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Commercial harvests of edible mushrooms from the forests of the Pacific Northwest United States: issues, management, and monitoring for sustainability

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Abstract

Widespread commercial harvesting of wild edible mushrooms from the forests of the Pacific Northwest United States (PNW-US) began 10–15 years ago. A large proportion of suitable forest habitat in this region is managed by the Forest Service (US Department of Agriculture) and Bureau of Land Management (US Department of the Interior). These lands are managed under an ecosystem management philosophy that entails multiple-use, sustainable forest product harvesting, resource monitoring, public participation in forest management issues, and holistic planning. Managing the harvest of edible mushrooms engages every aspect of this management philosophy. We examine a variety of issues raised by mushroom harvesting and how these issues interact with forest ecosystem management choices. We discuss regulations currently being used by managers to conserve the mushroom resource while further information is gathered, unique challenges and considerations inherent to sampling fungi, and current research and monitoring activities in the Pacific Northwest. Although current scientific evidence suggests that harvesting likely will not harm the resource in the short term, no statistically-based monitoring information exists about the cumulative impacts of intensive and widespread commercial harvesting over long-time periods. We outline a three pronged approach to long-term monitoring of the resource: (1) tracking harvest quantities in areas with intense commercial harvests; (2) sampling productivity in areas with no mushroom or timber harvests; and (3) conducting research to model the relations between forest management and mushroom productivity. Public participation and a broad collaboration among public land management agencies, private forest landowners, forest managers, researchers, and research organizations will make this approach cost effective and the results widely applicable. © 2001 Published by Elsevier Science B.V.

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1. Introduction

Edible mushrooms have been widely collected from the forests of the Pacific Northwest since the 1860s when European settlers began hunting for mushrooms similar to species they had collected in their homelands. Some Native American tribes harvested mushroom for various uses, but we lack evidence of widespread consumption. During the 1980s and early 1990s commercial mushroom harvesting expanded dramatically. The increased public demand for wild edible mushroom harvesting opportunities has affected all forest landowners in the Pacific Northwest, especially federal forests.

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Federal lands encompass a large portion of suitable mushroom habitat in the Pacific Northwest United States (PNW-US) an area that includes Oregon, Washington, northern California, Idaho, and western Montana. The US Department of Agriculture, Forest Service (USDA-FS) and US Department of Interior, Bureau of Land Management (USDI-BLM) manage their forests for multiple-use, including commercial forest products. Since the 1950s timber has been the major forest product, but environmental concerns have led to dramatic reductions in timber harvesting from federal lands during the 1990s and the adoption of an ecosystem management philosophy (Bormann et al., 1994; Jensen and Everett, 1994). Ecosystem management is a holistic approach to decision making that integrates biological, ecological, geophysical, silvicultural, and socioeconomic information to conserve biological diversity and maintain ecosystem functioning while meeting human needs for the sustainable production of forest products and amenities.

In response to reduced federal timber harvests, many forest workers broadened the range of commercial products that they harvested from forests. Their efforts to develop new livelihoods coincided with expanding national and international markets for speciality products, and now the harvest of nontimber forest products (NTFPs) is a widely recognized industry in the PNW-US and globally (Ciesla, 1998; Lund et al., 1998). The increased demand for opportunities to harvest NTFPs from public lands caught many managers unprepared, but the challenges they face exemplify every aspect of ecosystem management. Integration of forest fungi into ecosystem management plans is discussed in Pilz and Molina (1996). Here we review edible mushroom harvesting issues and concerns, interim regulations that managers have adopted to sustain the resource while more complete information is acquired, unique sampling challenges and considerations intrinsic to studying mushrooms, current research and monitoring activities, and a proposed format for a regional research and monitoring program.

2. Issues and concerns

More than 20 species of fungi are commercially harvested from forests of the PNW-US. Understanding their biology is essential to understanding management issues. The body or thallus of a fungus individual consists of a network of hyphae (one-cell-wide fungal filaments) or rhizomorphs (bundles of hyphae) extending into the substrate that it colonizes. Collectively, a network of hyphae is called a mycelium and a fungus individual may be referred to as a mycelial colony. Mushrooms (epigeous) and truffles (hypogeous) are the reproductive structures or sporocarps of fungi in the phyla Ascomycota and Basidiomycota. Fungi are not photosynthetic, hence they must obtain their food from organisms that are. Some edible forest fungi are saprobic, that is, they decompose organic matter. Others live symbiotically with host trees, forming structures called mycorrhizae, literally "fungus-roots". Mycorrhizal fungi colonize the fine roots of trees and also permeate the surrounding soil. The fungi absorb water and minerals that they translocate to a host tree, thus greatly extending the tree's effective root system. In return, the tree provides the fungi (often multiple species colonize a given tree's root system) with carbohydrates needed for growth and reproduction. The mycorrhizal fungi that produce edible mushrooms form a type of mycorrhizae called ectomycorrhizae, the prefix ecto-referring to a fungal sheath or mantle that forms around the root tip. Smith and Read (1997) for a complete review of mycorrhizal symbioses. The most important commercially harvested forest mushrooms in the PNW-US are listed in Table 1. With the exception of morels, all of them are obligately ectomycorrhizal. This symbiotic association between ectomycorrhizal fungi and forest trees has many implications for managing forests to sustain edible mushroom productivity.

The greatly increased harvest of forest mushrooms raises many issues and concerns among forest managers and the general public (Pilz and Molina, 1996; Liegel, 1998) especially within special interest groups, such as mushroom clubs, mycological societies, and conservation organizations. These issues and concerns can be grouped into five categories: (1) mushroom productivity; (2) mushroom harvesting effects; (3) forest management practices; (4) biology, ecology, and ecosystem functions of the fungi; and (5) people management.

2.1. Mushroom productivity

Questions about sustainability of mushroom crops must start with inventories of productivity. We define

Table 1
Important internationally-marketed wild edible mushrooms harvested from the forests of the PNW-US and typical prices paid to harvesters from 1992 to 1999

Local common names	Scientific name	Price per kg[a] (US$)
American or white matsutake, pine or tanoak mushroom	*T. magnivelare* (Peck) Redhead	33
Morels	Various *Morchella* species	11
Pacific golden chanterelle	*Cantharellus formosus* Corner (previously considered *C. cibarius* Fr., Redhead et al., 1997)	6
White chanterelle	*Cantharellus subalbidus* Smith and Morse	5
Hedgehogs	*Hydnum repandum* L. ex Fr., *Hydnum umbilicatum* Peck	7
King bolete	*Boletus edulis* Bull.:Fr.	11
Oregon white truffle	*Tuber gibbosum* Harkn.	50
Oregon black truffle	*Leucangium carthusianum* (Tul. and C. Tul.)	100

[a] These are conservative estimates of average prices (all grades throughout the season) paid to harvesters for fresh product during the years 1992–1999. Sources include discussions with harvesters and buyers, unpublished data, and cited literature. Schlosser and Blatner (1995) and Blatner and Alexander (1998) for buyer survey reports.

biological productivity as the total number or weight of mushrooms or truffles that fruit per unit area during the course of a fruiting season (although the term ‘‘fruiting’’ technically applies to flowering plants, it is commonly used in mycological literature to describe the formation of sporocarps). Commercial productivity is the amount collectors actually harvest in a given area during a season. Seasonal totals are necessary because many edible species will fruit repeatedly or continuously during a period of several months of favorable weather each year, therefore estimates based on one-time sampling would represent an unknown percentage of the seasonal crop. Repeated inventories (monitoring) over multiple fruiting seasons are required to adequately estimate habitat or site productivity, because there is substantial annual variation, often weather related, in productivity among fruiting seasons (Vogt et al., 1992; Liegel, 1998; Pilz et al., 1999). The high annual variability in production also necessitates long-term monitoring to detect statistically significant trends in productivity. Typical productivity of eight commercially important edible fungi collected in the PNW-US are presented in Table 2.

Predicting and enhancing productivity also interests many people. Prediction of annual fruiting often entails efforts to correlate weather patterns with fruiting (Vogt et al., 1992). Commercial harvesters report that summer rainfall is a salient factor influencing where, and in what quantity, fall-fruiting mushrooms will occur. Other harvesters have postulated that patterns of chilling and warming are important for inducing and maintaining flushes of fruiting (Pilz et al., 1999). Few researchers or harvesters claim an understanding of multi-year fruiting cycles or an ability to predict fruiting more than a few weeks in advance, therefore managers who wish to prepare for harvest seasons several months in advance must rely on guesswork.

Attempts to increase mushroom productivity include modifying the microenvironment of growing mushrooms to enhance their size or quality, irrigation to increase the number or weight of mushrooms, spreading spores or planting inoculated trees to establish new fungal colonies, or silvicultural manipulations to improve fruiting conditions or the health of mycorrhizal host trees. Asian researchers have explored these techniques as they apply to the Japanese matsutake (*Tricholoma matsutake* (S. Ito et Imai) Sing.) (Hosford et al., 1997; Ishikawa and Tekeuchi, 1970; Koo and Bilek, 1998). Silvicultural manipulations to enhance production of the American matsutake (*Tricholoma magnivelare* (Peck) Redhead) are described in Weigand (1998). The effectiveness and practicality of these methods vary and, to date, they

Table 2
Forest habitats that support commercial harvesting and typical biological productivity (average (range)) for eight species or species groups of commercially harvested fungi in the PNW-US

Mushroom	Commercial harvest habitats[a]	Mushrooms per ha[b]	Kilograms per ha[b] (fresh weight)
American matsutake	Well drained or infertile soils (i.e. pumice or sand). Broad host and geographic ranges (Hosford et al., 1997)	150 (100–500) (Pilz et al., 1999)	4.5 (3–15) (Pilz et al., 1999)
Morels	Forests affected by fire, tree mortality, soil disturbance, and flooding. Various species and habitats	500 (200–1200) (Pilz, unpublished data, 1995–1996)	2.5 (1–6) (Pilz, unpublished data, 1995–1996)
Pacific golden chanterelles	Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests, especially west of the Cascade Range	750 (300–3000) (Liegel, 1998)	5 (2–20) (Liegel, 1998)
White chanterelles	White chanterelles overlap the habitat of Pacific golden chanterelles but also occur at higher elevations with *Abies* species	235 (100–500)[c] (Pilz, unpublished data, 1996–1998)	No information
Hedgehogs	Same as golden chanterelles, peak of fruiting about a month later than chanterelles	No information	No information
King bolete	Often with Sitka spruce (*Picea sitchensis* (Bong.) Carr.) on the coast and Englemann spruce (*Picea engelmannii* Parry ex Engelm.) in the Cascade Range	No information	No information
Oregon white truffle	Douglas-fir in low elevation valley margins	No information	10 (5–30) (Lefevre, unpublished data, 1990s)[d]
Oregon black truffle	Douglas-fir in low elevation valley margins	No information	7 (5–10) (Lefevre, unpublished data, 1990s)[d]

[a] Distributions are not restricted to these habitats or host trees. Arora (1986) or other field guides for more complete host, habitat, and distribution descriptions.

[b] Typical biological productivity (average and (range)) found in habitats that support commercial harvesting. Sources include discussions with harvesters and buyers, unpublished data, and cited literature. The low end of each range is adjusted upwards to reflect minimum productivity levels that attract commercial harvesting and the high end is the maximum recorded in our surveys. Harvesters will visit known, discrete mushroom patches in forest stands that are otherwise less productive overall than shown here.

[c] Measured on a site where golden chanterelles and matsutake also fruit abundantly.

[d] Charles Lefevre, Department of Forest Science, Oregon State University, Corvallis, OR.

have not been widely applied. Silvicultural practices (Section 2.3) hold the greatest promise for ensuring continuous availability of optimal habitat through time as forest conditions change.

2.2. Mushroom harvesting effects

As commercial mushroom harvesting expanded, one of the first concerns was whether greatly increased harvesting would reduce subsequent fruiting. There are several aspects to this question.

Does harvesting, per se, diminish subsequent fruiting? Insofar as mushrooms are the reproductive structures of mycelial colonies, the picking of mushrooms has often been compared to picking apples from a tree; that is, the organism itself is thought to be only minimally impacted. Indeed, two studies with chanterelles indicate that, in the short term and on small scales, this is likely true. The Oregon Mycological Society Chanterelle Study (Norvell, 1995) examined harvesting per se and methods of harvest (plucking or cutting the mushrooms); after 10 years, no declines in productivity were noted. Egli et al. (1990) report that in Switzerland, 10 years of harvesting had no significant effect on the continued fruiting of 15 different ectomycorrhizal mushroom species. Trampling, however, dramatically reduced chanterelle (*Cantharellus lutescens* Fr.) fruiting for a year. This impact was attributed to damaged sporocarp primordia, because fruiting returned to previous levels the following year when trampling stopped.

Moving woody debris on the forest floor or raking forest litter layers to search for young mushrooms are additional concerns, they occur most often when harvesters search for new mushroom patches in areas they have not previously visited. These activities are predominantly associated with matsutake and truffle harvesting. Matsutake are far more valuable when they are young because they arrive at Japanese markets in better condition than do older specimens. Immature matsutake usually have not yet emerged from litter layers or spread their spores. Truffles fruit underground, rarely appearing on the surface. Raking litter layers to find matsutake or truffles can disturb the mycelium or disrupt the humid litter layer microenvironment that allows initial development of the sporocarp primordia. During the initial expansion of commercial harvesting, many recreational harvesters complained that their favorite patches had been destroyed by unscrupulous commercial harvesters who raked large areas. These claims often were exaggerated, or the damage localized, but resentment about raking damage was heightened by the increased competition that recreational harvesters experienced in locations they had traditionally visited. Unpublished data from recent research with American matsutake in the Oregon Coast Dunes and Cascade Mountain Range suggests that raking can decrease subsequent production for several years, but that the severity and duration of raking impacts can be lessened by replacing the removed litter layers. Experienced harvesters of matsutake can find young specimens by visiting known patches and observing or feeling for lumps in the forest floor. Truffle hunters could train dogs to sniff out ripe truffles, although few in the PNW-US follow this practice so commonly used to harvest truffles in Europe.

Many harvesters, both recreational and commercial, actively attempt to improve production and create new mushroom patches by spreading the caps (with spores) of mushrooms that are too old to sell or eat (Liegel, 1998). Some harvesters speculate that simply carrying mushrooms around during collection helps to distribute spores. It is even possible that harvesters are distributing spores with their shoes. No scientific evidence exists regarding the establishment of new mycelial colonies or improved sporocarp production from these modes of spore dispersal, but many harvesters claim success or believe it does no harm to try.

Although it appears that harvesting is unlikely to harm ectomycorrhizal mushroom species in the short term, the long-term impacts of widespread intensive harvesting are not known. Concern might be greater for saprobic species that colonize coarse woody debris than for ectomycorrhizal species. Examples of edible saprobic mushrooms from the PNW-US include chicken of the woods or sulfur shelf (*Laetiporus sulphureus* (Bull. ex Fr.) Murr.), lion's mane (*Hericium abietis* (Weir ex Hubert) K. Harrison), angel wings (*Pleurotus porrigens* (Pers. ex Fr.) Kummer), and the cauliflower mushroom (*Sparassis crispa* Wülf. ex Fr.). Several saprobic medicinal species are also collected commercially, namely *Ganoderma tsugae* Murr. and *Ganoderma oregonense* Murr. (Hobbs, 1995), and more species are likely to be identified. All of these wood decay fungi are less common and fruit less abundantly than ectomycorrhizal species. They also might be more dependent on repeatedly colonizing new substrates than ectomycorrhizal species, because the wood they decompose could be depleted of usable nutrients within a decade or two, while ectomycorrhizal species might persist for the life-time of their arboreal symbionts or longer if compatible host trees regenerate quickly after a stand replacement event. If wood decay species are dependent on regular spore dispersal for colonizing new substrates, or if they have fewer opportunities to reproduce due to timber harvests that do not leave coarse woody debris, then their reproduction might be hampered by widespread harvesting of their sporocarps. Saprobic species are easier to propagate than ectomycorrhizal species and increased cultivation could ameliorate concerns about harvesting wild populations (Stamets, 1993).

2.3. Effects of forest management practices

Forest management activities affect habitat for edible mushrooms in many ways. Effects differ by the lifestyle and reproductive strategies of each fungal species, the forest types they inhabit, and management goals and activities associated with each forest type. Forest practices that can affect the occurrence, productivity and reproduction of mushrooms include silvicultural practices, logging methods, tree species selection, fire, fertilization, pesticide use, and grazing.

Clearcut harvesting, for instance, interrupts the fruiting of most edible ectomycorrhizal fungi for a decade or more while they become reestablished on new tree hosts and the trees grow large enough to provide the fungi with sufficient carbohydrates or appropriate metabolites to support fruiting. By contrast, some of the tree hosts for ectomycorrhizal fungi are usually retained when stands are thinned. Thinning intensity influences to what degree and for how long fruiting is affected. Thinning also influences fruiting conditions by allowing rain and sunshine to penetrate the forest canopy more easily than in nonthinned stands, resulting in more rapid wetting and drying of the forest floor. Unpublished data from a thinning study on the Willamette National Forest in Oregon shows that heavy thinning (from 615 to 125 trees per ha) of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) reduces chanterelle fruiting by 90% in the following year. We do not yet know how quickly mushroom productivity will rebound as remaining trees reoccupy the site, but recovery rates are needed to understand the effects of thinning on total mushroom production during a timber rotation. Frequent light (few trees removed) thinning during a timber rotation might maintain mushroom productivity better than infrequent heavy thinning because the mycorrhizal host trees would retain nearly full photosynthetic occupancy of the site. Conversely (depending on logging systems) frequent light thinning could also result in more soil compaction than infrequent heavy thinning, thus impairing mycelial growth of the fungi in the soil and reducing long-term mushroom production (Amaranthus et al., 1996).

Ground-based logging systems cause more soil compaction than cable or helicopter suspension, or logging on top of snow, hence are more likely to diminish long-term mushroom productivity. Ground-based logging systems also cause more disruption of litter layers than suspension systems, potentially resulting in short-term effects similar to raking. The long-term effects of this disturbance on microenvironments for mushroom formation and growth are not known. Removal of logging slash by yarding, piling, or burning makes thinned forests easier and safer to walk through and mushrooms easier to find, but reduces organic matter on the forest floor. Reducing accumulations of litter or removing grassy sod can stimulate fruiting of some ectomycorrhizal fungi under certain circumstances (Hosford et al., 1997; Barr and Kuyper, 1993).

Ectomycorrhizal fungi exhibit varying degrees of specificity for host tree genera (Molina et al., 1992), therefore tree species selection during planting or thinning influences mushroom occurrence and production. PNW-US tree genera, such as *Abies*, *Alnus*, *Arbutus*, *Castanopsis*, *Larix*, *Lithocarpus*, *Populus*, *Picea*, *Pinus*, *Pseudotsuga*, *Quercus*, and *Tsuga* form ectomycorrhizae with fungi that produce sporocarps, whereas other genera, such as *Acer*, *Calocedrus*, *Chamaecyparis*, *Sequoia*, *Sequoiadendron*, *Taxus*, and *Thuja* form a different type of mycorrhizae (arbuscular mycorrhizae) with fungi that reproduce primarily with individual spores in the soil rather than sporocarps. Stand composition and dominance of ectomycorrhizal host trees relative to arbuscular mycorrhizal trees likely affects the quantity of carbohydrates available to ectomycorrhizal fungi for fruiting.

Fires that kill trees are known to shift the composition of ectomycorrhizal fungal communities (Visser, 1995; Horton et al., 1998; Barr et al., 1999). When soil litter layers are consumed, the abundance of ectomycorrhizae at the interface of organic and mineral soil layers is reduced (Stendell et al., 1999) but the effects of less intense fires are not as dramatic (Jonsson et al., 1999). Tree seedlings that establish in burned areas can be colonized by ectomycorrhizal fungi through persistent spores in the soil (Horton et al., 1998) wind blown spores, or residual mycelia associated with surviving trees or brush species (Amaranthus and Perry, 1994). Little is known, however, about the influence of forest fires on the productivity of edible ectomycorrhizal mushrooms other than the fact that stand replacement fires inhibit fruiting until a new stand develops.

By contrast, some species of morels fruit prolifically for the first year or two following forest fires. Other morel species fruit annually at moderate levels in nondisturbed forests, but will produce large crops when a forest is logged or killed by insect infestations. Most morels are considered saprobic because they grow rapidly in pure culture and can complete their life-cycle without host trees, but some species can form mycorrhizae (Buscot, 1994; Dahlstrom et al., 2001). Thinning and prescribed burning are increasingly being used in the montane forests of the intermountain west to reduce wildfire danger, curtail potential insect infestations, and produce timber. Opportunities to increase the size, regularity, or frequency of morel crops might be enhanced if managers better understood how each morel species responded to various disturbances.

Evidence from Europe suggests that nitrogen deposition from air pollution inhibits the growth of some ectomycorrhizal fungi and reduces the productivity of edible ectomycorrhizal mushrooms (Arnolds, 1991). This suggests that nitrogen fertilization of forest soils has the potential to reduce edible mushroom production. In general, trees allocate a lesser portion of photosynthates to roots and mycorrhizae on fertile sites than on infertile sites (Perry, 1994; Waring and Running, 1998), but the total quantity of carbohydrates available to edible mycorrhizal fungi for fruiting also depends on many other factors.

We know of no studies investigating the relations between pesticide applications and edible forest mushroom production or consumption. Herbicides are sometimes used to release newly planted conifers from competition by broadleaf trees and shrubs, but commercially harvested ectomycorrhizal mushrooms usually begin fruiting 5–15 years later as the conifer stand develops, so that only persistent compounds or recent drift from nearby areas are potential hazards. Aerial broadcasting of chemical insecticides would pose a greater concern for human consumption of mushrooms, especially if applied during the mushroom fruiting season. Given that forest mushrooms are often sold as natural, wild, or pure products, obvious marketing implications exist for the desirability and sales potential of mushrooms collected from forests where pesticides are used. Currently, the source of wild edible mushrooms is rarely identified in retail sales, although this could change as certification of NTFPs becomes more common.

We are not aware of any research investigating the influence of grazing on edible mushroom production, but if compaction becomes severe, hyphal growth near the soil surface could be inhibited. In the PNW-US, grazing occurs in drier forests where few edible mushrooms, other than morels, are commercially harvested.

2.4. Biology, ecology, and ecosystem functions of fungi

Given the numerous mushroom species harvested, the diversity of forest types they inhabit, and the wide range of silvicultural systems that foresters use, many opportunities remain to improve management of mushrooms through better understanding of their biology, ecology, and ecosystem functions. Additional information is needed about sexual and asexual modes of reproduction, spore dispersal mechanisms, and factors influencing colony establishment, health, growth, senescence, and death. Fungi have complex breeding patterns that complicate their population dynamics. Forest conditions that facilitate reproduction differ on time scales from days (favorable weather) to centuries (episodic disturbance events such as forest fires that create new habitats). Recent research (Dahlberg and Stenlid, 1994; de la Bastide et al., 1994; Bonello et al., 1998) is just beginning to characterize ectomycorrhizal colony sizes, longevity, and population structures, but species-specific investigations are needed to understand how colonies and populations of edible mushrooms will respond to forest management activities. Forest fungi, including edible mushrooms, contribute to healthy forests and food webs in ways too numerous to discuss here (Carroll and Wicklow, 1992; Molina et al., 1999; Read et al., 1992), and managers should consider these ecosystem roles and functions when developing mushroom harvest regulations or management plans.

2.5. People management

Although forests and fungi evolved for eons without human influence, people have played an integral role in shaping forest ecosystems since we began burning and clearing forests. Indeed, many edible mushroom species are found most abundantly in burned or young forests. Social, cultural, and economic values continue to determine forest use and management and are integral to addressing mushroom harvesting issues.

The extensive cultural diversity of mushroom harvesters in the PNW-US is a salient example (Arora, 1999). Harvester groups include Native Americans, descendents of European settlers, and recent Latin American and southeast Asian immigrants (Richards and Creasy, 1996; Liegel, 1998). Among and within each of these broad harvester categories are considerable differences in the way groups or individuals view their interactions with the forest and with each other. These differences are frequently rooted in homeland cultural traditions and fundamental concepts, such as ownership, rights, freedoms, security, livelihoods, and spiritual connections with nature. Income is only one of many motivations for commercial harvesting; other reasons include independence (Sullivan, 1998), the excitement of the hunt, beautiful natural surroundings, and social activities in camps. Differences between recreational and commercial harvesters also have political and policy ramifications (McLain et al., 1998).

On public lands, forest managers need to be sensitive to cultural nuances and differences if they are to simultaneously minimize conflicts and ensure resource conservation (Pilz et al., 1999). Some of the issues they face with all users include camping and sanitation facilities, traffic safety and road closures, fire danger, weapons, littering, wildlife disturbance, pathogen dispersal, impacts on other sensitive species or archeological sites, and conflicts among user groups, such as recreational harvesters, commercial harvesters, and big game hunters.

Complete ecosystem management plans must incorporate economic information too. Many forest-associated rural communities have suffered economically and socially from reductions of timber harvesting on federal lands. Development of NTFP enterprises can play a role in ameliorating these impacts, especially if companies can depend on reliable resource supplies from federal lands to support local processing and value-added activities.

Supplies are not the only salient issue, however. The volatility of international commerce in edible forest mushrooms (Blatner and Alexander, 1998) results in unpredictable demand for mushrooms. For example, the vast majority of matsutake are sold to Japan, but the mushroom commands such high prices that it is considered a luxury item. Economic cycles or changes in monetary exchange rates can considerably alter prices paid to harvesters and their resulting incentive to collect. Harvest levels in other countries also vary from year to year, so global competition is unpredictable for all internationally-marketed species (predominantly those listed in Table 1). Managers are well-advised to develop programs and regulations that accommodate fluctuations in demand. Likewise, local NTFP harvesters and industries can stabilize their income by diversifying the products they harvest or market.

As another example of economic issues, the value of annual mushroom harvesting has been used by conservation organizations as an argument for appealing timber sales. Although clearcut harvesting will arrest the fruiting of ectomycorrhizal mushrooms for a decade or more and thinning can suppress fruiting, mushroom harvesting and timber growing can be compatible activities during much of a timber rotation. We lack adequate information for accurate assessments of discounted present net worth for mushrooms, but several illustrative scenarios comparing timber and mushroom values have been developed (Liegel, 1998; Pilz et al., 1999) Using these methods, managers can modify assumptions or insert site-specific data to analyze the economic consequences of local decisions. Importantly, the harvest of mushrooms benefits different individuals, companies, and customers than does timber harvesting, and many other NTFPs and amenities are derived from any given forest.

3. Harvest regulations and resource conservation

Because federal forest lands are publicly owned, all citizens and companies are entitled to equitable access to commercial resources. Competitive auctions are typically used for timber sales or products, such as decorative boughs. This approach is problematic with mushrooms, however, because quantities are difficult to predict and individuals, rather than companies, do the harvesting. For these reasons, most National Forests (USDA-FS) sell commercial harvest permits to individuals at set prices. Permits usually allow unlimited collection during a specified season because rules limiting the quantities collected would be difficult to enforce. In some cases the number of permits are restricted. The Winema and Deschutes National Forests in Oregon set the number of available permits at the capacity of nearby designated campgrounds (Pilz et al., 1999). Matsutake fruiting in the Oregon Dunes National Recreation Area is fairly reliable and harvesters can estimate how much they will be able to collect in a season thus, a limited number of permits are issued by sealed bid auction. The USDI-BLM sells contracts for mushroom harvesting. Contracts stipulate the species that can be harvested, maximum quantities for each, specified areas for harvesting, and a limited time frame depending on the amount sold and number of anticipated harvesters. The per weight value of each species is determined by contacting local mushroom buying sheds. Contract prices are set at the maximum of either 10% of the wholesale value or the calculated results of a formula that includes items, such as shed price, purchaser's potential profit and risk, labor costs, transportation, and road maintenance. Some districts have minimum contract prices or quantities. All these methods have advantages and disadvantages for both managers and harvesters, but equity and compliance are improving as procedures are refined by experience and communication (Liegel, 1998).

A variety of measures have been adopted on federal lands to ensure conservation of the resource until more is known about the long-term impacts of intensive commercial mushroom harvesting. For instance, in the Winema and Deschutes National Forests, the commercial matsutake harvest season begins in mid-September, after the first hard frost. Matsutake that fruit earlier in the season are often riddled with insect larvae and have little commercial value. This arrangement allows the first flush to disseminate spores without greatly reducing the potential value of the commercial crop (Pilz et al., 1999).

Most federal forests also have areas off-limits to commercial activities; these include wilderness areas, research natural areas, mushroom research areas, designated recreation areas, or other areas of special environmental concern. All National Parks (USDI) in the region prohibit commercial mushroom harvesting. Some industrial and nonindustrial private forest landowners prohibit or restrict commercial harvesting on their properties. Even in areas where commercial activities are allowed, managers will sometimes rotate areas where collection is permitted to provide fallow periods. Adherence to various harvest restrictions is not uniform; compliance is influenced by mushroom prices, access difficulty, harvester attitudes about regulations, and enforcement.

Mushroom commerce is a global enterprise, and potential impacts concern forest managers wherever harvesting occurs. Regulations often are tailored to local land tenure (Hardin, 1968; Bromely, 1991; Lund et al., 1998) and traditions concerning access to harvesting opportunities. For example, Bandala et al. (1997) describe communally owned matsutake habitat in Oaxaca, Mexico where native tribes participate in matsutake harvesting, marketing, monitoring, conservation, and forest management. In Sweden and elsewhere in Europe there is a long tradition of access to private property for collecting edibles, such as mushrooms. It is called ''Allemansrätten'', literally translated as every man's right. Egli et al. (1995) has proposed standardizing regulations in Switzerland because each canton stipulates differing days of the week when mushrooms may be collected and individuals raid each other's cantons when they are prohibited from collecting locally.

Many of the issues, concerns, and regulatory approaches we have discussed also apply to the harvest of other NTFPs and affirm the utility of comprehensive and integrative approaches to management (Molina et al., 1997). Monitoring and research are essential components of management plans if decisions and regulations are to be improved over time. However, fungi in general and ectomycorrhizal mushrooms in particular pose some unique challenges for research and monitoring.

4. Sampling challenges and considerations

Most fungi are difficult to study in their native habitats because their thallus is microscopic, very delicate, diffuse, embedded in the substrate they have colonized, and intermixed with other soil fungi and microorganisms. Estimates of edible mushroom productivity do not necessarily reflect the extent or dominance of a species thallus in the soil or the number of ectomycorrhizae it forms relative to other species (Gardes and Bruns, 1996; Mehmann et al., 1995). Scientists have quantified morphological types of ectomycorrhizae extracted from soil cores, but until recently the fungal symbionts were identified only if the mycelium was distinctive. With the advent of molecular techniques of DNA analysis, fungi can be identified from ectomycorrhizal root tips (Goodman et al., 1996; Bruns et al., 1998) a development that is rapidly advancing ecological studies of ectomycorrhizal fungi.

Because weather patterns can cause large annual variations in mushroom productivity, many years of sampling are needed to estimate the average or potential productivity of a site or habitat over time (Luoma and Frenkel, 1991). Potential long-term productivity might be more precisely estimated if a covariate, such as the percentage of ectomycorrhizae colonized by the fungal species of interest, was also estimated. Processing individual root tips for genetic analysis is time consuming and labor intensive but, if marker systems using monoclonal antibodies were developed, quick counts of how many ectomycorrhizae were formed by a targeted species of fungus could be obtained from soil cores. Currently estimates of mushroom productivity are still derived from sampling the sporocarps.

Repeatedly-visited plots with fixed boundaries must be used to obtain total sporocarp production during the course of a fruiting season, because mushrooms recorded during a previous sampling visit must be marked or collected to avoid repeat sampling during subsequent visits. Selecting an optimal plot size for multi-year sampling can be a challenge. Mushrooms frequently fruit in spatially clustered patterns, hence fixed plot sampling designs can result in many plots with zero values unless the plots are large. Plots that are large enough to prevent this problem during years of poor fruiting may result in an unnecessarily large number of mushrooms sampled in years of good fruiting (Liegel, 1998).

Trampling of the forest floor by field crews is an important consideration for selecting plot shapes. Long, narrow (2 m wide) strip plots allow field personnel to reach in from either side to sample without actually walking on the plot. Mushrooms are often well camouflaged by forest floor litter or brush, and searching for them from opposite sides of a strip plot might also reduce detection error.

Recently developed methods of adaptive sampling (Thompson and Seber, 1996) have been suggested as a way to improve sampling efficiency for clustered populations, but the approach has several potential drawbacks when applied to the sampling of edible mushrooms. Adaptive sampling uses a set of predefined rules for adjacent subsampling when members of a clustered population are encountered, and then adjusts for the nonrandom design with appropriate analyses. Because mushrooms need to be sampled repeatedly during the course of a fruiting season, this approach would result in different areas being sampled during each sampling interval, and the data would not be directly cumulative for a seasonal total. Trampling also could be a problem because crews might walk on areas to be subsampled before they realize where the boundaries of subsample plots will be located. Subsampling is repeated until members of the population are no longer encountered, but this requires careful marking of areas already sampled, a difficult task on steep slopes or in areas with abundant brush. Last, field crews must consistently and carefully apply the sampling protocols to obtain reliable results. Training volunteers to use complicated sampling protocols could be cost-prohibitive because field workers should be familiar with sampling theory to respond appropriately to unanticipated circumstances.

To be properly interpreted, reports of mushroom productivity must be explicit in describing sampling methods, sampling intervals, and minimum size criteria. Unlike trees or other vegetation, mushrooms appear, change in size, and disappear rapidly. Sporocarp longevity of each species constrains the maximum time between sampling rounds. As an example, morels are relatively short-lived and weekly sampling is appropriate, whereas chanterelles are relatively long-lived and intervals of up to 3 weeks are adequate to sample all the sporocarps produced.

Investigators must decide whether to pick the mushrooms that are sampled. Counts are quick and easy to obtain, but if the mushrooms are not picked, then they must be marked to avoid resampling during the next visit. Flat, colored toothpicks are inexpensive, clearly visible, biodegradable, and do not split the cap of the mushroom. Weight productivity is simple to measure if the mushrooms are picked, but if the study objectives preclude picking, then weight must be estimated from mushroom dimensions. Fresh and dry weights can be adequately estimated from cap diameters in spite of variations in moisture content and irregular cap shapes (Liegel, 1998; Pilz et al., 1999). Because mushrooms vary daily in moisture content, dry weight is a more precise measure of productivity, however, drying and reweighing are time consuming and fresh weight productivity is often the variable of greatest interest anyway.

Estimates of weight productivity depend on decisions about when to harvest or measure a growing mushroom. If a daily sampling interval was selected and mushrooms were sampled when they appeared to reach maximum size, the productivity estimates might well be higher than if all mushrooms above a given minimum size are sampled at wider intervals.

Mushroom studies and inventories are further complicated by wildlife and human harvesters that seek and consume edible mushrooms, often avidly. Short of fencing sample plots, little can be done to prevent wildlife from eating mushrooms. Investigators in the PNW-US have tried a variety of methods to preclude humans from interfering with research or monitoring plots, including locating the plots in obscure or remote areas, posting signs, visiting the plots often, or publicizing and enforcing no-pick regulations. These approaches work best in combination, but often the plots are inadvertently placed in someones favorite mushroom patch. Sometimes this results in aggrieved harvesters who then ignore the no-pick signs or intentionally harvest or sabotage sample plots. One of the best solutions to this dilemma is to enlist the cooperation of responsible harvesters, thus averting ill will by providing them with ownership in the project. Harvesters are keenly observant and readily detect signs that others have harvested in an area, information that is useful for interpreting data.

Measuring commercial productivity can be easier than estimating biological productivity. The simplest approach is to give a cooperating harvester or group of harvesters exclusive access or rights to harvest a particular area in exchange for information about how much they harvested. Interpretation of commercial productivity data should account for the varied levels of harvest intensity that result during or between seasons due to mushroom prices or other factors that motivate harvesters.

Sampling designs must consider whether sites, habitats, watersheds, ownerships, or other categories are to be sampled. If estimating edible mushroom productivity on a particular site is the goal, then all areas within the site should theoretically have an equal chance of being sampled and plots must be located accordingly. By contrast, if the intent is to characterize the productivity of a habitat type then, during plot establishment, areas of inappropriate habitat for that mushroom species should be excluded. If estimating productivity across a watershed or area of land ownership is the objective, then Geographic Information Systems (GIS) can be used to extrapolate habitat estimates. Simplifying assumptions would be required for this approach because habitat types and their suitability for mushroom production usually vary and intergrade. Commercial harvest potential of GIS-mapped biological productivity could be modified by factors that influence harvester behavior, such as distance from roads or slope steepness.

5. Current research and monitoring in the PNW-US

Abundant mushroom habitat, a diversity of forest landowners, extensive mycological expertise, and avid public interest have provided a broad base of support for edible mushroom research in the PNW-US. University researchers and mycological societies have undertaken ecological (Largent and Sime, 1995; Hosford et al., 1997), harvest impact (Norvell, 1995), taxonomic (Redhead et al., 1997), sociological (Richards and Creasy, 1996; McLain et al., 1998; Liegel, 1998) and economic (Schlosser and Blatner, 1995; Blatner and Alexander, 1998) studies. Scientists with the Pacific Northwest Research Station (a branch of the USDA-FS) and Oregon State University (OSU) have conducted productivity (Liegel, 1998; Pilz et al., 1999), resource valuation (Liegel, 1998; Pilz et al., 1999), and forest management (Liegel, 1998; Weigand, 1998) research on edible fungi. Ongoing research (Pilz and Molina, 1996) includes the impact of raking soil litter layers to find young matsutake; the effectiveness of silvicultural treatments designed to enhance matsutake fruiting; how wildfire and other disturbances affect morel production; how thinning of young stands influences subsequent chanterelle production; revised taxonomic distinctions among species of chanterelles and morels; and describing the population genetics of morels, chanterelles, and matsutake.

Research and monitoring projects throughout the region are often sponsored by, or conducted in cooperation with, various USDA-FS and USDI-BLM districts because their managers have concerns about the impacts and sustainability of intensive mushroom harvesting in their forests. Developing practical, cost effective, and statistically valid sampling procedures for edible forest mushrooms was a goal common to all the productivity studies. Tested sampling procedures will provide a reliable and uniform foundation for long-term regional monitoring of harvest sustainability and the influence of forest management activities on productivity.

6. Regional research and monitoring in the future

Concern about the sustainability of large-scale commercial mushroom harvesting in the Pacific Northwest is partly based on declining crops in traditionally harvested areas of Europe and Japan (Arnolds, 1991; Arnolds, 1995; Hosford et al., 1997). Air pollution, climate change, industrial timber management, native and exotic diseases and pests, conversion of forest lands to other uses, road building, and intensive mushroom harvesting all have the potential to affect habitat and long-term production.

To address these concerns, we have outlined a collaborative regional research and monitoring program based on tested sampling protocols (Pilz and Molina, 1998). One component will consist of measuring commercial productivity on highly productive sites by cooperating with selected commercial harvesters to record what they collect in discrete areas where they have exclusive access. A second component entails estimating productivity in natural areas where neither mushroom nor timber harvesting occurs (hopefully with field assistance from mycological societies); these sites will be used to discern trends associated with pollution, climate change or habitat degradation and to interpret trends noted in commercially harvested areas. Both components require commitments by participating landowners to long-term, albeit frugal monitoring activities. A third component will create predictive models relating edible mushroom occurrence and productivity to habitat factors, such as site fertility, climate, or plant association, and silvicultural characteristics, such as stand age, density, growth rates, and species composition. This modeling component is a short-term project (approximately 7 years) and should help managers predict how their silvicultural activities can affect edible mushroom crops over long periods as the mosaic of forest conditions shifts across the landscape. Although edible mushrooms seem to be a resilient resource as long as they have appropriate habitat, the limits to their sustainable use remain unknown. Research and monitoring are fundamental to determining those limits and improving resource management guidelines.

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