurs as isolated islands near or on mountain peaks. In other areas, such as Colorado, more of the landscape is high elevation and morel habitat is more continuously distributed. Winter snow packs accumulate in most of these high-elevation forests, and convection thunderstorms or southwesterly fronts from the Gulf of Mexico cause sporadic heavy summer rainfall. Morels frequently occur in moist microhabitats and the morel season progresses upwards in elevation as summer weather warms (Miller 2003).

The U.S. federal government (typically the BLM, USFS, national parks, and national monuments) manages most of the forests in the region, so morels are found predominantly on federal lands, but some state, county, tribal, and private forest lands also include morel habitat.

As in other regions, black morels (both natural and burn morels) tend to fruit in coniferous forests, especially following tree death, wildfire, or soil disturbance. Yellow morels can be found in wetter or riparian forests with birch and cottonwood trees. Although some profitable timber harvesting occurs in the national forests of this region, forest health, fire protection, wildlife habitat, and watershed protection often are the more important goals. Thinning and prescribed burning are commonly used to achieve these goals. Although such operations are rarely designed to stimulate morel fruiting, they can inadvertently do so.

Regulations differ by landowner and circumstances, thus few generalizations apply to such a large geographic area. The USFS and BLM lands do have some uniform standards, such as requiring permits for any commercial activity. Specific regulations, however, differ greatly among local management districts and often from year to year depending upon anticipated harvesting pressure (for instance, in the wake of a large wildfire). Because commercial harvesting is relatively uncommon and small in scale throughout this region, most regulations are not complicated.

Mushroom export or brokerage companies must consider several factors when deciding where to locate large-scale buying stands. Reliable abundant crops of mushrooms that fruit during a relatively short period of time and large areas of productive habitat within a reasonable driving distance are important factors. The sporadic summer rainfall after snowmelt might actually prolong the potential morel season. However, in a region with such steep topographic gradients, morel flushes are more likely to be confined to a small area than in regions where climatic and geographic conditions are more uniform over large areas. For these reasons, most morels harvested in this region are either for personal use or marketed fresh in local towns and cities. Some entrepreneurs likely dry morels for sale later, but large-scale exports of fresh or dried morels are uncommon.

Sierra Nevada Range of California

Morels are widespread in the Sierra Nevada Mountain Range and occur in many ecological communities. Black morels (natural and burn species) are the most commonly harvested morels in the Sierras, although yellow morels are found occasionally. Just after snowmelt in the spring, areas burned by fires during the previous 2 years provide the most reliable source of morels in the Sierras. The timing of fruiting varies by elevation, snowpack, and temperature. Fruiting generally starts in early March at about 4,000 feet in the northern Sierras and about 5,000 feet in the southern Sierras, and increases in elevation as spring progresses. Burned riparian forests also can be productive collecting areas, especially in drainages along the eastern Sierras where willow, aspen, and cottonwood grow. Morels can be abundant in the western foothills of the Sierras in areas where snow is uncommon, but these crops are more influenced by unreliable rainfall than annual snowmelt; consequently, the season can be very short and unpredictable in any given year.

Morels that fruit in nonburned areas do so less profusely than those that fruit in burned areas but are preferred by connoisseurs because they are easier to clean and have a sweeter flavor if cooked fresh. The main groups who collect morel mushrooms from nonburned areas generally include people devoted to a particular reliable location, forest workers collecting opportunistically, and recreational harvesters. Habitats in nonburned areas include slightly mossy (*Polytrichum* species) open areas, coniferous forests, riparian areas, mixed-conifer forests with low amounts of large woody debris, mature mats of prostrate ceanothus (*Ceanothus prostratus*) along the eastern Sierran slopes, and areas with a dense layer of conifer needles but lacking other brush or debris.

Morel harvesting in the Sierras occurs primarily on USFS lands, but harvesters that lack awareness of land ownership boundaries often stray onto private property.

This can be common at the edges of national forest boundaries and in areas with checkerboard-ownership patterns. Such unintentional trespass makes management, law enforcement, and data collecting difficult.

Morel mushroom harvest and management activities on the national forests in the Sierras are less extensive than on national forests in northwestern California, Oregon, and Washington. This is not to say that commercial harvesting and rudimentary efforts at management of this resource have not occurred, but, to date, such efforts have been piecemeal and mushroom collecting is largely unregulated. In California, some state parks allow harvesting with a permit (California Code of Regulations 1996), although most parks in the Sierras pay little attention to such activities within the park and most harvesters are unaware of any required permits.

Large mycological societies and a few ethnic groups are the primary collectors of morel mushrooms in the Sierra Nevada Mountains. Forest botanists working for the national forests of this region often get inquiries from people of European descent about morel, chanterelle, and bolete species available in their area. Southeast Asian groups also harvest numerous mushroom species in the Sierras, but social barriers hinder collecting information about their activities. The Mycological Society of San Francisco, the Los Angeles Mycological Society, and other smaller clubs have many members who are well aware of the potential productivity of morels after a wildfire in the Sierra Nevada (Bomm 1995). Letters that request collecting opportunities often flood the mailboxes of USFS botanists and forest supervisors on national forests with recent wildfires.

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For instance, in August 1994, the Cottonwood Fire on the Tahoe National Forest consumed over 45,000 acres of eastern Sierran yellow pine and lowland riparian cottonwood forest ecosystems. By October 1994, the Tahoe National Forest was inundated with letters from members of the California mycological societies demanding that the forest issue harvest permits. Forest staff worried that if permits were not issued with resource protections, large amounts of damage would occur from unregulated harvesting activities. Tahoe National Forest botanists developed free use permits that stipulated resource protections and required individual harvesters to provide basic information about their identity, where and when they intended to harvest, and what quantities of mushrooms they planned to harvest. In spite of these precautions, officials eventually chose to completely close the area to the public owing to concerns about road damage in the wet spring, and other potential resource damage. Public safety in burned areas was another concern. Subsequently, USFS botanists working in the Cottonwood Fire area in spring 1995 noted large quantities of morel mushrooms fruiting in the fire area and evidence of illegal collecting in spite of the forest closure orders.

The unpredictable nature of morel crops in the Sierras, the relatively short season, and the lack of a commercial harvest infrastructure for any mushroom species have prevented commercial harvests from becoming well established. Much like in Mexico, the interior West, and the central and southern Rockies, most commercial morel harvesting remains small scale and local.

Coast and Cascade Ranges in Oregon and Washington

Throughout the mountainous forests of coastal Oregon and Washington and the western slopes of the Cascade Range, morels are known to fruit the first year after logging or after wildfires. Although some commercial harvesting of morels occurs in these areas, crops are neither as large nor as predictable as on the semi-arid southern and eastern slopes of the Cascade Range. National forests with consistently significant levels of commercial morel harvesting include Mount Hood, Deschutes, Fremont, Malheur, Siskiyou, and Rogue River (McLain 2000). Large morel crops also occur periodically in the semi-arid forests of central and eastern Washington, such as the Gifford Pinchot, Okanogan-Wenatchee, and Colville National Forests (Johnston 2001).

The morel harvest along the eastern slopes of the Cascade Range in Washington and Oregon begins in the south around Bly, Keno, and Gold Hill, Oregon, in March. From mid-April through mid-May, the action shifts to the towns of White Salmon near the Gifford Pinchot National Forest, Tygh Valley near the Mount Hood National Forest, and Sisters near the Deschutes National Forest. Although Sisters is farther south, it is also at higher elevation than Tygh Valley and White Salmon. From late May and into June, morels begin fruiting on the Wenatchee and Okanogan National Forests in Washington. Some harvesters continue at Sisters, Oregon, collecting morels and boletes into June, while others head east to the Wallowa and Blue Mountains, or to Idaho and Montana if there were major wildfires in these regions the previous summer.

Commercial morel harvesting along the eastern front of the Oregon and Washington Cascades takes place on lands managed by the BLM, the USFS, and, in some areas such as near Sisters, Oregon, and Cle Elum, Washington, on large private holdings managed for timber production. Only tribal members or authorized individuals may harvest on the Warm Springs, Yakima, and Colville Indian Reservations. The fine for trespassing on the Warm Springs Reservation is sufficiently high ($5,000) to discourage most harvesters from poaching. Crater Lake, Mount Rainer, North Cascade, and Olympic National Parks allow no commercial activities.

The BLM and USFS lands in this region are subject to the standards and guidelines of the Northwest Forest Plan. It stipulates that activities, including morel harvesting, should not have a negative impact on areas set aside as late-successional or riparian reserves. To address these concerns, some districts have closed such land management units to commercial harvesting, and many have begun to limit dispersed camping in riparian areas.

In addition to issuing permits for commercial mushroom harvesting and operation of buying stations on federal property (see "Permit Fees" in the "Policy and Regulation" section), most national forests in the area also require commercial harvesters to obtain industrial camping permits. In some cases, concessionaires operate designated campgrounds. The USFS law enforcement personnel patrol the roads and camps to monitor compliance with permit requirements, including fire safety and clean camp conditions. To date, managers remain largely unconcerned about whether morel harvesting is sustainable. As yet, there is little monitoring of morel crops or the effects that different forest activities, including harvesting, might have on them. National forest and BLM district permit systems are aimed primarily at keeping track of people.

To date, managers remain largely unconcerned about whether morel harvesting is sustainable.

The early part of the season takes place at a time when morels are scarce and prices are high. Buyers thus tend to market the early morels to domestic and international fresh market customers. Only a small percentage of the crop is sold locally–most is transported to Portland, Seattle, or Vancouver, British Columbia, and either sold in those cities or shipped elsewhere. By mid-May, enough morels have entered the market to bring the price down to the point where buyers and harvesters begin to dry their mushrooms. As the weather warms up, insects become a problem for marketing fresh morels, so by late May into June most of the crop is dried to kill larvae and flies.

Road densities in forests located in the eastern front of the Cascades are greater, and access to large domestic markets and export facilities is better than in the northern Rockies. For instance, in Montana and Idaho, vehicle access can be difficult and harvesters can spend a large portion of their day walking to and from their harvest spots (Brown and Marin-Hernandez 2000). By contrast, most of Oregon and Washington is within just a few hours of the two largest metropolitan areas, Seattle and Portland. Harvest sites between Bend, Oregon, and Twisp, Washington, thus constitute places where people who do not wish to travel far can reasonably compete with circuit harvesters. Sisters, Oregon, plays a particularly interesting role in the harvest of wild morels. Large crops of natural black morels are common in nearby forests in most years. The harvest years of 2003 and 2004, however, were exceptions because the large Eyerly and Cache Mountain Fires in 2002 and the Booth and Bear Butte Fires (combined as the B&B Fire) of 2003 had burned the previous years. Large quantities of black burn morels were harvested in the first year following each of the fires. Whether the reliable productivity of natural black morels returns in the extended aftermath of these wildfires remains to be seen. Sisters also attracts people who are interested in collecting spring boletes (*Boletus pinophilus*), as well as people who use the area as a fall-back zone when other morel harvest locations fruit late or do poorly. It also is a staging area for harvesters before they head east to harvest or buy on the burns in eastern Oregon, or in Idaho, and Montana.

Wallowa and Blue Mountains of Northeastern Oregon

The Wallowa and Blue Mountains are located in northeastern Oregon and extreme southeastern Washington and contain several mountain ranges with elevations sufficient to enhance precipitation and form islands of moisture and biodiversity. Commercial and recreational morel harvests from this region occur in the forests of these mountains. In 1992, the nearly 1 million pounds of morels were gathered in Oregon, mostly from mixed-conifer stands on national forests in the Blue Mountains (Parks and Schmitt 1997).

Much of the land in this region is federally managed as national forests with extensive wilderness areas. La Grande, in the Grande Ronde Valley, is the region's largest town. The Wallowa-Whitman National Forest is the largest national forest (2,392,508 acres, 10 counties) in the area and has been issuing permits for commercial harvesting of mushrooms since 1991 (see "Permit Fees" in the "Policy and Regulation" section). Because morel crops are somewhat dependent on fire activity, there is not a consistent level of harvest activity from year to year (table 4). In 1998, the three Blue Mountain forests (Malheur, Umatilla, and Wallowa-Whitman) began issuing a "tri-forest" mushroom permit. Individuals can purchase a permit from any district office on these forests and it is valid for use in the entire tri-forest area. This has proven to be quite successful, not only from the public's standpoint, but also from a law enforcement perspective. Currently, the forests plan to continue this method of permit issuance. There have been few forest fires within the tri-forest area in recent years; thus the number of issued permits has declined from the peak years of the 1990s.

Regulations for harvesting mushrooms from these national forests are listed in a mushroom guide that is given to individuals when they purchase a permit. Mushrooms may not be harvested in wilderness areas or from restricted botanical sites. The USFS law enforcement officers monitor permitted activities by checking individuals who are harvesting on national forest land to see if they have a valid permit and mushroom guide in their possession and if they are following forest regulations.

Table 4—Number and value of mushroom[a]-harvesting permits sold by the tri-forest permit collaboration of the Malheur, Umatilla, and Wallowa-Whitman National Forests

Year	Permits sold	Value
	Number	*Dollars*
1991	14	882
1992	699	9,066
1993	1,502	17,218
1994	1,537	21,438
1995	2,325	41,840
1996	700	17,926
1997	569	18,316
1998	463	6,436
1999	112	2,020
2000	368	6,854
2001	500	6,524
2002	284	5,192
2003	227	8,130
2004	92	2,800

[a] Although other mushrooms are collected on these forests, morels are the most commonly collected and in the largest quantities.

The mushroom season generally starts in early to mid April, depending on temperature patterns, snow, and precipitation, and can last into early July. Most harvesting activities occur in May and June. Morels can be found later in the year, but not in the quantities or of the quality needed for commercial harvest. Morels are mostly sold fresh to buyers who set up stations in nearby towns and communities. The local buyers in turn resell the mushrooms to mushroom brokers. In La Grande, Oregon, there is one established year-round mushroom buyer and processor. Two of the local restaurateurs actively seek to obtain fresh morels and showcase morel cuisine on their menu during the peak harvest.

Northern Rocky Mountains of Washington, Idaho, and Montana

This area encompasses the Selkirk Range of northeastern Washington, and the northern Rockies of the Idaho Panhandle and western Montana. Commercial morel harvesting occurs throughout these northern ranges, especially in the Bitterroot and Kootenai National Forests of Montana. For example, in the summer of 2000, the huge (292,070 acres) Valley Complex Fire on the Bitterroot National Forest enticed large numbers of commercial morel harvesters to visit in spring 2001.

The two major types of commercially harvested morels in western Montana are the burn morels and gray morels. Both fruit in greatest abundance during the spring

Private timberland owners typically concentrate on salvage logging after fires and have safety and liability concerns regarding mushroom harvesters during these operations.

through summer following a forest fire. Other varieties include blonds and naturals, which grow in nonburned mixed-conifer stands with somewhat open canopies or in small clearcuts. All these morels fruit most abundantly in association with some type of disturbance (McLain and others 2005).

Because this region lies in the rain shadow of the Cascade Range to the west, the mesic coniferous forest habitat that morels inhabit is found at fairly high elevations ranging from 2,500 to 7,000 feet. These forests receive most of their precipitation as winter snow, so wildfires that burn large areas are most common during the relatively dry summer months. Morels seem to fruit most abundantly in areas where a fire burned at moderate intensity, thus killing trees but not burning up their needles. This situation results in a layer of ash and recently fallen reddish needles on the forest floor the following spring and is a clue for harvesters to search the area (McFarlane and others 2005).

Natural black morels and black burn morels fruit in mixed, mid-elevation coniferous forests consisting of Douglas-fir, western hemlock, lodgepole pine, and western larch, and in higher-elevation alpine forests, Engelmann spruce, subalpine fir, subalpine larch, and whitebark pine. Gray morels also fruit in the higher elevation forests (McFarlane and others 2005, McLain and others 2005).

Morels are harvested on both private timberlands and national forests throughout the region, but most morel habitat that is accessible to commercial harvesters is on national forests. Private timberland owners typically concentrate on salvage logging after fires and have safety and liability concerns regarding mushroom harvesters during these operations. National forests also conduct some salvage logging and have the same concerns, but their multiple-use mandate limits the areas logged and stipulates that other forest users, such as morel harvesters, also be accommodated.

Because commercial morel crops occur so frequently in areas burned by wildfire in this region, forest management concerns revolve around issues such as compatibility with salvage logging, introduction of noxious weeds, off-road vehicle use on fragile burned soils, hazards such as falling snags or burned-out root wells, and heavy back-road traffic. Concerns related specifically to morel harvesting include conflicts between visiting and local harvesters, potential overharvesting, and possible harm to endangered species from foot traffic, all terrain vehicles (ATVs), and camping. The USFS is also concerned about providing adequate sanitation at campsites, controlling litter, and commercial harvesters using campsites intended for recreational forest visitors.[27]

[27] Floch, Rick. 2001, 2005. Personal communication. Assistant Forest Fire Management Officer, U.S. Department of Agriculture, Forest Service, Bitterroot National Forest, Forest Supervisor's Office, 1801 N First, Hamilton, MT 57840-3114.

As the main landowner in this region, the USFS predominantly controls issuance of permits and regulation of the commercial harvest on national forests, although local private landowners also set up campsites on their property and charge harvesters.[28] Each individual forest manager is responsible for outlining any special considerations. The Kootenai National Forest, for example, has special grizzly bear restrictions, whereas the Lolo National Forest restricts harvesting in gray wolf habitat. All forests prohibit commercial harvesting in wilderness areas. In general, enforcement of mushroom permits and regulations is a relatively low priority for the national forests in Idaho and Montana. In particularly active seasons, such as the one following the fires of 2000, however, the USFS has experienced problems with compliance (see footnote 27). Specialists, such as botanists, typically analyze a harvest season to identify needed modifications to monitoring, regulations, or enforcement.

The morel season in this region typically begins with a focus on marketing of fresh morels. As quantities increase, buyers shift to drying morels and then later in the season when volumes again decrease, buyers will shift back to selling fresh morels. Prices fluctuate throughout a season depending on the type of morel and harvest quantities. Gray morels, for example, are heftier than other types of morels and retain moisture and freshness better in transport; therefore, buyers prefer to sell them fresh. Gray morels also are often harvested in June when morel production is dropping off elsewhere around the world in temperate forests; hence fresh morels are more valuable on the world market when the gray morels fruit in this region. When possible, fresh morels are shipped to ports such as Seattle, where they can then be distributed internationally. Dried morels can be easily shipped anywhere throughout the off-season.

Western Canada

Generally, morel production in western Canada begins in late April or May at lower elevations and southern latitudes and proceeds to higher elevations and more northern latitudes. For example, burned areas on the high-elevation Chilcotin Plateau of central British Columbia produced morels in June through July. Near Cranbrook, morels were commercially harvested in 2004 from the beginning of May until early August. In the Northwest Territories, Obst and Brown (2000) reported the season near Yellowknife is July 1–30.

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[28] Svalberg, Larry. 2001. Personal communication. Zone Planning Coordinator, U.S. Department of Agriculture, Forest Service, Lolo National Forest, Fort Missoula Bldg. 24, Missoula, MT 59804.

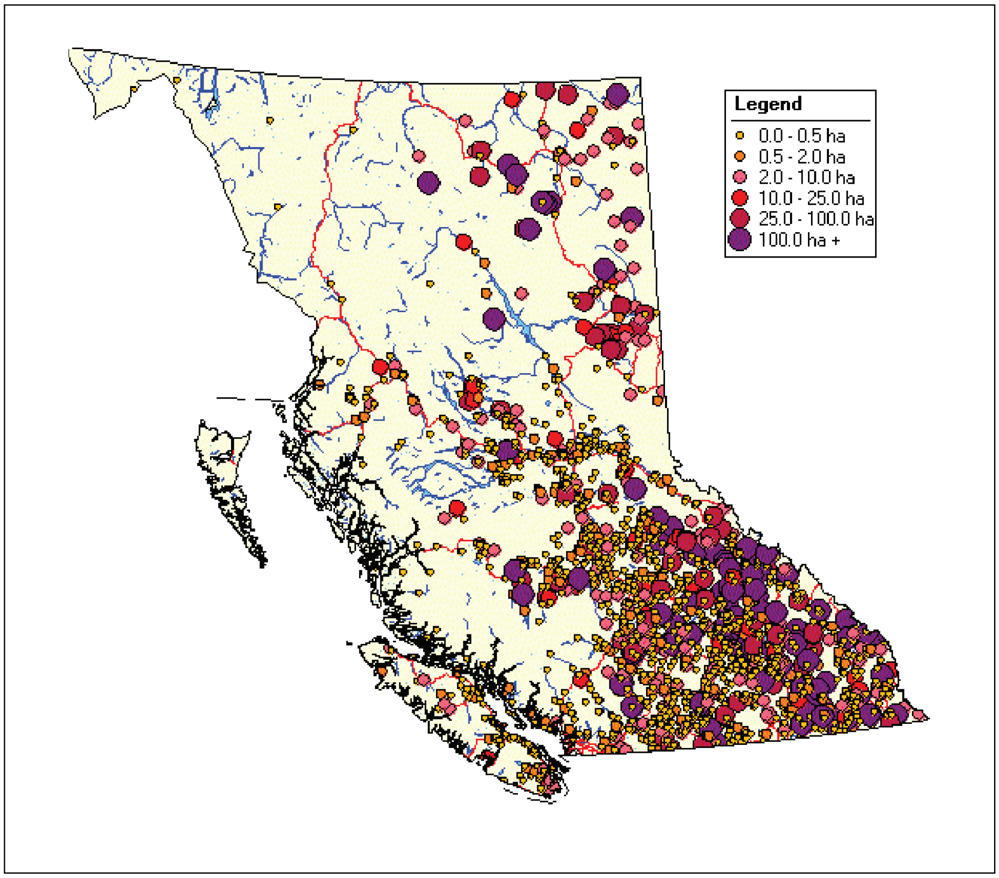

Figure 14—Forest fires in British Columbia in 2003. Protection Branch of the Ministry of Forests and Range. http://www.for.gov.bc.ca/protect/reports/FireLocations.htm.

Nonfire morels have been harvested commercially in British Columbia in recent years, for example, in the Williams Lake area.[29] More recently, the focus of commercial morel harvesting in British Columbia has shifted to fire morels (both black and gray). Wills and Lipsey (1999) reported that fire morels were harvested near Pemberton in the southern Okanagan Range, and around the Smithers area. Most forest fires in British Columbia occur in the relatively hot, dry ecosystems concentrated in the southeast part of the province, east of the Coast Mountains and south of Prince George (fig. 14). Therefore, most of the commercial morel production likely now occurs in this area. However, commercial morel harvesting certainly occurs on burns in virtually all other parts of the province as long as the fire is large enough to produce big crops worth harvesting and access is reasonable. For instance, in northeastern British Columbia, the Wapiti Fire (1987) and the 5,200-acre "M"

[29] Chapman, Bill. 2004. Personal communication. Research soils scientist, Southern Interior Region, BC Ministry of Forests, 200-640 Borland St., Williams Lake, BC V2G 4T1 Canada.

Fire near Emerslund Lakes (1991) were big fires that brought in morel buyers from outside the area.[30] Similarly, the 62,000-acre Telegraph Creek Fire[31] in northwestern British Columbia (1998) and the 74,000-acre Chilko Fire[32] in central British Columbia (2003) produced big commercial morel crops in forests killed by mountain pine beetle. The Cranbrook area also produced abundant morel crops in 2004 and 2005,[33] although they were not commercially harvested.

During the 1990s and early 2000s, the majority of morels harvested in western Canada came from the Yukon Territory. The Yukon Territory consistently produced morels in commercial quantities, most of which passed through Vancouver as part of the export trade (Wills and Lipsey 1999). British Columbia yielded considerably fewer morels during this period, a difference that Wills and Lipsey (1999) attributed to more aggressive fire suppression. The Yukon Territory has paved roads connecting most communities to each other and to the Alaskan Highway, so morels can be moved promptly to the markets in Vancouver (Wills and Lipsey 1999). Fires that produce commercial crops of morels occur mostly in the center and southwest areas near Whitehorse and Carmacks.[34] Although the harvesters are mostly local, morel buyers come into the area when productivity is high, as they did for the 143,000-acre Minto Fire (1995) and the 124,000-acre Fox Lake Fire (1998).

Although remote, the Yukon Territory is more accessible than the Northwest Territories. Obst and Brown (2000) noted that lack of access to harvesting sites and high cost of transporting morels from the forest to markets hinders development of the morel industry in the Northwest Territories. Nevertheless, some commercial morel harvesting does occur near population centers. Kenney (1996) reported that the availability of laborers often limits harvesting in remoter regions of the Yukon Territory. In Canada, as in some of the more remote areas of the Western United States, harvesters occasionally rent planes or helicopters to locate burns and identify areas of low-intensity fire (Brown and Marin-Hernandez 2000). If the harvesters can identify a highly productive site where no one else is harvesting, their investment may be recouped.

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[30] Kabzems, Richard. 2004. Personal communication. Research silviculturalist, Northern Interior Region, BC Ministry of Forests, 9000 - 17th St., Dawson Creek, BC. V1G 4A4 Canada.

[31] Kranabetter, Marty. 2004. Personal communication. Research pedologist, Northern Interior Region, BC Ministry of Forests, BAG 6000, 3333 Tatlow Rd, Smithers, BC V0J 2N0 Canada.

[32] Chapman, Bill. 2004. Personal communication. Research soils scientist, Southern Interior Region, BC Ministry of Forests, 200-640 Borland St., Williams Lake, BC V2G 4T1 Canada.

[33] Keefer, Michael[a] and Winder, Richard[b]. 2004. [a]Coordinator, Kootenays Forest Innovations Society, 3816 Highland Rd., Cranbrook, BC V1C 6X7 and [b]microbial ecologist. Canadian Forest Service, Pacific Forestry Centre, 506 West Burnside Rd., Victoria, BC V8Z 1M5 Canada.

[34] Skaalid, Susan. 2004. Personal communication. Manager, Forest Operations, Yukon Government, Box 2703 (K-918), Whitehorse, YT Y1A 2C6 Canada.

Little information has been published on the morel harvests in British Columbia or the Yukon Territory. Ecological and economic studies have only recently been conducted (Keefer 2005). Because most of the forest fires occur in the drier, warmer ecosystems in British Columbia, most of the burned stands were primarily coniferous, consisting of pine, subalpine fir, western larch, Douglas-fir, or spruce. In the Peace region, where fires that produce commercial morel crops are relatively uncommon, it is thought that morels are harvested from burned spruce and pine but not aspen stands (see footnote 30). In the Yukon Territory, most commercial morel crops are produced after mixed white spruce and pine stands burn. Pink burn morels are harvested early in the season and "grays" and "greenies" are harvested later.[35]

During a field trip with Dr. Nancy S. Weber in May 2004 to the Okanagan Mountain Fire in southeastern British Columbia, participants were able to collect a variety of black morels: putative species A (naturals), B (pink burn morels) and C (green burn morels) as described by Pilz and others (2004). Gray morels (putative species D) were also collected from the same burn sites a little later. The gray morels might be more common than the blacks at higher elevations and farther north,[36] and they fruit later in the season on the same burned areas where the other burn morels previously fruited (see footnote 29).

Although Pilz and others (2004) reported that mountain blond morels are likely only found in nonburned areas, blond-colored morels were observed fruiting at high elevations in early September in the Tokumn Verrendrye Fire. In this case, they were fruiting in burned soils near large dead Engelmann spruce trees.[37] Gray morels can lighten in color significantly with age, as illustrated in figure 2 in the "Species Description" section, so this observation might have entailed morphological misidentification.

In British Columbia, the province is 94.7 percent national Provincial Crown land. Land administered by the Ministry of Forests makes up 91.5 percent of these Crown lands and 86.7 percent of the province (Still and others 1994). Therefore, most morel harvesting probably occurs on Crown land, although trespass into burns on private lands and prohibited harvesting in parks probably occur. In the Northwest Territories, land ownership is split between the territorial government and the national government, with the territorial government having jurisdiction over public

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[35] Olivotto, Gerard, 2004, Personal communication. Forest resource modeller, Olivotto Timber, 203-733 Johnson St., Victoria, BC V8W 3C7 Canada.

[36] Winder, Richard. 2004. Personal communication. Microbial ecologist, Canadian Forest Service, Pacific Forestry Centre, 506 West Burnside Rd., Victoria, BC V8Z 1M5 Canada.

[37] Keefer, Michael. 2004. Personal communication. Coordinator, Kootenays Forest Innovations Society, 3816 Highland Rd., Cranbrook, BC V1C 6X7 Canada.

forest lands (Olynyk and Bergner 2002). In 2003, the Yukon territorial government assumed management authority over most of the Crown lands in its territory (Office of the Auditor General of Canada 2004). In the Yukon Territory, forest land makes up 59 percent of the total area. Of this, the government now manages 85 to 90 percent of public land referred to as "Commissioner's Land," 8 to 15 percent is managed by First Nations, and less than 1 percent by the Canadian government (Yukon Energy, Mines, and Resources 2004). The territorial governments in the Yukon and Northwest Territories settled land claims agreements with many of the First Nations within their boundaries beginning in 1984 (Olynyk and Bergner 2002). In the Yukon, 14 First Nations (indigenous peoples and their governments) will eventually control 9 percent of the territory; First Nation claims settlements to date encompass about 40 percent of the Northwest Territories land area (Olynyk and Bergner 2002). An overlay of un-extinguished aboriginal rights and titles also govern rights of access and use of much of British Columbia's public lands (Tedder and others 2002). Under the land claims settlements, First Nations will assume much greater authority to regulate resource harvesting on lands within their claim boundaries (Olynyk and Bergner 2002, Tedder and others 2002). It is too soon to tell how this will affect access to morel harvest areas in western Canada.

An overlay of un-extinguished aboriginal rights and titles also govern rights of access and use of much of British Columbia's public lands.

Mushroom harvesting from Crown lands in British Columbia is unregulated, and there are currently no plans by government agencies to manage the resource. Similarly, in the Yukon Territory, mushroom harvesting is neither regulated nor managed, but nontimber forest product regulations are currently being drafted that might affect future management of the commercial morel harvesting. Without government-wide policies, the focus of concern for forest districts where morel harvesting occurs is not the productivity of the morels but the activities of the harvesters: littering, getting lost, causing forest fires, or driving on logging roads. In the Southern Interior Forest Region, awareness of the importance of morel harvesting in burned areas led in 2004 to the creation of a Web page that provides information about fire maps, mushroom harvesting and identification, road use, camping and recreation, and fire prevention (http://www.for.gov.bc.ca/rsi/PublicUse/PublicUse.htm). During the long Canadian winter, morel harvesters and buyers also monitor the Web sites of the Protection Branch of the Ministry of Forests (http://www.for.gov.bc.ca/protect/reports/FireLocations.htm) and of the Yukon Government (http://www.community.gov.yk.ca/firemanagement/index.html) for the size and location of the previous summer's wildfires. They use this information to focus their efforts the following spring. Combined with local information, this allows the commercial morel industry to visit potential sites and assess their productivity starting in early spring.

Although morels are sold fresh locally to restaurants and stores in western Canada, most of the crop is shipped to Europe and elsewhere, including the United States. Some morels are shipped fresh, but depending on weather and transportation networks, many are dried before export. For instance, in the relatively accessible Kootenay region of southeastern British Columbia, a third of morels shipped in 2004 were dried (Keefer 2005).

Interior Alaska

Interior Alaska encompasses over 108 million acres. In this boreal forest region, the primary natural disturbance is wildfire, and in the majority of the land area of interior Alaska, wildfires are not suppressed (Alaska Wildland Fire Coordination Group 1998). An average of 708,700 acres burned each year in interior Alaska between 1961 and 2000 (a total of nearly 28 million acres), but during that interval, 55 percent of the total area (15.6 million acres) was burned in six particular years (Kasischke and others 2006).

The vast majority of land in Alaska is public land managed by the BLM and the Alaska Department of Natural Resources. The major private landowners are a variety of Native Corporations, which together own about 10 percent of all the land in Alaska. Alaska has very few roads and typically most land affected by wildfires in any given year is not accessible by road.

Although stories of large postfire morel crops in interior Alaska are common, few data are available. Wurtz and others (2005) reported finding morels in a variety of forest types, including riparian areas, stands of white spruce, steep south-facing slopes with dense stands of black spruce, and level benches with mixed stands of black spruce and paper birch. Morel productivity varied from year to year and site to site, but was at least similar to that reported by Pilz and others (2004). Research is underway (Helfferich 2005) to determine and describe the species of *Morchella* that occur in interior Alaska, but we know that between 2002 and 2005, peak fruiting periods lasted only 2 to 3 weeks (Wurtz and others 2005).

There has been comparatively little commercial morel harvesting in Alaska, although the number of Alaskans who pick occasionally is increasing. To date, there have been only two major influxes of commercial morel harvesters from outside the state: in 1991, to the area burned in the 1990 Tok River Fire, and in 2005, to a number of different fires that burned near Tok in 2004 (fig. 15). Between 150 and 300 people participated in these harvests; most of these individuals traveled to Alaska from Canada and the Lower 48 States. It was estimated that buyers from outside Alaska purchased over 300,000 pounds of morels in 1991 (Malchow 1991), and

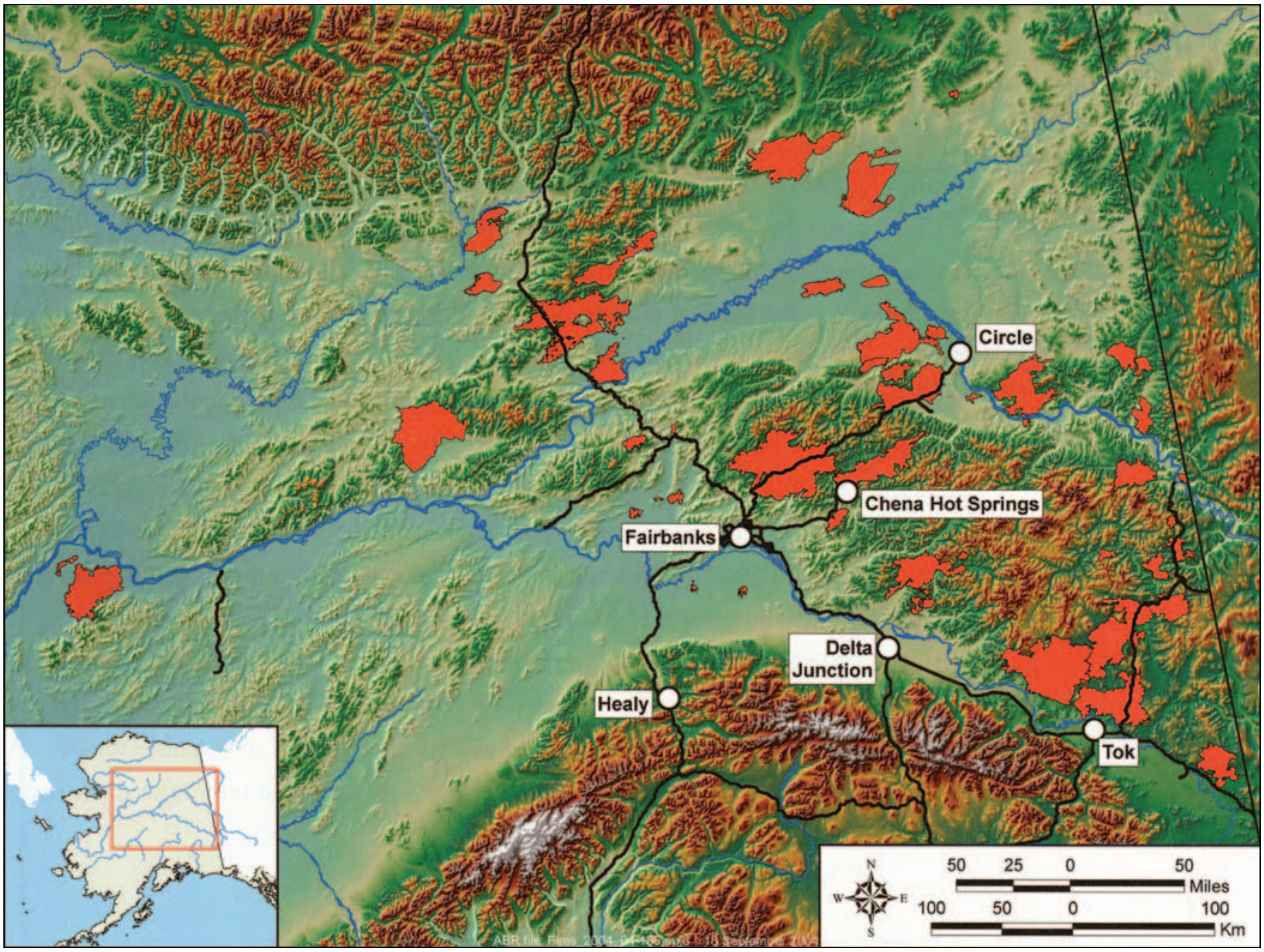

Figure 15—Interior Alaska, with the areas burned in major wildfires during summer 2004 in red. (Fire perimeters are as of September 2004 and are courtesy of the Alaska Fire Service. Image by Matt Macander, ABR Inc., Environmental Research & Services, Fairbanks. Reprinted from Wurtz and others [2005]).

approximately 175,000 pounds were purchased in 2005 (Yamin 2005). Both times, managers reported problems with garbage being left in the field, trespassing, and with the misuse of ATVs on public lands (Malchow 1991, Yamin 2005). In 2005, the State of Alaska, the BLM, and two Native Corporations issued permits for the commercial harvest and experienced a range of compliance and success (Yamin 2005). The University of Alaska Cooperative Extension Service and the U.S. Department of Agriculture Cooperative State Research, Education, and Extension Service published a practical extension guide on harvesting morels in Alaska (Moore and others 2005). The pamphlet discusses morel identification, personal safety, permits, harvest areas, forest protection, litter, harvest methods, harvest equipment, and morel handling, transporting, processing, drying, storing, home use, and marketing. It also provides addresses for land management agencies that regulate morel harvesting on their lands.

Constraints on the commercial harvest of morels in Alaska include the lack of road access to burned areas, the small size of local markets, lack of established markets for other nontimber forest products, and lack of experience within the Alaskan morel industry. At least one in-state supplier sells both Alaskan-harvested morels as well as morels harvested outside the state (Wurtz and others 2005), suggesting that demand for morels inside Alaska currently exceeds the quantity harvested. Niche markets may exist outside the state for mushroom products from Alaska, or products harvested by Alaska Natives (Pilz and others 2006a). No licenses or authorizations are currently required to either buy or sell wild mushrooms as a food product in Alaska.

The most common forest type in interior Alaska is black spruce forest. It is extremely flammable and accounts for most of the acres burned each year in the state. Most black spruce stands in Alaska are slow growing and unproductive, with no value as timber. Postwildfire morel crops might therefore represent the greatest economic return for a forest product from these forest types.

Management and Research

Sustainability

Many forest laws and regulations stipulate that natural resources should be managed for conservation, or in the case of commercial products, sustainable production. Defining "sustainability," however, can be complex in a forest environment that is constantly changing. For instance, natural or nondisturbance morels might appear easy to monitor for sustainable production. One would simply measure production each year and chart the values to see if they change over time. Unfortunately, mushroom productivity fluctuates greatly from year to year (Vogt and others 1992), therefore decades of monitoring is typically necessary to detect trends with a useful degree of statistical confidence. During such timeframes, however, the forest ages and changes, possibly enough to affect morel production more than harvesting. Hence it would be difficult to assign a reason for noted changes in productivity over time.

Morels that fruit abundantly in response to disturbances present an even more interesting challenge to defining "sustainable." Such disturbances can be unplanned and episodic (such as wildfire or insect infestations) or planned and periodic (such as logging or prescribed burning). Such morel crops can also occur over the vast areas typical of some wildfires such as those near Yellowknife in the Northwest Territories (Obst and Brown 2000) or in Yellowstone National Park (Kuo 2002). In any case, these disturbance morels do not produce annual commercial crops. Hypothetically, sustainable production could be defined as nondeclining yields of morels each time a delimited forest stand is disturbed. Morel production, however, is likely to vary widely depending on the condition of the stand at the time it is disturbed, the intensity of the disturbance, and the weather that year, so comparisons between crops widely separated in time also would be very hard to interpret with any confidence.

These considerations about how to define sustainable production are not unique to morels or even to harvested mushrooms in general. They are applicable to many harvested forest resources, including timber. Often the only way to reasonably monitor sustainable production is on the scale of landscapes and over periods of decades or centuries. To date, no land management agency has undertaken long-term monitoring of potential impacts that intensive commercial mushroom harvesting might have on mushroom populations across large areas (Pilz and Molina 1998). Nevertheless, forest managers must make decisions about how to harvest commercial products in a sustainable manner, and usually such decisions apply to small spatial scales and short timeframes. The most useful approach is to use current knowledge about the biology, reproductive potential, growth rates, and ecology of the organism being harvested to design forest management and product harvesting guidelines that reduce or mitigate the risks of potential overharvesting. Providing such information is a key purpose of this publication. In some cases, management can even proactively use this information to increase or enhance the availability of morel harvesting opportunities.

Often the only way to reasonably monitor sustainable production is on the scale of landscapes and over periods of decades or centuries.

In the remainder of this section, we examine some of the considerations that factor into evaluations of whether morel harvesting is sustainable. These include estimates of typical morel productivity, forest management activities that affect morel crops, management of morel harvesting activities, and useful morel research.

Productivity

Although there has been no long-term monitoring of morel productivity, we do have published estimates of typical productivity. One of the first published estimates (Duchesne and Weber 1993) reported extremely high values. Using 10.76-square-foot (1-square-meter) plots in a 0.52-acre (30- by 70-meter) portion of a burned Jack pine stand in eastern Ontario, they documented 2,550 pounds per acre of fresh morels. Assuming each morel weighed two-thirds of an ounce, this translates to approximately 60,000 morels per acre, 12 to 13 morels per square yard, or over 1

Table 5—Unbiased stand-level estimates of mean morel productivity (counts and fresh weight per acre per year) and 90-percent confidence intervals for nine forest stands in northeastern Oregon that were selected to represent three stand conditions[a]

Site location[b]	Stand condition[c]	1995[d]		1996	
		Count	Weight	Count	Weight
		Morels/acre	*Pounds/acre*	*Morels/acre*	*Pounds/acre*
45.08º N 118.49º W	Healthy	229 (± 131)	1.2 (± 0.9)	87 (± 38)	1.4 (± 0.9)
45.09º N 118.49º W	Insect-damaged	417 (± 132)	2.9 (± 1.2)	129 (± 68)	3.2 (± 2.1)
45.08º N 118.50º W	Wildfire in 1994	1194 (± 243)	3.7 (± 1.6)	182 (± 125)	8.1 (± 6.4)
45.04º N 118.48º W	Healthy	83 (± 60)	1.7 (± 2.3)	42 (± 45)	1.9 (± 2.0)
45.04º N 118.48º W	Insect-damaged	283 (± 123)	2.7 (± 2.2)	32 (± 27)	0.5 (± 0.5)
45.04º N 118.47º W	Wildfire in 1994	1761 (± 948)	3.4 (± 2.3)	117 (± 48)	2.0 (± 1.2)
44.68º N 118.64º W	Healthy	123 (± 84)	1.3 (± 0.8)	49 (± 35)	1.3 (± 1.4)
44.68º N 118.64º W	Insect-damaged	156 (± 59)	0.8 (± 0.7)	115 (± 70)	3.1 (± 4.1)
44.07º N 118.63º W	Wildfire in 1994	127 (± 82)	0.6 (± 0.4)	132 (± 81)	5.1 (± 4.9)

[a] Source: Pilz and others 2004.
[b] Latitude and longitude conversions from Township and Range legal descriptions were incorrectly transcribed in the original publication. They are correctly reported here.
[c] The wildfire occured in 1994, and the insect-damaged stands had been infested for the previous 5 years.
[d] Only burn morels fruited in the wildfire stands in 1995. Burn morels did not fruit in the nonburned stands that year or in any of the stands in 1996. Natural black and mountain blond morels fruited in the nonburned stands and in the burned stands the second year after the wildfire.

every square foot. Such densities would be a morel harvester's paradise but likely represent the high end of potential productivity. More typical morel productivity values are presented in tables 5 and 6. Although values differ by several orders of magnitude depending on the habitat, it appears common to find 1,000 or more morels per acre the first year after a forest fire.

Table 6—Morel productivity values from the first year following wildfires in Minnesota, Oregon, Alaska, British Columbia, and the Northwest Territories

General location	Lat. and long.	Name of fire	Year of fire	Year morels sampled	Burn intensity[a]	Mean count	Mean fresh weight	Reference
						Number/ac	*lbs/ac*	
Cook Co., MN			1976	1977	Light to moderate	607		Apfelbaum and others 1984[b]
Cook Co., MN			1976	1977	Severe	81		Apfelbaum and others 1984
Wallowa-Whitman National Forest	45.08º N 118.5º W	Tower	1994	1995	Moderate	1,194	3.70	Pilz and others 2004
Wallowa-Whitman National Forest	45.04º N 118.47º W	Tower	1994	1995	Moderate	1,761	3.39	Pilz and others 2004
Malheur National Forest	45.04º N 118.63º W	Summit	1994	1995	Moderate	127	0.58	Pilz and others 2004
Southwest of Fairbanks, AK	64.65º N 148.3º W	Survey line	2001	2002	Moderate to severe	398	5.86	Wurtz and others 2005[c]
Northeast of Fairbanks, AK	65.05º N 146.2º W	West Fork	2002	2003	Moderate to severe	4	0.02	Wurtz and others 2005[c]
North of Fairbanks, AK	65.38º N 148.91º W	Tolovana Hot Springs	2002	2003	Moderate to severe	91	2.34	Wurtz and others 2005[c]
Kootenay region of southwestern BC[d]		Lamb Creek, Plumbob, Mission Creek, White River, Middlefork, Tokumm	2003	2004	Varied by microsite[e]	1,472-3,062		Keefer 2005
Yellow-knife NWT	62.55º N 113.35º W	Tibbit Lake Lake	1998	1999	Moderate to severe	140-940	8.92	Obst and Brown 2000[f]

[a] Burn intensity can be characterized in many ways. We define our broad categories as follows: Light burn = trees alive, duff layer not consumed. Moderate burn = many trees killed, but needles not consumed, duff layer mostly consumed. Severe burn = all trees killed and needles burned, duff layer entirely consumed.

[b] Sampling methods for these data are not described.

[c] Sampling methods were similar to those described in Pilz and others 2004.

[d] Data from several fires were combined.

[e] Keefer (2005) compared morel productivity with burn intensity within sites and concluded that the highest morel productivity was sampled in areas of moderate burn intensity.

[f] Productivity sampling was not described as random. Some "hot spots" were sampled.

Forest Management

A key research question is whether mycelial colonies or sclerotia of morels persist in the soil through stand-replacement events.

Nondisturbed forests—Natural black, yellow, half-free, mountain blond, and red-brown blushing morels are all capable of fruiting in habitats that have not been disturbed. They can fruit annually if favorable conditions persist and the weather cooperates. Sustaining populations of these species entails maintaining forest habitat for them. No forest stand lives forever. Stand-replacement events happen in virtually all western North American forest ecosystems. Sometimes such events are natural (such as fire, blowdown, and volcanism) and sometimes planned by humans (such as logging). Sustaining populations of morels that fruit in nondisturbed habitat, therefore, likely entails managing forests for a mixture of stands in various age classes and in sufficiently close proximity for morels to spread their spores between stands. In this manner, morels in an older stand could reinoculate nearby newly established stands. A key research question is whether mycelial colonies or sclerotia of such morels persist in the soil through stand-replacement events. If so, the relative proximity of stands in different age classes might not matter much.

Tree death—Some morel species that fruit in nondisturbed areas can fruit as abundantly as fire morels when other disturbances occur, especially tree death. Massive crops of yellow morels at the bases of dying elms (Thompson 1994, Weber 1988) and extensive fruiting of natural black morels in insect-killed forest (Pilz and others 2004) are two examples. Insect infestations left uncontrolled might create large morel crops, but if the trees die, it could be a long time before new forests sustain new morel crops. In forests where insect infestations are controlled, managers might forgo immediate large crops of morels while sustaining annual production of smaller morel crops. Given our current state of knowledge, how all these considerations balance out is merely a matter of interesting speculation. Because timber is usually worth more than morels (Alexander and others 2002a), decisions about controlling insects usually are driven by considerations other than morel crops. Still, if managers realize a large morel crop is likely, they can plan for managing its harvest.

In a related question, could the total production of morels be affected by how quickly a tree dies? For instance, does a tree that declines over several years before dying from insect damage stimulate more morels to fruit than one that is cut down for timber? In the latter case, the roots would die more quickly and likely fewer nutrients would be transferred to mycorrhizal root tips as they die. On the flip side, morels are likely competing with other fungi for these root tip food sources, and if the tree dies quickly, morels might have a competitive advantage decomposing the root tips. This question could make interesting material for a graduate student who wanted to kill some trees in a controlled fashion.

Timber harvesting—Clearcut logging and thinning also can produce morel crops in the absence of fire, but to what extent they do so has not been documented in the literature. Nevertheless, any forest where morels grow and that is managed for timber production presents an opportunity to stimulate morel crops through logging. The seasonal timing of logging activities might influence the level of subsequent morel productivity, so if a manager wanted to co-produce timber and morels, testing this hypothesis would be a useful line of inquiry. The percentage of trees removed during a thinning operation, and the relative size, dominance, health, and crown class of the removed trees, could all conceivably influence the size of morel crops, both those associated with the thinning disturbance and those that follow annually in the thinned stand. For instance, if morels fruit in association with diseased or suppressed trees that are slowly dying, removing these from the stand during thinning might reduce subsequent morel fruiting. Conversely, if some morels function as full mycorrhizal partners with healthy trees, then stimulating the growth of residual trees in a stand by thinning might improve annual morel crops. In a study that examined the effect of young-stand thinning on chanterelle mushroom production, the productivity of this mycorrhizal fungus declined for several years following thinning, but rebounded within 6 years (Pilz and others 2006c). We have yet to determine if morels respond similarly.

Soil disturbance—Harvesters frequently note that morels tend to fruit where soil has been displaced, mixed, or compacted. We have observed morels fruiting along the edges of yarding roads in thinned forests and in the deep footprints left by previous harvesters on a burned site. Not yet known is whether the soil disturbance per se stimulates fruiting or whether a good spot is simply created for morels that would have fruited someplace anyway. Morels are often found fruiting in sheltered locations such as along the side of a log or in depressions, so soil disturbance might simply offer locations on the forest floor where developing morels are protected from desiccation by wind or sunlight. Even if soil disturbance does enhance morel fruiting, intentional disruption or compaction of soil has too many potential negative impacts on tree growth to consider its use for enhancing morel crops. Also, any such crops might only last a year, but soil compaction can last a long time. Here again though, when managers know that harvesting timber has produced some degree of soil disturbance in a given area, they can anticipate that morel harvesters will be looking there.

Intentional disruption or compaction of soil has too many potential negative impacts on tree growth to consider its use for enhancing morel crops.

Fires—Fire management is an integral component of managing western forests. Fire suppression is now recognized as having increased the risk of large catastrophic wildfires compared to the more frequent and less intense fires that preceded fire control (Pyne 1996). Mushroom harvesters and buyers commonly target large catastrophic wildfires because they promise sufficiently large morel crops to justify travel, harvesting, buying, and shipping expenses. But do infrequent intense fires produce more morels over time than frequent less intense fires would? This question would be relatively easy to address because managers of forests in fire-prone regions are increasingly using prescribed fire to reduce fuel accumulation and wildfire risk. The intensity of a prescribed fire is often manipulated by burning when fuel moisture regimes are deemed appropriate. This is done to reduce the risk that a prescribed burn might get out of control. Typically, this means fires are set in spring or early summer before fuels have fully dried out, or later in summer or autumn after a period of adequate precipitation. By contrast, wildfires more often get out of control and burn large areas when conditions are hottest and driest. As noted in the biology section, morels tend to fruit most abundantly in the "red needle zone" (McFarlane and others 2005) of a fire that corresponds to moderate fire intensity (Keefer 2005). But "moderate" intensity, in this case, means hot enough to kill dominant trees, a goal managers are unlikely to pursue with prescribed fires. Managers have been experimenting with setting prescribed burns in different seasons because the timing and intensity of such fires also influence other resources such as soil fertility, water quality, fish and wildlife populations, tree seedling establishment, forage availability, and rare plant populations (Biswell 1989, Walstad and others 1990). It would be a relatively simple matter to systematically assess the comparative size of morel crops produced by prescribed burns lit in different seasons or when different fuel and soil moisture regimes existed. Methods for such assessments could range in complexity and cost from informal harvester interviews to systematic sampling of replicated prescribed burns.

Morels from western North America could command a premium price if they can be marketed as collected from pristine areas.

Other issues—Fire suppression might not be the only way that humans are affecting morel habitat throughout western North America. Global warming might be shifting forest biomes further north and higher in elevation. These shifts could also be accompanied by changes in evaporation and precipitation patterns. Large-scale insect infestations such as the ongoing mountain pine beetle epidemic in British Columbia (http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/) might partly be a result of winters that are no longer sufficiently cold to kill the beetle larvae. Although this pine die-off does seem to be producing morel crops (see footnote 33) (Keefer 2005), will such forests be replaced by different tree species and will those species also produce morel crops? If climate continues to warm, this type of question could apply to shifting tree species dominance in many western forest habitats.

Morel crops in western forests also are being affected by pollution. For instance morels from western North America could command a premium price if they can be marketed as collected from pristine areas. But if morels are collected from areas where the soil is contaminated with mine tailings or mercury deposition from coal-fired power generation plants, high concentrations of heavy metals might make such morels dangerous to consume. As data from Obst and others (2001) suggest, morels might concentrate dangerous levels of lead near roads even though lead has not been added to gasoline in the United States and Canada for two decades.

Lastly, exotic pathogens such as Dutch elm disease created temporary morel crops as it devastated American elms. New exotic pathogens that attack western forest trees could easily be introduced or become established. For instance, western states have been battling for the last 20 years to prevent the introduced gypsy moth from becoming established. The larvae of this moth are voracious feeders on tree foliage and can cause tree mortality in the same manner as the native western spruce budworm. Morels might fruit more abundantly as infected trees are damaged or die, but few would argue that such tree mortality benefits the forest, people, or the long-term viability of morel populations.

Enhancing morel harvest opportunities—We do not know if logging and prescribed burning enhance the long-term production of morels over time in a given forest stand, but regular application of these forest management activities across a landscape (say for instance, a particular national forest) can insure annual opportunities to harvest morels. Another possible method of enhancing morel reproduction or productivity is spreading spores. Because morel spores are released in such great abundance during commercial drying operations, it would be easy to collect vast numbers and disperse them artificially across the landscape. We are unaware of any trials that have produced evidence that this approach is either effective or ineffective. As with backyard kits, the morels likely grow in ideal habitat anyway. Demonstrating that intentionally spreading spores is effective at enhancing morel production in forested settings might be difficult, because such trials likely would involve multiyear studies of productivity. (See the following "Useful Research" section regarding the efficacy of this approach for maintaining morel populations and diversity). Most morels commercially collected in forests are not yet mature, so removing them before they spread their spores might significantly reduce spore distribution compared to nonharvested areas. If the spores collected in drying operations have subsequently matured (easily tested), then distributing them might remediate reduced spore dispersal. On the other hand, broad distribution of collected spores could also shift naturally-evolved patterns of genetic diversity and adaptation to local environments within morel populations.

Harvest Management

Federal land managers have accomplished a great deal in their efforts to regulate the commercial harvest of wild mushrooms. Successful programs have been shared among forest managers throughout western North America and adapted to local laws and conditions. Many publications address the issue of commercial mushroom harvesting. They include articles (Arora 1999, Penticton Herald 2004, Rommelmann 2005), reports (Acker 1986; Brown and Marin-Hernandez 2000; Diario Oficial 1996, 2001; Kenney 1996; Obst and Brown 2000; Wills and Lipsey 1999; Yamin 2005, Zamora and others 2001), peer-reviewed publications (Bray and others 2003; Hansis 1998; Love and others 1998; Martínez-Carrera and others 2002; McFarlane and others 2005; McLain and others 1998, 2005; Molina and others 1993, 2001; Parks and Schmitt 1997; Pilz and Molina 2002; Pilz and others 2003; Tedder and others 2000, 2002; Wurtz and others 2005), theses (Keefer 2005, McLain 2000), book chapters (Alexander and Fight 2003, Alexander and others 2002b, Antypas and others 2002, Redhead 1997), and books (Palm and Chapela 1997, Jones and others 2002). These references are only that portion of the relevant literature that we cite elsewhere in this report. Alexander and Fight (2003) also outlined the various ways that permits, contracts, and access to nontimber forest products in the United States are regulated and structured. No local regulatory program is perfect though, and some issues remain inadequately addressed.

Equitable access—Both recreational and commercial harvesters appreciate opportunities to harvest morels on public lands. In areas where intensive commercial harvesting occurs, recreational harvesters can face stiff competition. Designating areas for only commercial harvesting or only personal-use harvesting is one way to address this concern. For instance, Montana National Forests have designated commercial-harvesting areas in recent years, while allowing personal harvesting elsewhere. The policy concentrates commercial activities in particular areas to facilitate provision of services such as sanitation and camping and to minimize potential conflicts among harvester groups.[38] Conversely, in keeping with their land use emphasis, the Sawtooth National Recreation Area on the Sawtooth National Forest in Idaho designated some wildfire areas for only personal-use morel harvesting during summer 2006 (http://fs.fed.us/r4/sawtooth/recreation/recreport.htm). National forests in Oregon and Washington have, to date, not required such designations because they could be difficult to enforce (see footnote 26).

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[38] DeWolf, Stacie. 2006. Personal communication. Special forest products coordinator, Regional Office, Region 1, U.S. Department of Agriculture, Forest Service. P.O. Box 7669, Missoula, MT 59807.

All federal lands in the United States have nondiscrimination policies that prohibit the agencies from favoring any ethnic or harvester group over another, but because commercial mushroom harvesters are so diverse (Arora 1999), proactive policies that enhance the ability of disadvantaged groups to participate can be very effective. A good example is providing harvest regulations and signs in multiple languages. Outreach programs that educate minority groups who are unfamiliar with U.S. laws and customs are also effective (Love and others 1998, Pilz and others 1999).

Sometimes local harvesters compete with transient or circuit harvesters, and conflicts ensue. As for recreational harvesters, portions of the landscape could be designated for harvest via contracts with local individuals or companies.

Land tenure and harvest pressure—How harvesters are allowed access to the land and the mushrooms growing there influences harvesting pressure on the resource. On lands that are communally owned, such as Native American lands, the governing bodies can control access, the number of harvesters, and quantities harvested. Private landowners, both individual and corporate, also have a good deal of control. By contrast, on public lands where the numbers of harvesters and the quantities they can collect are not typically limited, harvesters have a greater incentive to collect any mushrooms they find even if they are small. If they come back later when the mushrooms should have grown larger, other harvesters might already have taken them. Even on public lands, however, managers have tools to control the negative impacts that a "de facto open access" management regime can have on resource conditions (Bromley 1991). Managers can limit the number of harvesters or harvest permits, they can designate areas and seasons for harvesting, and they can provide commercial harvesting opportunities through exclusive contracts to particular areas. Whether any of these approaches are worthwhile depends on whether managers consider local mushroom harvesting pressure too great and whether they have the time, personnel, and budget to more carefully regulate harvesting. Conflict can be reduced and regulations are apt to be more widely accepted if managers involve all interested parties in making regulatory decisions (McLain and Jones 2001, Pilz and others 2006b).

Conflict can be reduced and regulations are apt to be more widely accepted if managers involve all interested parties in making regulatory decisions.

Liability insurance—In some states, all harvesters must obtain a direct sales contract to harvest forest products on state lands. In Idaho, direct sales contracts include a provision that contractors obtain liability insurance worth $1 million. Not surprisingly, no mushroom harvesters have ever obtained a commercial permit to harvest mushrooms on lands managed by the state of Idaho. Many large private landowners also require large amounts of liability insurance from harvesters.

Research on how small-scale operators in other forest products industries have managed to overcome this barrier could help facilitate the ability of harvesters to maintain or expand legal access to harvesting sites on state and privately owned land.

Certification systems—Either harvesters or products could be certified. Harvesters could receive certification that they have completed training in harvest methods, pertinent laws and regulations, and mushroom identification. Products such as morels could be certified as properly identified or harvested from particular lands. Certification could be instituted for public safety, used to improve compliance with regulations, or employed to enhance product value. For instance, as wild mushrooms become more common in farmers' markets, stores, and restaurants, pressures to certify mushroom identification are likely to increase. In some cases, managers already require people who apply for harvesting permits to attend brief training about the regulations (Pilz and others 1999). In this case, the permit becomes a form of certification. Adding a half-day mushroom identification class would not be difficult. Many harvesters might appreciate the opportunity to learn more about mushroom identification or to share their own knowledge. Some other countries already have such programs. For instance, Von Hagen and others (1996), in their annotated bibliography of nontimber forest product literature, summarized two Finnish articles (Härkönen 1988, Härkönen and Järvinen 1993) that describe a national program of trained "county mushroom advisors" who then give classes in mushroom identification to commercial harvesters. In the Umbria region of Italy, a law stipulates that truffle harvesters must pass exams about species identification, collecting methods, and other applicable laws (Giunta Regionale dell'Umbria 1987).

Certification of origin could be used to demonstrate the mushrooms were not collected near sources of pollution. In the case of Native Americans, certification of origin, or of who harvested the product, could be an effective marketing tool to add value to the products sold. Tribes in Alaska already do something similar with artwork and crafts. Authentic Alaska Native arts and crafts items may display a "Silver Hand" symbol, with the words "Authentic Native Handicraft from Alaska." The Alaska Department of Education and Early Development, Alaska State Council on the Arts (http://www.eed.state.ak.us/aksca/) administers the program (Pilz and others 2006a). Certification of nontimber forest products or harvesters is an evolving field with participants and practitioners balancing the work involved with anticipated benefits (Shanley and others 2002).

Useful Research

Many scientific papers conclude that more research is needed to understand the topic, but considered in the context of agency budgets, managerial priorities, and personal perspectives, "need" is always relative. In this section, we mention some research that would be useful for enhancing our understanding of morels, improving management of their populations, and designing better harvest regulations. Our intent is to provide a list of topics for future research that would pertain to management of the commercial resource or management of the forests where they grow. Some research topics also were discussed in the previous "Forest Management" section.

Taxonomy—The jumbled taxonomy of North American *Morchella* species and their lack of valid species names is perhaps the biggest current impediment to morel research (Weber 1988). Without identification of the organism being studied, it is difficult to extrapolate research results to other morels or interpret ecological relationships (Weber 1997). While the taxonomy of *Morchella* in North America is being worked out, morel researchers should keep studied specimens in herbaria for future reference. Unfortunately, until recently, relatively few *Morchella* specimens have been added to either personal collections or public herbaria (Weber 1997). Apparently early collectors considered them too common to accession into herbaria; they preferred to document rarer species.

The jumbled taxonomy of North American *Morchella* species and their lack of valid species names is perhaps the biggest current impediment to morel research.

Recent work has begun to remedy some of these limitations. For instance, the online Morel Data Collection Project (Kuo 2006) has compiled more than 500 morel collections from across North America. Each is identified by collector's name, the date it was collected, and county and state where it was found. Some collections also have associated images and notes on habitat. Many have been genetically analyzed for sorting into putative taxons and then deposited in the public herbarium at the Field Museum in Chicago.

Weber and others (1997) described techniques for collecting, recording, describing, and preserving field samples of ascomycetes, including morels. Mueller and others (2004) provided a comprehensive guide to sampling, culturing, inventorying, monitoring, and preserving methods for various types of fungi. By linking morel collections to precisely georeferenced collecting sites, ecological information on habitat and substrate, and any DNA analyses that are conducted, researchers will be better able to interpret the role of such fungi in their native ecosystems. Crous and Cother (2003) argued succinctly for the value of linking DNA databases with freely available specimens deposited in public herbaria in order to facilitate species identification and cross-reference research findings. Ultimately, morel taxonomy in North America will only be resolved to most scientists' satisfaction when the DNA of publicly available specimens is independently examined by several labs and the results are correlated to species descriptions published by trained taxonomists in peer-reviewed journals by using standards set in the International Code of Botanical Nomenclature (Greuter and others 2000).

Ecology—As morel species become better delimited and named, the next logical step is to develop basic range maps for each, create thorough descriptions of their habitats, and describe the conditions that stimulate fruiting. Mushroom field guides could then be revised to provide accurate information to managers, harvesters, and researchers. More accurate ecological information will assist forest managers with decisions regarding their morel resource and managing its commercial harvest; help morel harvesters, buyers, and sellers better distinguish the market and culinary characteristics of each; give recreational harvesters a better idea where and when to search for their favorite species of morels; and allow researchers to more easily compare and interpret their results.

The management of morels also is hindered by limited understanding of how each species of *Morchella* obtains most of its nutrition and how the nutritional sources they use might change over time or with circumstances. We also know little about how, and under what conditions, the mycelial colonies of each species become established, grow, persist through time, senesce, and die out. For instance, do mycelial colonies in nature senesce quickly like those in pure culture, or does heterokaryogamy and repeated anastomosis with hyphae from germinating spores maintain colony vigor? If so, how long do such colonies survive? Do colonies die out after they produce massive crops of morels in response to a disturbance, or do they persist in the soil as a new forest becomes established? In wet or cold forests that typically only burn every century or two, have the fire morels that fruit following a fire been growing in the soil since the last fire without fruiting in the interim? Answering these questions would help us evaluate the importance of spore dispersal and determine whether harvesting immature morels before they spread viable spores could impair morel reproduction.

Reproduction and population genetics—The importance of spore dispersal can also be addressed through studies of population genetics that examine the relatedness of morels growing at various distances from each other. In the “Population Genetics” subsection of the “Morel Biology” section we discuss some of the recent work. Morel species might differ in their reproductive biology, so conducting this work with at least several species would help us understand potential differences. Examining potential dissimilarities between the yellow versus black clades and the fire versus nonfire morels would be especially interesting. Such studies would also be easier to interpret if researchers evaluate the heterokaryotic nature of morel mycelia and the possibility that morel fruiting bodies are a mixture of genetically different hyphae. Designing a population genetics study to ascertain whether artificial spore dispersal is an effective method of maintaining morel populations and their diversity also might be possible. If spores were collected from one morel population and spread over a genetically different morel population of the same species, it might be possible to use DNA analyses to determine if genetic information from the spore-producing population shows up in subsequent fruiting bodies of the recipient population. It might even be possible to correlate the density of spore dispersal in a given area with how much genetic information is incorporated by the recipient population. This approach is suggested only for experimental purposes. In practical application, spores should only be spread near where they are collected until more is known about the dynamics of morel populations, how natural patterns of *Morchella* adaptation and diversity might be altered, and the potential for ecological harm.

Morel commodity chains—Government policies play an important role in ensuring that businesses can obtain adequate supplies of morels and other wild edible fungi. Tax incentives, export and import restrictions, and the provision of easily accessible and up-to-date information on sources of supply, prices, and markets can influence the ability of businesses to compete in global markets. The capacity of state, federal, and provincial governments in western North America to support the wild mushroom industry, however, is hampered by a profound lack of published information about morel commodity chains; that is, How do morels move from initial harvest to final sales, and how does value and profit accrue along the way? The structure and function of such commodity chains are the result of economic policy, marketing arrangements, and the social interactions and power relationships among participants. Additional information about morel commodity chains, domestic and international, would improve the ability of economic development organizations and extension agencies to help a broad range of business enterprises participate more effectively in this global industry.

The capacity of state, federal, and provincial governments in western North America to support the wild mushroom industry is hampered by a profound lack of published information about morel commodity chains.

Closing Remarks

Our discussion of morels has been replete with evocative quotations, phrases, and words. Morel hunters use terms like “morel madness,” “fungal lust,” “the sickness,” “screams of delight,” and “angst relief,” whereas Lewis and Clark called them “truly an insippid taistless food.” Commercial harvesters talk of “farming morels,” “patch-lines,” “rural legends,” and “roadhunting.” Economists call commercial mushroom harvesting an “informal economy.” Preserved morels have been called “dried-up brains.” In the forest, they have been described as “infuriatingly elusive.” An “80 ton falling film ice slurry system” has been used to cultivate them. They have “toxic look-alikes” and accumulate “heavy metals.” They “usually fruit outdoors” in response to “episodic catastrophic disturbances” such as “wildfires” or “dead and dying trees.” They eat “necromass,” have been called the “necrophiles of the alpine forest," and fruit in the "red needle zone" of burned forests. Ecologically they have been called "phoenicoid fungi" that exhibit "psychrotolerance," "environmental plasticity," and "broad ecological amplitude." Their "polymorphic" appearance has led to "problematic taxonomy." Their cells are "heterokaryotic," and they might be capable of rare "haploid meiosis." What should we make of such unique and diverse organisms (other than dinner)?

Morels might appear to be the weeds of the mushroom world insofar as they fruit abundantly in episodically disturbed environments, but does the organism actually persist in the same forests through the long years of stability in between as do other edible mycorrhizal mushrooms? They might seem like good fungal competitors, but do they grow better under snow because other fungi are at a competitive advantage in warmer soils? Do they use energy from sclerotia to quickly colonize necromass in the upper layers of a burned soil because they could not otherwise compete with other soil micro-organisms? The potential diversity of their food sources and their modes of reproduction could be interpreted to imply that they are not at risk from harvesting, but like many mushrooms, most commercially harvested morels are collected before their spores have matured or been distributed. Therefore, we simply do not know what impact large-scale commercial collecting might have on morel reproduction, populations, or diversity. There might be negative impacts, or, for all we know, morel harvesters might be spreading more morel spores further on their boots than would be spread by the wind. From a scientific perspective, most of these questions can be addressed with current methods of field and laboratory research. In the meantime, from a managerial perspective, there remain options for sustaining the resource and providing ample harvesting opportunities. Happy hunting (fig. 16)

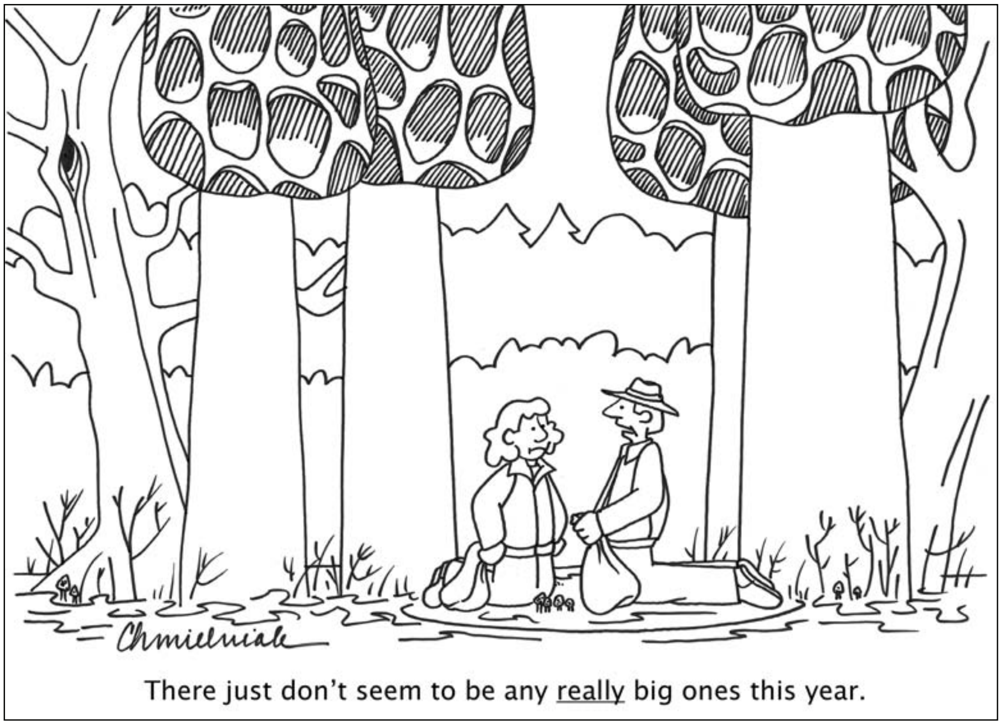

Figure 16—Given the effective camouflage and mysterious qualities of morels, harvesters benefit from a sense of humor. Cartoon by Betty Chmielniak Grace (2005). Do not reproduce without permission.

Glossary

See Kirk and others (2001) or Ulloa and Hanlin (2000) for a complete glossary of mycological terms.

allele—Any one of a number of DNA variations of the same gene occupying the same position on a chromosome.

anastomosis—Fusion between hyphae resulting in shared cytoplasm and sometimes nuclei.

ascomycetes—Fungi belonging to the phylum Ascomycota.

ascus, asci (plural)—Specialized cells where haploid spores (typically eight) are produced during meiosis by fungi in the phylum Ascomycota. In *Morchella*, asci are elongated sac-like structures where spores are lined up for ejection.

ascospores—Sexual spores produced inside asci by fungi in the Ascomycota.

asexual—Nonsexual; not involving the genetic recombinant and chromosome reduction process of meiosis.

basidium, basidia (plural)—A microscopic club-shaped structure that produces sexual spores in fungi that belong to the phylum Basidiomycota. This phylum includes many commercially harvested mushrooms species. This structure corresponds to the ascus in *Morchella,* a member of the phylum Ascomycota.

chromosome—A very long, continuous piece of DNA that carries genetic information in cells. Complex organisms store their genetic information on a set of chromosomes. A diploid nuclei contains two of each chromosome in the set (with genes that perform the same functions located at the same position along the strand of DNA). These pared chromosomes are called homologous.

clade—A group of organisms, regardless of taxonomic ranking, that evolved together through time. Recent DNA analyses frequently delineate clades of genetically similar fungi that include some species that were previously placed in dissimilar genera, families, and orders when classifications were predominantly based on morphological distinctions.

conidiophore—Hyphal structures that produce conidia.

conidium, conidia (plural)—An asexual (usually clonal) spore produced by simple hyphal structures or cells. Also called a conidiospore.

cytoplasm—The jelly-like aqueous contents of a cell including organelles, salts, an assortment of organic molecules, and enzymes that catalyze reactions.

dikaryotic—Two, and only two, genetically different nuclei per cell. Generally the nuclei are haploid, of compatible mating types, and are paired in proximity, but the nuclei have not fused to form a diploid nucleus.

diploid—Containing two copies of each chromosome in a nucleus, typically one from each parent.

DNA—Deoxyribonucleic acid is a nucleic acid that contains the genetic instructions specifying the biological development of all cellular forms of life.

ectomycorrhiza—A type of mycorrhiza where the fungus covers the root tip with an outer ("ecto") mantle of hyphae, penetrates between the outer cells of the root tip, but does not penetrate into the root's cells. Ectomycorrhizae (plural) are common on trees in temperate forests and with fungi that produce mushrooms and truffles.

fruiting body (American usage) or fruit body (elsewhere)—An organ or structure that bears haploid (sexual) spores produced through meiosis. Also called a sporocarp. In the case of *Morchella* species, the morel mushroom itself.

fungivore—An organism that eats fungi, typically animals, insects, or mollusks.

genome—All of the hereditary information of an organism that is encoded in its DNA.

haploid—Containing one copy of each chromosome in a nucleus.

Hartig net—A structure, typically formed by ectomycorrhizal fungi, that consists of a network of fungal hyphae growing between the epidermal and cortical cells of a root tip.

heterokaryotic—Two or more genetically different, and generally haploid, nuclei per cell. (See "dikaryotic")

hymenium—Spore-bearing surface of a mushroom. The hymenium can take the form of gills (as in button mushrooms), ridges (as in chanterelles), tubes (as in boletes), or other structures. In the case of morels, it lines the surface of the pits in the head.

hypha, hyphae (plural)—A one-cell-wide filament of cells produced by multicellular fungi. Collectively, a web of hyphae is referred to as mycelium. Hyphae converge to form all fungal structures, for example, rhizomorphs, mycorrhizae, or mushrooms.

hypogeous—Fruiting underground (in reference to the fruiting habits of fungi that produce sporocarps).

karyon—A cell nucleus that is either haploid or diploid.

macroscopic—Visible without magnification.

meiosis—The last phase of the cellular process of sexual reproduction (after fusion of the cytoplasm and haploid nuclei). Typically some alleles are swapped between paired chromosomes and through one doubling and two subsequent nuclear divisions, eight recombinant haploid nuclei are formed.

multikaryotic—More than one nucleus per cell. Also referred to as multinucleate. The nuclei could all be identical copies or differ (see "heterokaryosis").

multinucleate—More than one nucleus per cell, regardless of whether they are haploid or diploid. Also referred to as multikaryotic.

mycelium, mycelia (plural)—A web of fungal hyphae that colonizes a substrate such as soil or decaying organic matter. Sometimes used in conjunction with the word "colony" to refer to a fungus individual, as in "mycelial colony."

mycology—The study of fungi.

mycophagy—Eating fungi.

mycophilic—Fond of fungi, especially eating them.

mycophobic—Fearful of fungi, especially eating them.

mycorrhiza, mycorrhizae or mycorrhizas (plural)—From Greek, "mykes" = fungus and "rhiza" = root. The structure formed when the mycelium of a fungus associates symbiotically with the root tips of a plant. The fungus acts as the fine root system for the plant, providing it with water and mineral nutrients absorbed from the surrounding soil, and the plant in return provides the fungus with carbohydrates produced through photosynthesis. Mycorrhizae is the plural form commonly used in North America; mycorrhizas often is used elsewhere.

nucleus, nuclei (plural)—The membrane-bound subcellular organelle found in plants, fungi, and animals that contains one set of an organism's chromosomes if the nucleus is haploid or two paired sets if the nucleus is diploid.

polymorphic—Assuming multiple forms or appearances.

primordium, primordia (plural)—The initial stage in the development of a structure, in this case the initial formation of a morel "bud" or "button" that can grow into a mature fruit body if conditions remain favorable.

rhizomorphs—Root-like structures formed by densely coalesced hyphae that specialize in transporting nutrients or cytoplasm from one location to another.

riparian—River or streamside.

saprobe, saprobic—Decomposer, decomposing. Previously called saprophytes, but "phytes" means plants, not fungi.

sclerotium, sclerotia (plural)—Nodules of tightly woven hyphae that store nutrients and are resistant to desiccation and cold.

sensu lato—Latin for "in a broad sense." The term is used after species names to indicate that the definition of a species is being interpreted broadly or loosely in that specific context. It is abbreviated "s.l." When "sensu" is used between a scientific name and a citation, it means taxonomic criteria or distinctions should be considered in the sense described in the publication.

septum, septa (plural)—Wall or separation between adjacent cells of a fungal hypha. Morel septa have pores that allow the physiologically controlled transfer of cell cytoplasm and nuclei.

sporocarp—Spore-bearing organ or structure. Also called fruiting body (American usage) or fruit body (elsewhere). In the case of *Morchella* species, the morel mushroom itself.

stipe—Mushroom stem.

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Metric Equivalents

When you know:	Multiply by:	To find:
Inches	25,400	Microns, micrometers (µm)
Inches	25.4	Millimeters (mm)
Inches	2.54	Centimeters (cm)
Feet	.305	Meters (m)
Yards	.9144	Meters (m)
Square feet	.0929	Square meters (m^2)
Square yards	.8361	Square meters (m^2)
Miles	1.609	Kilometers (km)
Acres	.4047	Hectares (ha)
Pounds	.4535	Kilograms (kg)
Short (US) tons	.907	Metric tons (t)
Pounds (lb)	.00045	Metric tons (t)
Pounds per acre (lb/ac)	1.12085	Kilograms per ha
Morels per acre	2.475	Morels per ha
Farenheit (°F)	.556 (°F - 32)	Celsius (°C)

Literature Cited[39]

Acker, R. 1986. Harvesting wild edible mushrooms in Washington: an issue paper. Prepared for the Wild Edible Mushroom Task Group, November 3, 1986. Olympia, WA: Department of Natural Resources: 115–150.

Aegerter, M. 1995. How many morel species? Mushroom, The Journal of Wild Mushrooming. 50: 5–6.

Alaska Wildland Fire Coordination Group. 1998. Alaska Interagency Wildland Fire Management Plan. http://www.dnr.state.ak.us/forestry/pdfs/98AIFMP.pdf.

Alexander, S.J.; Fight, R.D. 2003. Managing access to nontimber forest products. In: Monserud, R.A.; Haynes, R.W.; Johnson, A.C., eds. Compatible forest management. Norwell, MA: Kluwer Academic Publishers: 383–400.

Alexander, S.J.; Pilz, D.; Weber, N.S. [and others]. 2002a. Value estimates of commercial mushrooms and timber in the Pacific Northwest. Environmental Management. 30(1): 129–141.

Alexander, S.J.; Weigand, J.F.; Blatner, K.A. 2002b. Nontimber forest products commerce. In: Jones, E.T.; McLain, R.J.; Weigand, J.F., eds. Nontimber forest products in the United States. Lawrence, KS: University Press of Kansas: 115–150.

[39] All Web sites listed in the "Literature Cited" were last accessed 20 December 2006.

Alexopoulos, C.J.; Mims, C.W.; Blackwell, M. 1996. Introductory mycology. 4th ed. New York: John Wiley & Sons, Inc. 869 p.

Amaranthus, M.; Pilz, D. 1996. Productivity and sustainable harvest of wild mushrooms. In: Pilz, D.; Molina, R., eds. Managing forest ecosystems to conserve fungus diversity and sustain wild mushroom harvests. Gen. Tech. Rep. PNW-GTR-371. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 42–61.

Ambrose, S.E. 1996. Undaunted courage. New York: Touchstone. 372 p.

Amir, R.; Levanon, D.; Hadar, Y. [and others]. 1992. Formation of sclerotia by *Morchella esculenta*: relationship between media composition and turgor potential in the mycelium. Mycological Research. 96(11): 943–948.

Amir, R.; Levanon, D.; Hadar, Y. [and others]. 1993. Morphology and physiology of *Morchella esculenta* during sclerotia formation. Mycological Research. 97(6): 683–689.

Amir, R.; Levanon, D.; Hadar, Y. [and others]. 1994. The role of source-sink relationships in translocation during sclerotial formation by *Morchella esculenta*. Mycological Research. 98(12): 1409–1414.

Amir, R.; Levanon, D.; Hadar, Y. [and others]. 1995a. Factors affecting translocation and sclerotial formation in *Morchella esculenta*. Experimental Mycology. 19: 61–70.

Amir, R.; Steudle, E.; Levanon, D. [and others]. 1995b. Turgor changes in *Morchella esculenta* during translocation and sclerotial formation. Experimental Mycology. 19: 129–136.

Antypas, A.; McLain, R.J.; Gilden, J.; Dyson, G. 2002. Federal nontimber forest products policy and management. In: Jones, E.T.; McLain, R.J.; Weigand, J., eds. Nontimber forest products in the United States. Lawrence, KS: University of Kansas Press: 347–374.

Apfelbaum, S.I.; Haney, A.; Dole, R.E. 1984. Ascocarp formation by *Morchella angusticeps* after wildfire. Michigan Botanist. 23(3): 99–102.

Apple, R.W., Jr. 1998. On the trail of the magnificent morel. New York Times. May 20; Sect. B: B1 & B11.

Arkan, O. 1992. *Morchella conica* Pers. monoaskospor kültürlerinde hif fizyonlari ve heterokaryon oluşumu [Hyphal fusions and heterokaryon formation between monoascosporous strains of *Morchella conica* Pers.] Turkish Journal of Biology. 16: 203–216. [In Turkish, English abstract].

Arkan, O.; Güler, P. 1991. *Morchella conica* Pers. sclerotial oluşumlari. [The sclerotia formations in *Morchella conica* Pers.] Turkish Journal of Biology. 16(3): 217–226. [In Turkish, English abstract]

Arnolds, E. 1995. Conservation and management of natural populations of edible fungi. Canadian Journal of Botany. 73(Supplement 1): S987–S998.

Arora, D. 1986. Mushrooms demystified. 2nd ed. Berkeley, CA: Ten Speed Press: 782–816.

Arora, D. 1999. The way of the wild mushroom. California Wild. 52(4): 8–19.

Arora, D. 2000. Migrant mushroomers: tales of adventure, nature love, and money on the globalocal mushroom trail. Whole Earth (Spring): 60–69. http://www.wholeearthmag.com/ArticleBin/333.html.

Arora, D.K.; Bridge, P.D.; Bhatnagar, D., eds. 2004. Handbook of fungal biotechnology. 2nd ed. New York: Marcel Dekker, Inc. 592 p.

Barnes, S.; Wilson, A. 1998. Cropping the French black morel: a preliminary investigation. RIRDC Publication No. 98/44. Barton, ACT, Australia: Rural Industries Research and Development Corporation, Australian Government. 14 p.

Benjamin, D.R. 1995. Mushrooms: poisons and panaceas: a handbook for naturalists, mycologists, and physicians. New York: W.H. Freeman and Company. 422 p.

Bensoussan, M.; Tissserand, E.; Kabbaj, W. [and others]. 1995. Partial characterization of aroma produced by submerged culture of morel mushroom mycelium. Cryptogamie Mycologie. 16(1): 65–75.

Beug, M.W. 2004. An overview of mushroom poisonings in North America. The Mycophile. 45(2): 4–5. http://www.sph.umich.edu/~kwcee/mpcr/reports.htm.

Birren, B.; Fink, G.; Lander, E. 2003. Fungal genome initiative; a white paper for fungal comparative genomics. Cambridge, MA: Whitehead Institute Center for Genome Research. www.broad.mit.edu/annotation/fungi/fgi/FGI3SEQ.pdf.

Biswell, H.H. 1989. Prescribed burning in California wildlands vegetation management. Los Angeles, CA: University of California Press. 255 p.

Blanco-Dios, J.B. 2002. Notas teratolóxicas (II). Unha forma anómala de *Morchella conica* Pers. [Teratologic notes (II). An anomalous form of *Morchella conica* Pers.]. Mykes. 5: 11–16. [In Galician, English abstract].

Blatner, K.A.; Alexander, S.J. 1998. Recent price trends for nontimber forest products in the Pacific Northwest. Forest Products Journal. 48(10): 28–34.

Boa, E. 2004. Wild edible fungi: a global overview of their use and importance to people. Rome, Italy: Food and Agriculture Organization of the United Nations. 147 p. http://www.fao.org/documents/show_cdr.asp?url_file=//docrep/007/y5489e/y5489e00.htm.

Boom, M. 1995. Fungal lust. Berkeley, CA: East Bay Express. May 12: 10–18.

Bray, B,D.; Merino-Pérez, L.; Negreros-Castillo, P. [and others]. 2003. Mexico's community-managed forest as a global model for sustainable landscapes. Conservation Biology. 17(3): 672–677.

Brock, T.D. 1951. Studies on the nutrition of *Morchella esculenta* Fries. Mycologia. 43: 402–422.

Bromley, D.W. 1991. Environment and economy: property rights and public policy. Cambridge, MA: Blackwell. 247 p.

Brower, L. [N.d.]. Vegetacion de Mexico [Map]. Sweet Briar VA: Sweet Briar College. http://www.learner.org/jnorth/images/graphics/monarch/lpb/LPB.0361.jpg.

Brown, B.A.; Marin-Hernandez, A. 2000. Voices from the woods: lives and experiences of nontimber forest workers. Wolf Creek, OR: Jefferson Center for Education and Research. 51 p.

Brown, C. 2005. Regulating the wild mushroom. L.A. County halts sales at farmers markets: Could restaurants and supermarkets be next? Los Angeles Times. March 16: F1.

Bunyard, B.A.; Nicholson, M.S.; Royse, D.J. 1994. A systematic assessment of *Morchella* using RFLP analysis of the 28S ribosomal RNA gene. Mycologia. 86: 762–772.

Bunyard, B.A.; Nicholson, M.S.; Royse, D.J. 1995. Phylogenetic resolution of *Morchella*, *Verpa*, and *Disciotis* [Pezizales: Morchellaceae] based on restriction enzyme analysis of the 28S ribosomal RNA gene. Experimental Mycology. 19: 223–233.

Burros, M. 1985. Northwest's new-found riches: its own fine food." New York Times. April 17: C1.

Buscot, F. 1989. Field observations on growth and development of *Morchella rotunda* and *Mitrophora semilibera* in relation to forest soil temperature. Canadian Journal of Botany. 67: 589–593.

Buscot, F. 1992a. Mycorrhizal succession and morel biology. In: Read, D.J.; Lewis, D.H.; Fitter, A.H. [and others], eds. Mycorrhizas in ecosystems. Wallingford, Oxon, United Kingdom: CAB International: 220–224.

Buscot, F. 1992b. Strategies écologiques et biologiques des morilles. [Ecological and biological strategies of morels]. Cryptogamie Mycologie. 13: 171–179. [In French, English abstract].

Buscot, F. 1992c. Synthesis of two types of association between *Morchella esculenta* and *Picea abies* under controlled culture conditions. Journal of Plant Physiology. 141: 12–17.

Buscot, F. 1993. Mycelial differentiation of *Morchella esculenta* in pure culture. Mycological Research. 97: 136–140.

Buscot, F. 1994. Ectomycorrhizal types and endobacteria associated with ectomycorrhizas of *Morchella elata* (Fr.) Boudier with *Picea abies* (L.) Karst. Mycorrhiza. 4: 223–232.

Buscot, F.; Bernillon, J. 1991. Mycosporins and related compounds in field and cultured mycelial structures of *Morchella esculenta*. Mycological Research. 95(6): 752–754.

Buscot, F.; Kottke, I. 1990. The association of *Morchella rotunda* (Pers.) Boudier with roots of *Picea abies* (L.) Karst. New Phytologist. 116: 425–430.

Buscot, F.; Roux, J. 1987. Association between living roots and ascocarps of *Morchella rotunda*. Transactions of the British Mycological Society. 89(2): 249–252.

Buscot, F.; Wipf, D.; Di Battista, C. [and others]. 1996. DNA polymorphism in morels. I. PCR/RFLP analysis of the ribosomal DNA spacers and microsatellite-primed PCR. Mycological Research. 100: 63–71.

CAB International [CABI]; Centraalbureau voor Schimmelcultures [CBS]; Landcare Research. [N.d.]. Index fungorum. Egham, Surrey, UK: CABI Bioscience; Utrecht, The Netherlands: Centraalbureau voor Schimmelculture; Lincoln, NZ: Landcare Research. http://www.indexfungorum.org.

California Code of Regulations. 1996. California Administrative Code, Natural Resources, Department of Parks and Recreation, Plants and Driftwood. 14: 4306.

Carpenter, S.; Trappe, J.M.; Ammirati, J., Jr. 1987. Observations of fungal succession in the Mount St. Helens devastation zone, 1980-1983. Canadian Journal of Botany. 65: 716–728.

Casey, K. 1995. Those magnificent morels. Seattle Post-Intelligencer. May 17; Sect. C: 1,4.

Chandra, A. 1989. Elsevier's dictionary of edible mushrooms. Botanical and common names in various languages of the world. Amsterdam, Netherlands: Elsevier. 259 p.

Chang, S.-T.; Miles, P. 2004. Mushrooms: cultivation, nutritional value, medicinal effect, and environmental impact. 2nd ed. New York: CRC Press. 451 p.

Cobanoglu, S.; Bayram, S. 1998. Mites (Acari) and flies (Insecta: Diptera) from natural edible mushrooms (*Morchella*: Ascomycetes) in Ankara, Turkey. Bulletin and Annales de la Societe Royale Belge d'Entomologie. 134(3): 187–198.

Constantin, J. 1936. La culture de la morille et sa forme conidienne. [Morel culture and its conidial form]. Annales des sciences naturelles. Botanique. Ser. 10(18): 111–129. [In French].

Coombs, D. 1986. Growing morels. Mushroom, The Journal of Wild Mushrooming. 4(13): 5-6, 23–24.

Coombs, D. 1994. Cultivated morels are promised, but—. Mushroom, The Journal of Wild Mushrooming. 12(4): 7.

Crisan, E.V.; Sands, A. 1978. Nutritional value. In: Chang, S.T.; Hayes, W.A., eds. The biology and cultivation of edible mushrooms. New York: Academic Press: 137–168.

Crous, P.W.; Cother, E.J. 2003. The reality of a virtual laboratory: reference to personal herbaria and culture collections is bad science. Inoculum. 54(5): 2–3.

Czarnecki, J. 1986. Joe's book of mushroom cookery. New York: Macmillan. 340 p.

Czimczik, C.I.; Preston, C.M.; Schmidt, M.W.I. [and others]. 2003. How surface fire in Siberian Scots pine forests affects soil organic carbon in the forest floor. Global Biogeochemical Cycles. 17(1): 1–14.

Dahlstrom, J.L.; Smith, J.E.; Weber, N.S. 2000. Mycorrhiza-like interaction by *Morchella* with species of the Pinaceae in pure culture synthesis. Mycorrhiza. 9: 279–285.

Dähncke, R.M.; Dähncke, S.M. 1984. 700 Pilze in Farbfotos [Color photos of 700 mushrooms]. Aarau, Switzerland: AT Verlag. 686 p. [In German].

Dalgleish, H.J.; Jacobson, K.M. 2005. A first assessment of genetic variation among *Morchella esculenta* (morel) populations. Journal of Heredity. 96(4): 396–403.

de Geus, P.M.J. 1995. Botanical forest products in British Columbia: an overview. Victoria, BC: Integrated Resources Policy Branch, British Columbia Ministry of Forests. 51 p.

DeWolf, S. 2001. Updated Region 1 figures for mushroom permits. Email communication from sdewolf@fs.fed.us (13 September 2001). On file with: Rebecca McLain, Institute for Culture and Ecology. P.O. Box 6688. Portland, OR 97228. mclain@ifcae.org.

Diario Oficial. 1996. NORMA Oficial Mexicana NOM-010-RECNAT-1996, que establece los procedimientos y especificaciones para realizar el aprovechamiento, transporte y almacenamiento de hongos. [NORMA Oficial Mexicana NOM-010-RECNAT-1996, to establish the procedures and specifications for picking, transportation and storage of mushrooms] Mexico City: Diario Oficial de la Federación. [pagination unknown]. [In Spanish].

Diario Oficial. 2001. NORMA Oficial Mexicana NOM-059-ECOL-2001, Protección ambiental-Especies nativas de México de flora y fauna silvestres—Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio—Lista de especies en riesgo. [NORMA Oficial Mexicana NOM-059-ECOL-2001, Environmental protection—Wild native animals and plants of Mexico—Categorization of risks and specifications for inclusion, exclusion or status change]. Mexico City: Diario Oficial de la Federación. http://www.ine.gob.mx/ueajei/norma59a.html. [In Spanish].

Diversified Natural Products. 2005. Gourmet and functional foods: Midsummer Exotics Gourmet Mix. http://www.dnpco.com/gourmet%20and%20functional.htm.

Duchesne, L.C.; Weber, M.G. 1993. High incidence of the edible morel *Morchella conica* in a Jack pine, *Pinus banksiana*, forest following prescribed burning. Canadian Field-Naturalist. 107: 114–116.

Egger, K.N. 1986. Substrate hydrolysis of postfire Ascomycetes (Pezizales). Mycologia. 78(5): 771–780.

Electric Power Research Institute [EPRI]. 1998. 1997-1998 Annual Report, EPRI HVAC&R Center, Thermal Storage Applications Research Center. Unpublished report. On file at: The HVAC&R Center and TSARC, EPRI-sponsored Technology Centers at The University of Wisconsin–Madison, College of Engineering, 949 East Washington Avenue, Suite 2, Madison, WI 53703-2937. http://www.hvacr.wisc.edu/publications.htm.

Fabricant, F. 1980. Plentiful mushrooms: The gift of autumn. New York Times. October 22: C1.

Faris, H.; Broderick, A.; Nair, N.G. 1996. Occurrence and initial observations of *Morchella* in Australia. In: The 2nd international conference on mushroom biology and mushroom products. University Park, PA: World Society for Mushroom Biology and Mushroom Production: 7.

Ferndock, M. (Each, P.; Mikkelsen, A., eds.) 1986. Malfred Ferndock's morel cookbook. Dennison, MN: Ferndock Publishing. 117 p.

Food and Drug Administration [FDA]. 1996. Revision of import alert #25-02: Detention without physical examination of morel mushrooms, 19 September 1996. U.S. Food and Drug Administration, Office of Regulatory Affairs, Import Program, FDA Import Alert Retrieval System (FIARS)–Import Alerts. http://www.fda.gov/ora/fiars/ora_import_ia2502.html.

Fine, G.A. 1998. Morel tales: the culture of mushrooming. Cambridge, MA: Harvard University Press. 324 p.

Fire-Trol Holdings, L.L.C. 1999. Material safety data sheet: Fire-Trol®LCG-R, Liquid Concentrate. Phoenix, AZ: Fire-Trol Holdings, L.L.C. http://www.firetrolholdings.com/.

Fischer, D.W.; Bessette, A.E. 1992. Edible wild mushrooms of North America: a field-to-kitchen guide. Austin, TX: University of Texas Press. 254 p.

Fries, E.M. 1822. System mycologicum. Lund, Sweden and Greifswald, Germany: Lund & Greifswald. 274 p. Vol. 2. [In Latin].

Fritze, H.; Pennanen, T.; Kitunen, V. 1998. Characterization of dissolved organic carbon from burned humus and its effects on microbial activity and community structure. Soil Biology and Biochemistry. 30(6): 687–693.

Fritze, H.; Smolander, A.; Levula, T. [and others]. 1994. Wood-ash fertilization and fire treatments in a Scots pine forest stand: effects on the organic layer, microbial biomass, and microbial activity. Biology and Fertility of Soils. 17: 57–63.

Fujimura, K.E.; Smith, J.E.; Horton, T.R. [and others]. 2005. Pezizalean mycorrhizas and sporocarps in ponderosa pine (*Pinus ponderosa*) after prescribed fires in eastern Oregon, USA. Mycorrhiza. 15: 79–86.

Gadbow, D. 2001a. Fungal frenzy: mushroom boom attracts legions of harvesters. Wildfire Journal 2001 Season. The Missoulian. July 1. http://www.missoulian.com/specials/fires2001/resources/morel-070101.html.

Gadbow, D. 2001b. Mushroom cloud: eruption of morel harvesters descends on acres of burned national forest. Wildfire Journal 2001 Season. The Missoulian. May 3. http://www.missoulian.com/specials/fires2001/resources/morel-050301.html.

Galagan, J.E.; Henn, M.R.; Ma, L.-J.; [and others]. 2005. Genomics of the fungal kingdom: insights into eukaryotic biology. Genome Research. 15: 1620–1631. http://www.genome.org/cgi/doi/10.1101/gr.3767105.

Gamundí, I.J.; Minter, D.W.; Romero, A.I. [and others]. 2004. Checklist of the Discomycetes (fungi) of Patagonia, Tierra del Fuego and adjacent Antarctic areas. Darwiniana. 42(1-4): 63–164.

Gecan, J.S.; Cichowicz, S.M. 1993. Toxic mushroom contamination of wild mushrooms in commercial distribution. Journal of Food Protection. 56(8): 730–734.

Gessner, R.V. 1995. Genetics and systematics of North American populations of *Morchella*. Canadian Journal of Botany. 73(Suppl. 1): S967-S972.

Gessner, R.V.; Romano, M.M.; Schultz, R.W. 1987. Allelic variation and segregation in *Morchella deliciosa* and *M. esculenta*. Mycologia. 79(5): 683–687.

Ghosh, S.; Majumdar, S.K. 1986. Effect of some minerals on the production of *Morchella*. Journal of Food Science and Technology. 23(4): 232–233.

Gilbert, F. 1961. The submerged culture of *Morchella*. Mycologia. 52: 201–209.

Gilmore, M.R. 1919. Uses of plants by the Indians of the Missouri River region. Thirty-third annual report of the Bureau of American Ethnology to the Secretary of the Smithsonian Institution. 1911-1912. Washington, DC: Government Printing

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Office. Online at the Southwest School of Botanical Medicine. http://www.swsbm.com/Ethnobotany/MissouriValley-Gilmore-1.pdf.

Giunta Regionale dell'Umbria. 1987. Norme concernenti la disciplina della raccolta, coltivazione, conservazione e commercio dei tartufi [Legal norms concerning the collecting, cultivation, conservation and commercialization of truffles]. Regional law (3 Nov. 1987) 47. Bollettino Ufficiale della Regione dell'Umbria. 18(81, parts 1, 2, and 3): 2156–2161. [In Italian].

Goldway, M.; Amir, R.; Goldberg, D. [and others]. 2000. *Morchella conica* exhibiting a long fruiting season. Mycological Research. 104(8): 1000–1004.

González-Pérez, J.A.; González-Vila, F.J.; Almendros, G. [and others]. 2004. The effect of fire on soil organic matter—a review. Environment International. 30: 855–870.

Gove, P.B.; Merriam-Webster Editorial Staff, eds. 1993. Webster's third new international dictionary of the English language, unabridged. Springfield, MA: Merriam-Webster, Inc. 2662 p.

Grace, B.C. 2005. Outside jokes: cartoons about nature and the outdoors. 2nd ed. Albany, MO: Panther Creek Publishing. 116 p.

Greis, H. 1940. Befruchtungsarten bei *Morchella*. [Kinds of fertilization in *Morchella*] Jahrbücher für Wissenschaft Botanik. 89: 245–253. [In German].

Greuter, W.; McNeill, J.; Barrie, E.R. [and others], eds. 2000. International code of botanical nomenclature (St. Louis Code). Regnum Vegetabile 138. Königstein: Koeltz Scientific Books. 474 p.

Guin, J. 1997. Matsutake mushroom: "white" goldrush of the 1990s. Happy Camp, CA: Naturegraph Publishers, Inc. 95 p.

Güler, P. 2000. Cultural characteristics of *Morchella esculenta* mycelium on some nutrients. Turkish Journal of Biology. 24: 783–794.

Guzmán, G. 1977. Identificación de los hongos comestibles, venenosos, alucinantes y destructores de la madera [Identification of edible, poisonous, hallucinogenic and wood-destoying fungi]. Mexico City: Editorial Limusa. 236 p. [In Spanish].

Guzmán, G.; Tapia, F. 1998. The known morels in Mexico, a description of a new blushing species, *Morchella rufobrunnea*, and new data on *M. guatemalensis*. Mycologia. 90(4): 705–714.

Guzmán-Dávalos, L.; Rodríguez-Alcantar, O. 1993. Registro de *Morchella guatemalensis* para Mexico. [Registry of *Morchella guatemalensis* for Mexico].

Boletín del Instituto de Botánica de la Universidad de Guadalajara. 1: 471–475. [In Spanish].

Hall, I.R.; Stephenson, S.L.; Buchanan, P.K. [and others] 2003. Edible and poisonous mushrooms of the world. Portland, OR: Timber Press. 371 p.

Hallen, H.; Volk, T.; Adams, G. 2001. May is morel month in Michigan. East Lansing, MI: Michigan State University Extension. 35 p.

Hammond, C. 1999. A taste of the woods. Endeavors. Fall 1999. 16(1). http://research.unc.edu/endeavors/fall99/mushroom.htm.

Hanlin, R.T.; Hahn, C.G. (illustr.). 1990. Illustrated genera of Ascomycetes. St. Paul, MN: The American Pathological Society: 66.

Hansis, R. 1998. A political ecology of picking: nontimber forest products in the Pacific Northwest. Human Ecology. 26(1): 67–86.

Harbin, M.; Volk, T.J. 1999. The relationship of morels with plant roots [Abstract]. XVI International Botanical Congress/Mycological Society of America Meeting. St. Louis, MO: Missouri Botanical Gardens: 59.

Härkönen, M. 1988. Training people to collect and sell natural products in Finland. Acta Botanica Fennica. 136: 15–18.

Härkönen, M.; Järvinen, I. 1993. Evaluation of courses for mushroom advisors in Finland. Aquilo Serie Botanica. 31: 93–97.

Hart, S.C.; DeLuca, T.H.; Newman, G.S. [and others]. 2005. Postfire vegetative dynamics as drivers of microbial community structure and function in forest soils. Forest Ecology and Management. 220: 166–184.

Haugen, J. 1994. Morel Mountain sold. The Mushroom Grower's Newsletter. July. 3(3): 1.

Haugen, J. 1998. Commercial morel cultivation. The Mushroom Grower's Newsletter. May. 7(1): 3.

Hemmes, D.E.; Desjardin, D.E. 2002. Mushrooms of Hawaii. Berkeley, CA: Ten Speed Press. 212 p.

Helfferich, D. 2005. Morels: a morsel after the fire. Agroborealis. 37(1): 4–9.

Hervey, A.; Bitis, G.; Leong, I. 1978. Cultural studies of single ascospore isolates of *Morchella esculenta*. Mycologia. 70: 1269–1273.

Hobbie, E.A.; Weber, N.S.; Trappe, J.M. 2001. Mycorrhizal vs. saprotrophic status of fungi: the isotopic evidence. New Phytologist. 150: 601–610.

Hosford, D.; Pilz, D.; Molina, R.; Amaranthus, M.P. 1997. Ecology and management of the commercially harvested American matsutake mushroom. Gen. Tech. Rep. PNW-GTR-412. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 68 p.

Huffman, D.M.; Tiffany, L.H. 2001. Spring morels and false morels of midcontinental U.S. Bioscience. 27(4): 3–11.

Instituto Nacional de Estadística Geografía e Informática [INEGI]. [N.d.]. *Morchella conica, elata y esculenta*. Especies y productos vegetales. [*Morchella conica, elata* and *esculenta*. Catalogue of species and plant products] México, D.F.: [National system of geographic statistics and information] (INEGI). http://www.inegi.gob.mx/est/contenidos/espanol/metodologias/censos/cepafop/. [In Spanish].

Iqbal, M. 1993. International trade in non-wood forest products: an overview. Working Paper Misc/93/11. Rome, Italy: Food and Agriculture Organization of the United Nations. Sec. 7.1 http://www.fao.org/documents/show_cdr.asp?url_file=/docrep/x5326e/x5326e00.htm.

Jacobs, M.E. 1982. Beta-alanine and tanning polymorphisms. Comparative biochemistry and physiology. 72(2): 173–177.

Jacquetant, E. 1984. Les morilles. [The morels]. Lausanne, Switzerland: Piantanida. 114 p. [In French].

Jenkins, N.H. 1985. Growing U.S. taste for mushrooms. New York Times. October 23: C1,2.

Johnson, N.C.; Graham, J.H.; Smith, F.A. 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. New Phytologist. 135: 575–585.

Johnston, G. 2001. Mad about morels: a Cascade treasure hunt for the mighty mushroom. Seattle Post-Intelligencer. May 24. http://seattlepi.nwsource.com/getaways/24288_shrooms24.shtml.

Jones, E.T.; McLain, R.J.; Weigand, J.F., eds. 2002. Nontimber forest products in the United States. Lawrence, KS: University Press of Kansas. 445 p.

Jung, S.W.; Gessner, R.V.; Keudell, K.C.; Ramano, M.A. 1993. Systematics of *Morchella esculenta* complex using enzyme-linked immunosorbent assay. Mycologia. 85: 677–684.

Kalač, P. 2001. A review of edible mushroom radioactivity. Food and Chemistry. 75: 29–35.

Kasischke, E.S.; Rupp, T.S.; Verbyla, D.L. 2006. Fire trends in the Alaskan boreal forest. In: Chapin, F.S., III; Oswood, M.W.; Van Cleve, K. [and others], eds. Alaska's changing boreal forest. New York: Oxford University Press: 285–301.

Kaul, T.N. 1975. Studies of the genus *Morchella* in Jammu and Kashmir I. Soil composition in relation to carpophore development. Bulletin of the Botantical Society of Bengal. 29: 127–134.

Kaul, T.N. 1997. Recent developments in morel biology. In: Rai, R.D.; Dhar, B.L.; Verma, R.N., eds. Advances in mushroom biology and production. Solan, India: Mycological Society of India: 59–81.

Keefer, M.E. 2005. The ecology and economy of morels in British Columbia's East Kootenay. Victoria, BC: Royal Roads University. 99 p. M.S. thesis.

Kendrick, B. 2001. The fifth kingdom. Sidney, BC: Mycologue Publications. 373 p.

Kenney, N.W. 1996. An overview of the Yukon morel mushroom industry. Whitehorse, Yukon: Government of Yukon, Yukon Economic Development, and Yukon Renewable Resources. 70 p.

King, R.C.; Stansfield, W.D. 2002. A dictionary of genetics. 6th ed. New York : Oxford University Press. 530 p.

Kirk, P.M.; Cannon, P.F.; David, J.C. [and others], eds. 2001. Ainsworth and Bisby's dictionary of the fungi. 9th ed. Wallingford, Oxon, United Kingdom: CABI Publishing. 655 p.

Korhonen, M. 1986. Uusi sienikirja [The new mushroom book]. Helsinki: Kustannusosakeyhtiö Otava. 318 p. [In Finnish].

Kreisel, H. 2005. Liste der ethnomykologisch und biotechnologisch relevanten Pilze. Feddes Repertorium 166 (5-6): 339–391. [In German, English summary].

Kuo, M. 2002 (December). When and where morels grow. http://www.mushroomexpert.com/morels/whenwhere.html.

Kuo, M. 2005. Morels. 1st ed. Ann Arbor, MI: University of Michigan Press. 230 p.

Kuo, M. 2006 (February). North American morels in the morel data collection project. http://mushroomexpert.com/morels/index.html.

Lakhanpal, T.N.; Shad, O.S.; Sagar, A. 1991. Mycorrhiza: a possible deterrent in artificial cultivation of morels. Current Science. 60: 375–377.

Leonard, T.J.; Volk, T.J. 1992. Production of specialty mushrooms in North America: shiitake and morels. In: Leatham, G.F., ed. Frontiers in industrial mycology. New York: Chapman Hall: 1–23.

LeVaux, A. 2005. Foraging for profit: cash crop for migrant workers, Oregon mushroom buyers. Eugene, OR: Eugene Weekly. August 18: 12-14. http://www.eugeneweekly.com/2005/08/18/coverstory.html.

Lonik, L. 2002. Basically morels: cooking, lore, & advice. Chelsa, MI: RKT Publishing. 144 p.

Love, T.; Jones, E. 2001. Why is nontimber forest product harvesting an "issue"? Excluding local knowledge and the paradigm crisis of temperate forestry. Journal of Sustainable Forestry. 13(3/4): 105–121.

Love, T.; Jones, E.; Liegel, L. 1998. Valuing the temperate rainforest: wild mushrooming on the Olympic Peninsula Biosphere Reserve. AMBIO Special Report 9: 16–25.

Low, J. 1995. Missouri's magnificent morels. Jefferson City, MO: Missouri conservationist. 56 (April): 20–23.

Lutzoni, F.; Kauff, F.; Cox, C.J. [and others]. 2004. Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. American Journal of Botany. 91(10): 1146–1480.

Mader, R. 2005. Exploring Oaxaca, San Antonio Cuajimoloyas guide: edible, eco mushroom fair. http://www.planeta.com/ecotravel/mexico/oaxaca/hongos.html.

Malchow, D. 1991 (27 December). Letter to Les Fortune, Northern Regional Forester. Morel mushroom revenue and regulation opportunities. 2 p. On file with: USDA Forest Service, Boreal Ecology Cooperative Research Unit, Box 756780, University of Alaska Fairbanks, Fairbanks, AK 99775.

Martínez-Carrera, D.; Morales, P.; Pellicer-González, H. [and others]. 2002. Rural management of matsutake mushrooms in Oaxaca, Mexico. Micologia Aplicada Internacional. 14(2): 1–18.

Masaphy, S. 2005. External ultrastructure of fruit body initiation in *Morchella*. Mycological Research. 109(4): 508–512.

Matruchot, L. 1892. Recherches sur le Développement de Quelques Mucédinées. [Research on the development of some Moniliella]. Paris: A. Colin. 11 p. [In French].

McFarlane, E.; Pilz, D.; Weber, N.S. 2005. High-elevation gray morels and other *Morchella* species harvested as nontimber forest products in Idaho and Montana. Mycologist. 19(2): 62–68.

McKnight, K.H. 1987. A field guide to mushrooms [of] North America. The Peterson Field Guide Series: 34. Boston, MA: Houghton Mifflin Co. 429 p.

McLain, R.J. 2000. Controlling the forest understory: wild mushroom politics in central Oregon. Seattle, WA: University of Washington. 331 p. Ph.D. dissertation.

McLain, R.J.; Christensen, H.H.; Shannon, M.A. 1998. When amateurs are the experts: amateur mycologists and wild mushroom politics in the Pacific Northwest, USA. Society and Natural Resources. 11: 615–626.

McLain, R.J.; Jones, E.T. 2001. Expanding nontimber forest product harvester/buyer participation in Pacific Northwest forest policy. In: Emery, M.R.; McLain, R.J., eds., Nontimber forest products: medicinal herbs, fungi, edible fruits and nuts, and other natural products from the forest Binghamton, NY: Haworth Press: 147–161.

McLain, R.J.; McFarlane, E.; Alexander, S.J. 2005. Commercial morel harvesters and buyers in western Montana: an exploratory study during the 2001 harvesting season. Gen. Tech. Rep. PNW-GTR-643. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 38 p.

McRobert, G. 1985. A walk on the wild side. Oregon Business. October: 105–106.

Methodus Consultora S.C. 2005. V Regional edible mushroom and other nontimber products fair. Oaxaca, México. http://www.raises.org/somos/METHODUS/methodusprincipal/eventos.htm.

Miller, H. 2003. Morel mushroom monitoring in a Colorado burn area: June–September, 2003. http://www.mushroomexpert.com/miller_01.html.

Miller, J. 2004a. Brownfield authority OK's plan. Ludington, MI: Ludington Daily News. February 5, 2004. http://www.ludingtondailynews.com/.

Miller, J. 2004b. Mushrooms to give bean plant new life. Ludington, MI: Ludington Daily News. January 22, 2004. http://www.ludingtondailynews.com/.

Miller, S.L.; Torres, P.; McClean, T.M. 1994. Persistence of basidiospores and sclerotia of ectomycorrhizal fungi and *Morchella* in soil. Mycologia. 86: 89–95.

Minnesota Statutes. 1998. State mushroom: morel (*Morchella esculenta*) 1.149. http://www.sos.state.mn.us/student/mushroom.html.

Moerman, D.E. 1998. Native American ethnobotany. Portland, OR: Timber Press. 927 p.

Molina, R.; Massicotte, H.; Trappe, J.M. 1992. Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. In: Allen, M.F., ed. Mycorrhizal functioning: an integrative plant-fungal process. New York: Chapman & Hall: 357–423.

Molina, R.; O'Dell, T.; Luoma, D. [and others]. 1993. Biology, ecology and social aspects of wild edible mushrooms in the forests of the Pacific Northwest: a preface to managing commercial harvest. Gen. Tech. Rep. PNW-GTR-309. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 42 p.

Molina, R.; Pilz, D.; Smith, J. [and others]. 2001. Conservation and management of forest fungi in the Pacific Northwestern United States: an integrated ecosystem approach. In: Moore, D.; Nauta, M.M.; Evans, S.E.; Rotheroe, M., eds. Fungal conservation: issues and solutions. A special volume of the British Mycological Society. Cambridge, United Kingdom: Cambridge University Press: 19–63. Chapter 3.

Molliard, M.M. 1904a. Forme conidienne et sclérotes de *Morchella esculenta* Pers. [The form of conidia and sclerotia of *Morchella esculenta* Pers.] Revue Général de Botanique. 16: 209–218. [In French].

Molliard, M.M. 1904b. Mycélium et Forme Conidienne de la Morille. [Mycelium and the conidial form of morels] Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences. 138: 516–517. [In French].

Montana Code Annotated [MCA]. 2005. Regulation of wildcrafting. Title 76, Chapter 10. http://data.opi.state.mt.us/bills/mca_toc/76_10_1.htm.

Montoya, A.; Hernández-Totomoch O.; Estrada-Torres A.; Kong A. 2003. Traditional knowledge about mushrooms in a Nahua community in the state of Tlaxcala, México. Mycologia. 95(5): 793–806.

Montréal Process Working Group. 1999. Criteria and indicators for the conservation and sustainable management of temperate and boreal forests. 2nd ed. Ottowa, ON: Montréal Process Liaison Office. http://www.mpci.org/.

Montréal Process Working Group. 2003. Mantenimiento y mejoramiento de los multiples beneficios socioeconomicos de largo plazo para cubrir las necesidades de las sociedades. Criterio seis. [Maintaining and improving long-term multiple socioeconomic benefits to cover societies needs]. The Montréal Process Country Forest Reports: Mexico. Ottawa, ON: Montréal Process Liaison Office. 174 p. http://www.mpci.org/rep-pub/2003/2003mexicocriterion06.pdf. [In Spanish].

Moore, J.; Seifert, B.; Long, K. [and others]. 2005. Alaskan mushroom guide for harvesting morels. Fairbanks, AK: University of Alaska Cooperative Extension Service; U.S. Department of Agriculture Cooperative State Research, Education, and Extension Service. 6 p.

Moser, M. 1949. Über das Massenauftreten von Formen der Gattung *Morchella* auf Waldbrandflächen. [On the mass fruiting of forms of the genus *Morchella* on burned forest soils]. Sydowia. Ser. II(3): 174–195. [In German].

Mueller, G.M.; Bills, G.F.; Foster, M.S., eds. 2004. Biodiversity of fungi: inventory and monitoring methods. New York: Elsevier Academic Press. 777 p.

Natural Resources Canada. 2004. Mushroom research follows in wake of province's wildfires. Victoria, BC: Pacific Forestry Centre, Information Forestry. http://www.pfc.forestry.ca/news/InfoForestry/Aug2004/mushrooms_e.html.

Natural Resources Canada. 2005. Forest pathology herbarium collections database. http://www.pfc.cfs.nrcan.gc.ca/biodiversity/herbarium/searchbyfungus_e.html.

Nelsen, S. 2002. Meriwether Lewis on morels. Field Mycology. 3(2): 47.

Obst, J.; Brown, W. 2000. Feasibility of a morel mushroom harvest in the Northwest Territories. Prepared by Arctic Ecology and Development (AED) Consulting and Deton'cho Corporation. Yellowknife, Northern Territories, Canada: Government of the Northwest Territories Department of Resources, Wildlife and Economic Development, Division of Economic Development, Trade and Investment Office. 42 p.

Obst J.; Coedy, W.; Bromley, R.G. 2001. Heavy metal analyses of wild edible mushrooms in the North Great Slave Lake Region, Northwest Territories, Canada. Unpublished report prepared for the Department of Indian and Northern Affairs Canada, Government of Canada, in Yellowknife, Northwest Territories. 71 p. Available from: Joachim Obst. Arctic Ecology and Development Consulting. P.O. Box 1888, Yellowknife, NT. X1A 2P4 Canada.

O'Donnell, K.O.; Cigelnik, E.; Weber, N.S. [and others]. 1997. Phylogenetic relationships among ascomycetous truffles and the true and false morels from 18S and 28S ribosomal DNA sequence analyses. Mycologia. 89(1): 48–65.

O'Donnell, K.O.; Weber, N.S.; Haines, J.H. [and others]. 1993. Molecular systematics and phylogenetics of Morchellaceae [Abstract]. Inoculum. 44(2): 51.

O'Donnell, K.; Weber, N.S.; Rehner, S. [and others]. 2003. Phylogeny and biogeography of *Morchella*. The 22nd Fungal genetics conference. Kansas City, MO: Fungal Genetics Stock Center. Fungal Genetics Newsletter. 50(Supplement): Abstract 443.

O'Driscoll, P. 2001. Delicacy sprouts from the ashes. USA Today. April 26; Sect. Nation: 3A.

Office of the Auditor General of Canada. 2004. November 2003 Report of the Auditor General of Canada. Chapter 8.4 Key tasks for the implementation of the Yukon Northern Affairs Program Devolution Transfer Agreement. Ottawa, ON: Office of the Auditor General of Canada. http://www.oag-bvg.gc.ca/domino/reports.nsf/html/20031108ce.html#ch8hd4e.

Olynyk, J.; Bergner, K. 2002. Update on land claims and devolution in the Yukon and the Northwest Territories. Fourth annual far north oil and gas conference. Vancouver, BC: Lawson Lundell, LLP. www.lawsonlundell.com/resources/updateonlandclaims-oct02.pdf.

Oregon Revised Statutes [ORS]. 1995. Unlawful cutting and transport of special forest products. ORS 164.813. http://www.statelawyers.com/Statutes/Index.cfm/StateID:37/ID:47354.

Ower, R. 1982. Notes on the development of the morel ascocarp: *Morchella esculenta*. Mycologia. 74: 142–144.

Ower, R.D.; Mills, G.L.; Malachowski, J.A. 1986 (June 17). Cultivation of *Morchella*. U.S. Patent 4,594,809.

Ower, R.D.; Mills, G.L.; Malachowski, J.A. 1988 (July 19). Cultivation of *Morchella*. U.S. Patent 4,757,640.

Ower, R.D.; Mills, G.L.; Malachowski, J.A. 1989 (September 19). Cultivation of *Morchella*. U.S. Patent 4,866,878.

Palm, M.E.; Chapela, I.H., eds. 1997. Mycology in sustainable development: expanding concepts and vanishing borders. Boone, NC: Parkway Publishers, Inc. 306 p.

Parks, C.G.; Schmitt, C.L. 1997. Wild edible mushrooms in the Blue Mountains: resource and issues. Gen. Tech. Rep. PNW-GTR-393. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 22 p.

Penticton Herald. 2004. Mushroom harvesters leave garbage strewn in woods. Penticton BC: Penticton Herald. July 5. http://www.pentictonherald.ca/.

Perry, J.P., Jr.; Graham, A.; Richardson, D.M. 1998. The history of pines in Mexico and Central America. In: Ecology and biogeography of *Pinus.* Richardson, D.M., ed. Cambridge, MA: Cambridge University Press: 137–149.

Persoon, C.H. 1797. Tentamen dispositionis methodicae fungorum in classes, ordines genera et familias. Leipsig. [In Latin].

Peterson, R.L.; Massicotte, H.B.; Melville, L.H. 2004. Mycorrhizas: anatomy and cell biology. Ottawa ON: NRC Research Press. 173 p.

Philippoussis, A.; Balis, C. 1995. Studies on the morphogenesis of sclerotia and subterranean mycelial network of ascocarps in *Morchella* species. In: Elliott, T.J., ed. Science and cultivation of edible fungi; Proceedings of the 14th international congress on the science and cultivation of edible fungi. Oxford, England; Rotterdam: A.A. Balkema: 847–855.

Pietikäinen, J. 1999. Soil microbes in boreal forest humus after fire. Res. Pap. 750. Vantaa, Finland: Finnish Forest Research Institute. 50+78 p. http://ethesis.helsinki.fi/julkaisut/maa/mekol/vk/pietikainen/soilmicr.html.

Pietikäinen, J.; Hiukka, R.; Fritze, H. 2000. Does short-term heating of forest humus change its properties as a substrate for microbes? Soil Biology and Biochemistry. 32(2): 277–288.

Pilz, D.; Alexander, S.; Smith, J. [and others]. 2006a. Alaskan nontimber forest product opportunities. Gen. Tech. Rep. PNW-GTR-671. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 79 p.

Pilz, D.; Ballard, H.L.; Jones, E.T. 2006b. Broadening participation in biological monitoring: a handbook for scientists and managers. Gen. Tech. Rep. PNW-GTR-680. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 131 p.

Pilz, D.; Molina, R. 1998. A proposal for regional monitoring of edible forest mushrooms. Mushroom, The Journal of Wild Mushrooming. (16)3: 19–23.

Pilz, D.; Molina, R. 2002. Commercial harvests of edible mushrooms from the forests of the Pacific Northwest United States: issues, management, and monitoring for sustainability. Forest Ecology and Management. 155(1–3): 3–16.

Pilz, D.; Molina, R.; Mayo, J. 2006c. Effects of thinning young forests on chanterelle mushroom production. Journal of Forestry. 104(1): 9–14.

Pilz, D.; Norvell, L.; Danell, E.; Molina, R. 2003. Ecology and management of commercially harvested chanterelle mushrooms. Gen. Tech. Rep. PNW-GTR-576. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 84 p.

Pilz, D.; Smith, J.; Amaranthus, M.P. [and others]. 1999. Mushrooms and timber: managing commercial harvesting in the Oregon Cascades. Journal of Forestry. 97(3): 4–11.

Pilz, D.; Weber, N.S.; Carter, M.C. [and others]. 2004. Productivity and diversity of morel mushrooms in healthy, burned and insect-damaged forests of northeastern Oregon. Forest Ecology and Management. 198: 367–386.

Prasad, P.; Chauhan, K.; Kandari, L.S. [and others]. 2002. *Morchella esculenta* (Guchhi): need for scientific intervention for its cultivation in Central Himalaya. Current Science. 82(9): 1098–1100.

Pugh, G.J.F.; Boddy, L. 1988. A view of disturbance and life strategies in fungi. Proceedings of the Royal Society of Edinburgh. 94B: 3–11.

Pyne, S.J.; Andrews, P.L.; Laven, R.D. 1996. Introduction to wildland fire. 2nd ed. New York: John Wiley & Sons, Inc. 769 p.

Ramsbottom, J. 1953. Mushrooms and toadstools: a study of the activities of fungi. London: Collins. 306 p.

Rédei, G.P. 2003. Encyclopedic dictionary of genetics, genomics, and proteomics. 2nd ed. Hoboken, NJ: Wiley-Liss. 1379 p.

Redhead, S.A. 1997. The pine mushroom industry in Canada and the United States: why it exists and where it is going. In: Palm, M.E.; Chapela, I.H., eds. Mycology in sustainable development: expanding concepts, vanishing borders. Boone, NC: Parkway Publishers: 15–54.

Revised Code of Washington [RCW]. 1967. Specialized forest products. Chapter 76.48. http://apps.leg.wa.gov/RCW/default.aspx?cite=76.48.

Robbins, W.J.; Hervey, A. 1959. Wood extract and growth of *Morchella*. Mycologia. 51(3): 356–363.

Rolfe, R.T.; Rolfe, F.W. 1925. Romance of the fungus world: an account of fungus life in its numerous guises, both real and legendary. London: Chapman and Hall. 309 p.

Rommelmann, N. 2005. The great Alaskan morel rush of '05**:** being the true story of intrepid pickers, cutthroat buyers, anxious distributors, curious scientists, conflicted locals and other denizens of the mushroom circuit, all of whom headed north in search of the mother lode. Los Angeles Times Magazine. July 10, 2005. Cover story.

Royse, D.J.; May, B. 1990. Interspecific allozyme variation among *Morchella* spp. and its inferences for systematics within the genus. Biochemical Systematics and Ecology. 18: 475–479.

Schadt, C.W.; Martin, A.P.; Lipson, D.A. [and others]. 2003. Seasonal dynamics of previously unknown fungal lineages in tundra soils. Science. 301: 1359–1361.

Schlosser, W.E.; Blatner, K.A. 1995. The wild edible mushroom industry of Washington, Oregon and Idaho: a 1992 survey. Journal of Forestry. 93(3): 31–36.

Schlosser, W.E.; Blatner, K.A. 1997. Special forest products: an east-side perspective. Gen. Tech. Rep. PNW-GTR-380. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 27 p.

Schmidt, E.L. 1979. Puffing in *Morchella*. Bulletin of the British Mycological Society. 13(2): 126–127.

Schmidt, E.L. 1983. Spore germination of and carbohydrate colonization by *Morchella esculenta* at different soil temperatures. Mycologia. 75(5): 870–875.

Secretaria del Medio Ambiente, Recursos Naturales y Pesca [SEMARNAP]. 2004. Aprovechamiento 2003–2004 vida Silvestre: Unidad de Manejo Ambiental (UMA) con taza de aprovechamiento autorizado. [Forestry and wildlife permits 2003–2004: environmental management units with list of fees for use permits] México, D.F.: [The Secretariat of Environment and Natural Resources], SEMARNAP. http://www.semarnat.gob.mx/Pages/inicio.aspx. [In Spanish].

Secretaria del Medio Ambiente, Recursos Naturales y Pesca [SEMARNAP]; Proyecto de Conservacion y Manejo Sustentable de Recursos Forestales [PROCYMAF]. [N.d.]. Especies con Usos No Maderables en Bosques de Encino, Pino y Pino-Encino en los Estados de Chihuahua, Durango, Jalisco, Michoacán, Guerrero y Oaxaca: *Morchella elata* y *Morchella esculenta*. [Species of nontimber forest products in Oak, Pine, and Pine-Oak forests of Chihuahua, Durango, Jalisco, Michoacán, Guerrero and Oaxaca: *Morchella elata* and

Morchella esculenta.] México, D.F.: [The Secretariat of Environment and Natural Resources], SEMARNAP and [Project of Conservation and Sustainable Management of Forest Resources] PROCYMAF. http://www.semarnat.gob.mx/Pages/inicio.aspx. [In Spanish].

Shad, O.; Sagar, A.; Lakhanpal, T.N. 1990. The mycorrhizal association of morels in NW Himalayas. Current trends in mycorrhizal research: proceedings of the national conference on mycorrhiza. Hisar, India: Haryana Agricultural University: 128–129.

Shanley, P.; Pierce, A.R.; Laird, S.A.; Guillen, S.A. 2002. Tapping the green market: management and certification of nontimber forest products. London: Earthscan. 456 p.

Sharma, B.M.; Deepika, S.; Singh, B.M. [and others]. 1997a. Natural occurrence of two strains of *Morchella esculenta* in Himachal Pradesh. Mushroom Research—International Journal of Mushroom Research and Development. 6(2): 63–64.

Sharma, B.M.; Deepika, S.; Singh, B.M. [and others]. 1997b. Production of sclerotial spawn for the cultivation of *Morchella esculenta*. Proceedings of the Indian National Science Academy, Part B, Reviews and Tracts, Biological Sciences. 63(6): 647–654.

Singh, S.K.; Dhar, B.L.; Verma, R.N. 1999. Mass production of carpogenic sclerotial spawn in *Morchella esculenta*—an attempt at its domestication. In: The 3rd international conference on mushroom biology and mushroom products. Sydney, Australia: World Society for Mushroom Biology and Mushroom Production: 6.

Singh, S.K.; Kamal, S.; Tiwari, M. [and others]. 2004. Myco-ecological studies of natural morel bearing sites in Shivalik hills of Himachal Pradesh, India. Micologia Aplicada International. 16(1): 1–6.

Singh, S.K.; Verma, R.N. 2000. Effects of nutrients on mycelial growth and sclerotia formation in *Morchella esculenta*. In: Van Griensven, L.J.L.D., ed. Science and cultivation of edible fungi; Proceedings of the 15th international congress on the science and cultivation of edible fungi. Maastricht Netherlands: Rotterdam: A.A. Balkema: 531–534.

Smith, A.H.; Smith, H.V.; Weber, N.S. 1981. How to know the non-gilled mushrooms. Dubuque, IA: Wm. C. Brown Co. 324 p.

Smith, S.E.; Read, D.J. 1997. Mycorrhizal symbiosis. San Diego, CA: Academic Press. 605 p.

Stabenow, D. 1995. Play with fire: a Kate Shugak mystery. New York: Berkley Prime Crime. 282 p.

Stamets, P. 1993. Cultivating morels. Mushroom, The Journal of Wild Mushrooming. 11(41): 9–15.

Stamets, P. 2000. Growing gourmet and medicinal mushrooms. Berkeley, CA: Ten Speed Press. 574 p.

Stamets, P. 2005. Mycelium running: how mushrooms can help save the world. Berkeley: Ten Speed Press. 340 p.

Still, G.; MacKinnon, A.; Planden, R. 1994. Forest, range and recreation resource analysis 1994. Catalogue code: 025–532. Victoria, BC: Crown Publications Inc. http://www.for.gov.bc.ca/hfd/library/frra/1994/.

Stott, K.G.; Gill, W.; Mohammed, C.; Brown, M. 2002. Specialty gourmet and medicinal fungi research in Tasmania. In: The 4th international conference on mushroom biology and mushroom products. Cuernavaca, Mexico: World Society for Mushroom Biology and Mushroom Production. 11 p.

Stott, K.G.; Mohammed, C. 2004. Specialty mushroom production systems: maitake and morels. RIRDC Publication No. 04/024. Barton, ACT, Australia: Rural Industries Research and Development Corporation, Australian Government. 86 p.

Sturgis, W.C. 1905. Remarkable occurrence of *Morchella esculenta* (L.) Pers. Journal of Mycology. 11: 269.

Svrček, M. 1983. Dausien's Grosses Pilzbuch in Farbe [Dausien's big mushroom book in color]. 2nd ed. Hanau, Germany: Verlag Werner Dausien. 313 p. [In German].

Szuecs, J. 1958 (September 9). Method of growing mushroom mycelium and the resulting products. United States Patent No. 2,850,841. 3 p.

Szuecs, J.; Wiles, G.M. 1950 (May 2). Essence of mushroom and its preparation. United States Patent No. 2,505,801. 3 p.

Taylor, J.W.; Jacobson, D.J.; Kroken, S. [and others]. 2000. Phylogenetic species recognition and species concepts in fungi. Fungal Genetics and Biology. 31: 21–32.

Taylor, J.W.; Spatafora, J.; Berbee, M. 1996. Ascomycota: sac fungi. The tree of life Web project. http://tolweb.org/tree?group=Ascomycota&contgroup=Fungi.

Tedder, S.; Mitchell, D.; Farran, R. 2000. Seeing the forest beneath the trees: the social and economic potential of nontimber forest products and services in the Queen Charlotte Islands/Haida Gwaii, BC. Victoria, BC: Ministry of Forests. 134 p. http://www.for.gov.bc.ca/hre/ntfp/online.htm.

Tedder, S.; Mitchell, D.; Hillyear, A. 2002. Property rights in the sustainable management of nontimber forest products. Victoria, BC: British Columbia Ministry of Forestry, Forest Renewal BC. 130 p. http://www.for.gov.bc.ca/hre/ntfp/online.htm.

Thompson, V.V. 1994. Morel: a lifetime pursuit. Glencoe, MO: Missouri Mycological Society. 36 p.

Tiffany, L.H.; Knaphus, G.; Huffman, D.M. 1998. Distribution and ecology of the morels and false morels of Iowa. Journal of the Iowa Academy of Science. 105(1): 1–15.

Trappe, J.M. 1996. What is a mycorrhiza? In: Azcon-Aguilar, C.; Barea, J.M., eds. Mycorrhizas in integrated systems from genes to plant development: proceedings of the fourth European symposium on mycorrhizas. European Commission Report EUR 16728 EN. Brussels: European Commission Directorate-General XII, Science, Research, and Development: 3–6.

Trappe, J.M.; Molina, R.; Castellano, M. 1984. Reactions of mycorrhizal fungi and mycorrhiza formation to pesticides. Annual Review of Phytopathology. 22: 331–359.

Treseder, K.K.; Mack, M.C.; Cross, A. 2004. Relationships among fires, fungi, and soil dynamics in Alaskan boreal forests. Ecological Applications. 14(6): 1826–1838.

Tumlin, H. 2005. Proposed prohibition of wild mushrooms in Los Angeles County. Letter to Dr. Thomas Garthwaite, Director of Health Services. Los Angeles, CA. February 17, 2005. In: Southland Farmers' Market Association. Los Angeles County Department of Health Services first bans, then rescinds ban, of wild mushroom sales in certified farmers' markets. [On-line newsletter] 21 March 2005. http://www.cafarmersmarkets.org/.

Ulloa, M.; Hanlin, R.T. 2000. Illustrated dictionary of mycology. St. Paul, MN: American Pathological Society Press. 448 p.

United Nations Environment Programme-World Conservation Monitoring Centre [UNEP-WCMC]; Methodus Consultora S.C. 2003. Informe sobre el mercado de hongos silvestres, Proyecto de comercialización de productos forestales no maderables, factores de exito y fracaso, el mercado de los hongos silvestres. [Report on the market of wild fungi, project for commercialization of nontimber forest products, factors of success and failure, market for wild fungi]. Cambridge, United Kingdom: United Nations Environment Programme-World Conservation Monitoring Centre. Oaxaca, México: Methodus Consultora S.C. 45 p. http://www.raises.org/centros/Manejocampesino/Recursosnomaderables/Reportemercadohongos.PDF. [In Spanish].

U.S. Department of Agriculture, Forest Service [USDA FS]. 2000. Morel mushroom meeting minutes. Region 1 December 7. Unpublished document. On file with: Rebecca McLain, Institute for Culture and Ecology, P.O. Box 6688, Portland, OR 97228. mclain@ifcae.org.

U.S. Department of Agriculture, Forest Service [USDA FS]. 2004a. Land areas of the national forest system: Table 4–Areas by state. http://www.fs.fed.us/land/staff/lar/LAR04/table4.htm.

U.S. Department of Agriculture, Forest Service [USDA FS]. 2004b. National report on sustainable forests–2003. [Indicators 14, 30, and 34]. Washington, DC: U.S. Department of Agriculture, Forest Service. FS-766. 152 p. http://www.fs.fed.us/research/sustain/.

U.S. Department of Agriculture, Forest Service [USDA FS]. 2004c. Passes and permits: mushroom gathering permits. Baker City, OR: Wallowa-Whitman National Forest. http://www.fs.fed.us/r6/w-w/passes/mushrooms.shtml.

U.S. Department of the Interior, Bureau of Land Management [USDI BLM]. 1996. Public land statistics 1996. Table 1–3: Comparison of federally owned land with total acreage of states. http://www.access.gpo.gov/blm/pls96/contents.html.

U.S. Department of the Interior, Bureau of Land Management [USDI BLM]. 2003. Update of Montana/Dakotas minimum price list for forest and vegetative products. Billings, MT: Montana State Office. http://www.blm.gov/nhp/efoia/mt/2003/im/03mtm038.pdf.

Vehling, J.D., ed. and transl. 1977. Apicius cookery and dining in imperial Rome: a biography, critical review and translation of the ancient book known as *Apicius de re Coquinaria*. New York: Dover Publications. 301 p.

Villarreal, L.; Gómez, A. 1997. Inventory and monitoring wild edible mushrooms in Mexico: challenge and opportunity for sustainable development. In: Palm, M.E.; Chapela, I.H., eds. Mycology in sustainable development: expanding concepts, vanishing borders. Boone, NC: Parkway Publishers: 99–109.

Villarreal, L.; Pérez-Moreno, J. 1989. Los hongos comestibles silvestres de Mexico, un enfoque integral. [Wild edible fungi of Mexico, an integral approach] Micologia Neotropical Aplicada. 2: 77–114. [In Spanish, English abstract].

Villarreal-Ruiz, L. 1994. Analisis ecologico silvicola de la productividad natural de hongos comestibles silvestres en los bosques del Cofre de Perote, Veracruz. [Ecological and silvicultural analyses of the natural productivity of wild edible mushrooms in the forests of Cofre de Perote, Veracruz] Montecillo, Edo. de Mexico: Colegio de Postgraduados en Ciencias Agrícolas. 158 p. M.S. thesis. [In Spanish].

Villarreal-Ruiz, L., ed. 1996. Los hongos silvestres: componentes de la biodiversidad y alternativa para la sustentabilidad de los bosques templados de México. [Wild mushrooms: biodiversity components and alternative for the sustainable management of temperate forest in Mexico]. Informe final, Proyecto-CONABIO C066. Montecillo, Edo. de Mexico: Instituto de Recursos Genéticos y Productividad, Colegio de Postgraduados en Ciencias Agrícolas. 97 p. Unpublished report. On file with: Library of Colegio de Postgraduados en Ciencias Agricolas, Campus Montecillo, Km. 36.5 Carretera México-Texcoco, Montecillo, Edo. de México, C.P. 56230. http://www.colpos.mx/biblioteca/servicios.htm. [In Spanish].

Vogt, K.A.; Bloomfield, J.; Ammirati, J.F.; Ammirati, S.R. 1992. Sporocarp production by Basidiomycetes, with emphasis on forest ecosystems. In: Carroll, G.C.; Wicklow, D.T., eds. The fungal community: its organization and role in the ecosystem, 2nd ed. New York: Marcel Dekker: 563–581.

Volk, T.J. 1990. The current state of morel cultivation. Mushroom News. 38(8): 24–27.

Volk, T.J. 1991. Understanding the morel life cycle: key to cultivation. McIlvainea. 10: 76–81.

Volk, T.J.; Kozak, M.E.; Krawczyk, J. 1997. Ecological guides to the cultivation of edible mushrooms. Mushroom News. 45(5): 26–36.

Volk, T.J.; Leonard, T.J. 1989a. Experimental studies on the morel. I. Heterokaryon formation between monoascosporous strains of *Morchella*. Mycologia. 81(4): 523–531.

Volk, T.J.; Leonard, T.J. 1989b. Physiological and environmental studies of sclerotium formation and maturation in isolates of *Morchella crassipes.* Applied and Environmental Microbiology. 55(12): 3095–3100.

Volk, T.J.; Leonard, T.J. 1990. Cytology of the life-cycle of *Morchella*. Mycological Research. 94: 399–406.

Von Hagen, B.; Weigand, J.F.; McLain, R. [and others]. 1996. Conservation and development of nontimber products in the Pacific Northwest: an annotated bibliography. Gen. Tech. Rep. PNW-GTR-375. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 246 p.

Vrålstad, T.; Holst-Jensen, A.; Schumacher, T. 1998. The postfire discomycete *Geopyxis carbonaria* (Ascomycota) is a biotrophic root associate with Norway spruce (*Picea abies*) in nature. Molecular Ecology. 7: 609–616.

Walstad, J.D.; Radosevich, S.R.; Sandberg, D.V. eds. 1990. Natural and prescribed fire in Pacific Northwest forests. Corvallis, OR: Oregon State University Press. 317 p.

Weber, N.S. 1988. A morel hunter's companion: a guide to the true and false morels of Michigan. Lansing, MI: TwoPeninsula Press. 209 p.

Weber, N.S. 1995. Overview of research pertinent to morels or *Morchella* spp. as special forest products. In: Schnepf, C., ed. Dancing with the elephant: proceedings, the business and science of special forest products—a conference and exposition. Moscow, ID: University of Idaho Extension Service: 129–133.

Weber, N.S. 1997. Morels and allied cup-fungi of the interior Columbia River basin. In: Kaye, T.N.; Liston, A.; Love, R.M. [and others], eds. Conservation and management of native plants and fungi. Corvallis, OR: Native Plant Society of Oregon: 227–233.

Weber, N.S.; Pilz, D.; Carter, C. 1996. Morel life histories: beginning to address the unknowns with a case study in the Fremont National Forest near Lakeview, Oregon. In: Pilz, D.; Molina, R., eds. Managing forest ecosystems to conserve fungus diversity and sustain wild mushroom harvests. Gen. Tech. Rep. PNW-GTR-371. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 62–68.

Weber, N.S.; Trappe, J.M.; Denison, W.C. 1997. Studies on western American Pezizales. Collecting and describing ascomata macroscopic features. Mycotaxon. 61: 153–176.

Wedin, M.; Döring, H.; Gilenstam, G. 2004. Saprotrophy and lichenization as options for the same fungal species on different substrata: environmental plasticity and fungal lifestyles in the *Stictis-Conotrema* complex. New Phytologist. 164: 459–465.

Werner, P. 2002. The secret life of morel bugs. Mycena News. 53(9): 1,3.

Wheeler, S. 1996. Mushroom magic: 100 fabulous feasts with wild and cultivated mushrooms. New York: Lorenz Books. 128 p.

Willetts, H.J. 1972. The morphogenesis and possible evolutionary origins of fungal sclerotia. Biological Reviews. 47: 516–536.

Wills, R.M.; Lipsey, R.G. 1999. An economic strategy to develop nontimber forest products and services in British Columbia. Forest Renewal BC Project PA97538-ORE. Bowen Island, BC: Cognetics International Research. 113 p.

Winder, R. 2006. Cultural studies of *Morchella elata* (Fries) Fries. Mycological Research. 110: 612–623.

Wipf, D.; Bedell, J.-P.; Munch, J.C. [and others]. 1996a. Polymorphism in morels: isozyme electrophoretic analysis. Canadian Journal of Microbiology. 42: 819–827.

Wipf, D.; Fribourg, A.; Munch, J.C. [and others] 1999. Diversity of the internal transcribed spacer of rDNA in morels. Canadian Journal of Microbiology. 42: 769–778.

Wipf, D.; Munch, J.C.; Botton, B.; Buscot, F. 1996b. DNA polymorphism in morels: complete sequences of the internal transcribed spacer of genes coding for rRNA in *Morchella esculenta* (yellow morel) and *Morchella conica* (black morel). Applied and Environmental Microbiology. 62(9): 3541–3543.

World Bank. 1995. Mexico: resource conservation and forest sector review. Report No. 13114-ME. Washington, DC: World Bank, Natural Resources and Rural Poverty Operations Division, Latin America and the Caribbean Regional Office. 29 p.

World Bank. 1997. Staff appraisal report, Mexico, community forestry project. Report No. 16134-ME. Washington, DC. http://www-wds.worldbank.org/servlet/WDSContentServer/WDSP/IB/2000/01/19/000009265_3970625093529/Rendered/INDEX/multi_page.txt.

Wurtz, T.L.; Wiita, A.L.; Weber, N.S. [and others]. 2005. Harvesting morels after wildfire in Alaska. Res. Note PNW-RN-546. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 31 p.

Yamin, S. 2005. Morel harvest in Alaska: an ethnographic overview of the 2005 season. Unpublished report. On file with: Cooperative Extension Service, University of Alaska. Fairbanks State Office, CES Building, P.O. Box 756180, Fairbanks, AK 99775-6180. http://www.uaf.edu/coop-ext/.

Yoon, C.-S.; Gessner, R.V.; Romano, M.M. 1990. Population genetics and systematics of the *Morchella esculenta* complex. Mycologia. 82(2): 227–235.

Yukon Energy, Mines, and Resources. 2004. Discussion paper–towards a Yukon forest policy framework. Whitehorse, Yukon: Government of Yukon, Yukon First Nations and Resource Councils. 33 p. http://www.emr.gov.yk.ca/pdf/forest_policy_framework_0604.pdf.

Zamora, M.; Torres, J.M.; Zamora, L. 2001. Analisis de la informacion sobre productos forestales no madereros en Mexico. Proyecto informacion y analisis para el manejo forestal sostenible: integrando esfuerzos nacionales e internacionales en 13 paises tropicales en America Latina CGCP/RLA/133/EC. [Analyses of nontimber forest products in Mexico. Project on analysis of information for forestry sustainable management: national and international joined efforts in 13 tropical Latin American countries]. Santiago de Chile: FAO/EU. 120 p. http://www.rlc.fao.org/proyecto/rla133ec/PFNM-pdf/PFNM%20Mex.PDF. [In Spanish].

Zickler, D.; Arnaise, S.; Coppin, E. [and others]. 1995. Altered mating-type identity in the fungus *Podospora anserina* leads to selfish nuclei, uniparental progeny, and haploid meiosis. Genetics. 140: 493–503.

Appendix—Common and Scientific Names[a]

Common English names	Scientific names
True morels[b]:	
Asexual conidial stage of *Morchella* mycelium	*Costantinella cristata* Matr. anamorphic Leotiales
Morels	*Morchella* species
(Black) burn morel	*Morchella angusticeps* Peck (European species only?)
Gray morel (fuzzy or black-foot morel)	*Morchella esculenta* var. *atrotomentosa* M.M. Moser
	Morchella atrotomentosa (Moser) Bride
	Both scientific names using "atrotomentosa" are invalid, European species only?
(Black) burn morel	*Morchella conica* Krombh. (European species only?)
None known	*Morchella costata* J.C. Schmidt & Kunze (variety of M. conica?)
Yellow morel	*Morchella crassipes* (Vent.) Pers. (European species only?) (Mature stage of "*M. esculenta*" in North America)
White morel	*Morchella deliciosa* Fr. (European species only?)
Natural black morel	*Morchella elata* Fr. (European species only?)
Yellow morel	*Morchella esculenta* (L.) Pers. (European species only?)
Guatemalan morel	*Morchella guatemalensis* Guzmán, M.F. Torres & Logem.
None known (named after Herediana, Costa Rica)	*Morchella herediana* Gómez
Garden morel	*Morchella hortensis* Boud.
None known	*Morchella intermedia* Boud. (variety of *M. conica*?)
None known	*Morchella rigidoides* R. Heim
Round blond morel	*Morchella rotunda* (Fr.) Boud. (=*Morchella esculenta*?)
Red-brown blushing morel	*Morchella rufobrunnea* Guzmán & F. Tapia
Half-free morel	*Morchella semilibera* DC. (*Mitrophora semilibera*)
None known	*Morchella umbrina* Boud. (variety of *M. esculenta*?)
Mountain blond morel	not yet named
Green morel	not yet named
Pink morel	not yet named
Morel look-alikes and related genera:	
Pig's ears	*Discina* species
Veined cup-fungus	*Disciotis venosa* (Pers.) Arnould

Common English names	Scientific names
Snowbank or giant false morel	*Gyromitra gigas* s.l. (Krombh.) Cooke
False morel	*Gyromitra esculenta* (Pers.) Fr.
False morels, lorchels	*Gyromitra* species
Elfin saddles	*Gyromitra* and *Helvella* species
Early morel	*Verpa bohemica* (Krombh.) J. Schröt.
Thimble morels	*Verpa* species
Other fungi:	
Agaric	Any gilled mushroom
Black poplar mushroom	*Agrocybe aegerita* (V. Brig.) Singer
Button mushroom	*Agaricus brunnescens* Peck
Boletes (commercially, often in reference to king [autumn] and spring boletes)	*Boletus* species
King bolete	*Boletus edulis* Bull.
Spring bolete	*Boletus pinophilus* Pilát & Dermek
Cedar-apple rust	*Gymnosporangium juniperi-virginianae* Schwein.
Chanterelle (specific usage)	Species of the genus *Cantharellus*
Chanterelles (inclusive or broad usage)	Species of the genera *Cantharellus, Craterellus, Gomphus,* and *Polyozellus.*
Pixie cup	*Geopyxis carbonaria* (Alb. & Schwein.) Sacc.
Shiitake	*Lentinula edodes* (Berk.) Pegler
Dutch elm disease	*Ophiostoma ulmi* (Buisman) Nannf.
Cinnamon nameko	*Pholiota nameko* (T. Itô) S. Ito & S. Imai
Oyster	*Pleurotus* species
None known	*Podospora anserina* (Rabenh.) Niessl
None known	*Sclerotina sclerotiorum* (Libert) de Bary
American matsutake (pine mushroom)	*Tricholoma magnivelare* (Peck) Redhead
Matsutake (generic term for any *Tricholoma* species harvested for culinary use, but typically the native Eurasian species, *Tricholoma matsutake*)	*Tricholoma matsutake* (S. Ito & S. Imai) Singer, *Tricholoma magnivelare* (Peck) Redhead, or *Tricholoma caligatum* (Viv.) Ricken
Truffles (In the specific sense it is used for fungi belonging to the genus *Tuber.* The term "truffles" is also more generally used to denote all culinary truffles, or more broadly, all fungi that produce fruiting bodies underground. The latter are technically called "hypogeous" fungi.)	*Tuber* species
Nonwoody plants:	
Beargrass	*Xerophyllum tenax* (Pursh) Nutt.
Fiddlehead ferns (braken ferns)	*Pteridium aquilinum* (L.) Kuhn

Common English names	Scientific names
Polytrichum moss	*Polytrichum* species
Strawberries	*Fragaria* species
Trillium	*Trillium* species
Shrubs:	
Huckleberries	*Vaccinium* species
Lilacs	*Syringa vulgaris* L.
Ocean spray	*Holodiscus discolor* (Pursh.) Maxim.
Prostrate ceanothus	*Ceanothus prostratus* Benth.
Salal	*Gaultheria shallon* Pursh
Wooly blackberry	*Rubus tomentosus* Borkh.
Trees:	
Alder	*Alnus* species
Apple	*Malus pumila* P. Mill.
Ash	*Fraxinus* species
Aspen	*Populus* species
Beech	*Fagus* species
Black cherry	*Prunus serotina* Ehrh.
Black spruce	*Picea mariana* (P. Mill.) B.S.P.
Birch	*Betula* species
Blue gum tree, Tasmanian blue gum tree, Australian fever tree	*Eucalyptus globus* Labill.
Cherry laurel	*Prunus laurocerasus* L.
Chestnut	*Castanea sativa* P. Mill
Chilean cedar	*Austrocedrus chilensis* (D. Don) Florin et Boutelje
Cottonwood	*Populus* species
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco
Elm	*Ulmus* species
Engelmann spruce	*Picea engelmannii* Perry ex Engelm.
European alder	*Alnus glutinosa* (L.) Gaertn.
Hickel's fir	*Abies hickelii* Flous & Gauss.
Hickory	*Carya* species
Jack pine	*Pinus banksiana* Lamb.
Juniper	*Juniperus* species
Locust	*Robinia pseudoacacia* L.
Lodgepole or shore pine	*Pinus contorta* Dougl. ex Loud. var. *contorta*
Maple	*Acer* species
Monterey pine	*Pinus radiata* D. Donn
Norway spruce	*Picea abies* (L.) Karst.
Oak	*Quercus* species
Oyamel fir	*Abies religiosa* (Kunth.) Schltdl. et Cham.
Paper birch	*Betula papyrifera* Marsh.
Pines	*Pinus* species
Ponderosa pine	*Pinus ponderosa* P. & C. Lawson
Poplars	*Populus* species

Common English names	Scientific names
Sierran yellow pine (community)	*Pinus jeffreyi* Grev. & Balf., *Pinus ponderosa* P. & C. Lawson, and *Pinus coulteri* D. Don pine stands
Southern beech	*Nothofagus* species
Subalpine fir	*Abies lasiocarpa* (Hook.) Nutt.
Subalpine larch	*Larix lyallii* Parl.
Sweet gum	*Liquidambar* species
Sycamore	*Platanus* species
True firs	*Abies* species
Tulip poplar	*Liriodendron tulipifera* L.
Weeping pine	*Pinus patula* Schiede ex Schlecht. & Cham.
Western hemlock	*Tsuga heterophylla* (Raf.) Sarg.
Western larch	*Larix occidentalis* Nutt.
White-alder	*Clethra* species
White fir	*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.
White spruce	*Picea glauca* (Moench) Voss.
Whitebark pine	*Pinus albicaulis* Dougl.
Willow	*Salix* species
Insects:	
Douglas-fir tussock moth	*Orgyia pseudotsugata* McDunnough
Flat bug	*Aradus debilis* Uhler
Gypsy moth	*Lymantria dispar* Linnaeus
Millipedes	Class Diplopoda
Mountain pine beetle	*Dendroctonus ponderosae* Hopkins
Rove beetles	Family Staphylinidae
Western spruce bud worm	*Choristoneura occidentalis* Freeman
Wireworms (click beetle larvae)	Family Elateridae
Animals:	
Elk	*Cervus canadensis* Borowski
Grizzly bear	*Ursus arctos* Linnaeus var. *horribilis*
Gray wolf	*Canis lupus* Linnaeus

[a] Fungi are listed alphabetically by scientific names because we used these extensively in the text. Other organisms are listed alphabetically by the common names we predominantly used. Our source for scientific names and naming authorities for fungal species is the IndexFungorum Database maintained by CABI Bioscience and The Centraalbureau voor Schimmelcultures, an institute of the Royal Netherlands Academy of Arts and Sciences. The database is available online at: http://www.indexfungorum.org/Names/NAMES.ASP. Readers are advised that fungal taxonomy is controversial and changing. This publication is not intended as a definite source. When in doubt, check the database or other references as needed. Our source for scientific names and naming authorities for trees, shrubs, and nonwoody vascular plants in the United States is the U.S. Department of Agriculture, Natural Resources Conservation Service, National Plant Data Center, Plants Database available for online searches at: http://plants.usda.gov/index.html.

[b] Scientific names of most of the morels listed here are derived from our citation of European literature and likely do not apply to most North American species. The common names associated with European scientific names do not necessarily reflect usage in North America either. Please see table 1 for the names we use for western North American species in this publication.

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