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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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45 Federal lands encompass a large portion of suitable
 46 mushroom habitat in the Pacific Northwest United
 47 States (PNW-US) an area that includes Oregon,
 48 Washington, northern California, Idaho, and western
 49 Montana. The US Department of Agriculture, Forest
 50 Service (USDA-FS) and US Department of Interior,
 51 Bureau of Land Management (USDI-BLM) manage
 52 their forests for multiple-use, including commercial
 53 forest products. Since the 1950s timber has been the
 54 major forest product, but environmental concerns have
 55 led to dramatic reductions in timber harvesting from
 56 federal lands during the 1990s and the adoption of an
 57 ecosystem management philosophy (Bormann et al.,
 58 1994; Jensen and Everett, 1994). Ecosystem manage-
 59 ment is a holistic approach to decision making that
 60 integrates biological, ecological, geophysical, silvi-
 61 cultural, and socioeconomic information to conserve
 62 biological diversity and maintain ecosystem function-
 63 ing while meeting human needs for the sustainable
 64 production of forest products and amenities.

65 In response to reduced federal timber harvests, many
 66 forest workers broadened the range of commercial
 67 products that they harvested from forests. Their efforts
 68 to develop new livelihoods coincided with expanding
 69 national and international markets for speciality pro-
 70 ducts, and now the harvest of nontimber forest products
 71 (NTFPs) is a widely recognized industry in the PNW-
 72 US and globally (Ciesla, 1998; Lund et al., 1998). The
 73 increased demand for opportunities to harvest NTFPs
 74 from public lands caught many managers unprepared,
 75 but the challenges they face exemplify every aspect of
 76 ecosystem management. Integration of forest fungi into
 77 ecosystem management plans is discussed in Pilz and
 78 Molina (1996). Here we review edible mushroom
 79 harvesting issues and concerns, interim regulations that
 80 managers have adopted to sustain the resource while
 81 more complete information is acquired, unique sam-
 82 pling challenges and considerations intrinsic to study-
 83 ing mushrooms, current research and monitoring
 84 activities, and a proposed format for a regional research
 85 and monitoring program.

86 2. Issues and concerns

87 More than 20 species of fungi are commercially
 88 harvested from forests of the PNW-US. Understanding
 89 their biology is essential to understanding manage-

ment issues. The body or thallus of a fungus individual 90
 consists of a network of hyphae (one-cell-wide fungal 91
 filaments) or rhizomorphs (bundles of hyphae) extend- 92
 ing into the substrate that it colonizes. Collectively, a 93
 network of hyphae is called a mycelium and a fungus 94
 individual may be referred to as a mycelial colony. 95
 Mushrooms (epigeous) and truffles (hypogeous) are the 96
 reproductive structures or sporocarps of fungi in the 97
 phyla Ascomycota and Basidiomycota. Fungi are not 98
 photosynthetic, hence they must obtain their food from 99
 organisms that are. Some edible forest fungi are sapro- 100
 bic, that is, they decompose organic matter. Others live 101
 symbiotically with host trees, forming structures called 102
 mycorrhizae, literally “fungus-roots”. Mycorrhizal 103
 fungi colonize the fine roots of trees and also permeate 104
 the surrounding soil. The fungi absorb water and 105
 minerals that they translocate to a host tree, thus greatly 106
 extending the tree’s effective root system. In return, the 107
 tree provides the fungi (often multiple species colonize 108
 a given tree’s root system) with carbohydrates needed 109
 for growth and reproduction. The mycorrhizal fungi 110
 that produce edible mushrooms form a type of mycor- 111
 rhizae called ectomycorrhizae, the prefix ecto-referring 112
 to a fungal sheath or mantle that forms around the root 113
 tip. Smith and Read (1997) for a complete review of 114
 mycorrhizal symbioses. The most important commer- 115
 cially harvested forest mushrooms in the PNW-US are 116
 listed in Table 1. With the exception of morels, all of 117
 them are obligately ectomycorrhizal. This symbiotic 118
 association between ectomycorrhizal fungi and forest 119
 trees has many implications for managing forests to 120
 sustain edible mushroom productivity. 121

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

2.1. Mushroom productivity 133

134 Questions about sustainability of mushroom crops
 135 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	<i>T. magnivelare</i> (Peck) Redhead	33
Morels	Various <i>Morchella</i> species	11
Pacific golden chanterelle	<i>Cantharellus formosus</i> Corner (previously considered <i>C. cibarius</i> Fr., Redhead et al., 1997)	6
White chanterelle	<i>Cantharellus subalbidus</i> Smith and Morse	5
Hedgehogs	<i>Hydnum repandum</i> L. ex Fr., <i>Hydnum</i> <i>umbilicatum</i> Peck	7
King bolete	<i>Boletus edulis</i> Bull.:Fr.	11
Oregon white truffle	<i>Tuber gibbosum</i> Harkn.	50
Oregon black truffle	<i>Leucangium carthusianum</i> (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.

136 biological productivity as the total number or weight
137 of mushrooms or truffles that fruit per unit area during
138 the course of a fruiting season (although the term
139 “fruiting” technically applies to flowering plants, it is
140 commonly used in mycological literature to describe
141 the formation of sporocarps). Commercial productiv-
142 ity is the amount collectors actually harvest in a given
143 area during a season. Seasonal totals are necessary
144 because many edible species will fruit repeatedly or
145 continuously during a period of several months of
146 favorable weather each year, therefore estimates based
147 on one-time sampling would represent an unknown
148 percentage of the seasonal crop. Repeated inventories
149 (monitoring) over multiple fruiting seasons are
150 required to adequately estimate habitat or site produc-
151 tivity, because there is substantial annual variation,
152 often weather related, in productivity among fruiting
153 seasons (Vogt et al., 1992; Liegel, 1998; Pilz et al.,
154 1999). The high annual variability in production also
155 necessitates long-term monitoring to detect statisti-
156 cally significant trends in productivity. Typical pro-
157 ductivity of eight commercially important edible fungi
158 collected in the PNW-US are presented in Table 2.

159 Predicting and enhancing productivity also interests
160 many people. Prediction of annual fruiting often
161 entails efforts to correlate weather patterns with fruit-
162 ing (Vogt et al., 1992). Commercial harvesters report

that summer rainfall is a salient factor influencing 163
where, and in what quantity, fall-fruiting mushrooms 164
will occur. Other harvesters have postulated that pat- 165
terns of chilling and warming are important for indu- 166
cing and maintaining flushes of fruiting (Pilz et al., 167
1999). Few researchers or harvesters claim an under- 168
standing of multi-year fruiting cycles or an ability to 169
predict fruiting more than a few weeks in advance, 170
therefore managers who wish to prepare for harvest 171
seasons several months in advance must rely on guess- 172
work. 173

Attempts to increase mushroom productivity 174
include modifying the microenvironment of growing 175
mushrooms to enhance their size or quality, irrigation 176
to increase the number or weight of mushrooms, 177
spreading spores or planting inoculated trees to estab- 178
lish new fungal colonies, or silvicultural manipula- 179
tions to improve fruiting conditions or the health of 180
mycorrhizal host trees. Asian researchers have 181
explored these techniques as they apply to the Japa- 182
nese matsutake (*Tricholoma matsutake* (S. Ito et Imai) 183
Sing.) (Hosford et al., 1997; Ishikawa and Tekeuchi, 184
1970; Koo and Bilek, 1998). Silvicultural manipula- 185
tions to enhance production of the American matsu- 186
take (*Tricholoma magnivelare* (Peck) Redhead) are 187
described in Weigand (1998). The effectiveness and 188
practicality of these methods vary and, to date, they 189

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 (<i>Tsuga heterophylla</i> (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 <i>Abies</i> 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 (<i>Picea sitchensis</i> (Bong.) Carr.) on the coast and Englemann spruce (<i>Picea engelmannii</i> 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.

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

194 2.2. Mushroom harvesting effects

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

199 Does harvesting, per se, diminish subsequent fruit-
 200 ing? Insofar as mushrooms are the reproductive struc-
 201 tures of mycelial colonies, the picking of mushrooms
 202 has often been compared to picking apples from a tree;
 203 that is, the organism itself is thought to be only
 204 minimally impacted. Indeed, two studies with chan-
 205 terelles indicate that, in the short term and on small
 206 scales, this is likely true. The Oregon Mycological
 207 Society Chanterelle Study (Norvell, 1995) examined
 208 harvesting per se and methods of harvest (plucking or
 209 cutting the mushrooms); after 10 years, no declines in
 210 productivity were noted. Egli et al. (1990) report that
 211 in Switzerland, 10 years of harvesting had no signifi-
 212 cant effect on the continued fruiting of 15 different
 213 ectomycorrhizal mushroom species. Trampling, how-
 214 ever, dramatically reduced chanterelle (*Cantharellus*
 215 *lutescens* Fr.) fruiting for a year. This impact was
 216 attributed to damaged sporocarp primordia, because
 217 fruiting returned to previous levels the following year
 218 when trampling stopped.

219 Moving woody debris on the forest floor or raking
 220 forest litter layers to search for young mushrooms are
 221 additional concerns, they occur most often when
 222 harvesters search for new mushroom patches in areas
 223 they have not previously visited. These activities are
 224 predominantly associated with matsutake and truffle
 225 harvesting. Matsutake are far more valuable when they
 226 are young because they arrive at Japanese markets in
 227 better condition than do older specimens. Immature
 228 matsutake usually have not yet emerged from litter
 229 layers or spread their spores. Truffles fruit under-
 230 ground, rarely appearing on the surface. Raking litter
 231 layers to find matsutake or truffles can disturb the
 232 mycelium or disrupt the humid litter layer microen-
 233 vironment that allows initial development of the spor-
 234 ocarp primordia. During the initial expansion of
 235 commercial harvesting, many recreational harvesters

236 complained that their favorite patches had been
 237 destroyed by unscrupulous commercial harvesters
 238 who raked large areas. These claims often were exag-
 239 gerated, or the damage localized, but resentment about
 240 raking damage was heightened by the increased com-
 241 petition that recreational harvesters experienced in
 242 locations they had traditionally visited. Unpublished
 243 data from recent research with American matsutake in
 244 the Oregon Coast Dunes and Cascade Mountain
 245 Range suggests that raking can decrease subsequent
 246 production for several years, but that the severity and
 247 duration of raking impacts can be lessened by replac-
 248 ing the removed litter layers. Experienced harvesters
 249 of matsutake can find young specimens by visiting
 250 known patches and observing or feeling for lumps in
 251 the forest floor. Truffle hunters could train dogs to sniff
 252 out ripe truffles, although few in the PNW-US follow
 253 this practice so commonly used to harvest truffles in
 254 Europe.

255 Many harvesters, both recreational and commercial,
 256 actively attempt to improve production and create new
 257 mushroom patches by spreading the caps (with spores)
 258 of mushrooms that are too old to sell or eat (Liegel,
 259 1998). Some harvesters speculate that simply carrying
 260 mushrooms around during collection helps to distri-
 261 bute spores. It is even possible that harvesters are
 262 distributing spores with their shoes. No scientific
 263 evidence exists regarding the establishment of new
 264 mycelial colonies or improved sporocarp production
 265 from these modes of spore dispersal, but many har-
 266 vesters claim success or believe it does no harm to try.

267 Although it appears that harvesting is unlikely to
 268 harm ectomycorrhizal mushroom species in the short
 269 term, the long-term impacts of widespread intensive
 270 harvesting are not known. Concern might be greater
 271 for saprobic species that colonize coarse woody debris
 272 than for ectomycorrhizal species. Examples of edible
 273 saprobic mushrooms from the PNW-US include
 274 chicken of the woods or sulfur shelf (*Laetiporus*
 275 *sulphureus* (Bull. ex Fr.) Murr.), lion's mane (*Heri-
 276 cium abietis* (Weir ex Hubert) K. Harrison), angel
 277 wings (*Pleurotus porrigens* (Pers. ex Fr.) Kummer),
 278 and the cauliflower mushroom (*Sparassis crispa* Wulf.
 279 ex Fr.). Several saprobic medicinal species are also
 280 collected commercially, namely *Ganoderma tsugae*
 281 Murr. and *Ganoderma oregonense* Murr. (Hobbs,
 282 1995), and more species are likely to be identified.
 283 All of these wood decay fungi are less common and

284 fruit less abundantly than ectomycorrhizal species.
 285 They also might be more dependent on repeatedly
 286 colonizing new substrates than ectomycorrhizal spe-
 287 cies, because the wood they decompose could be
 288 depleted of usable nutrients within a decade or two,
 289 while ectomycorrhizal species might persist for the
 290 life-time of their arboreal symbionts or longer if
 291 compatible host trees regenerate quickly after a stand
 292 replacement event. If wood decay species are depen-
 293 dent on regular spore dispersal for colonizing new
 294 substrates, or if they have fewer opportunities to
 295 reproduce due to timber harvests that do not leave
 296 coarse woody debris, then their reproduction might be
 297 hampered by widespread harvesting of their sporo-
 298 carps. Saprobic species are easier to propagate than
 299 ectomycorrhizal species and increased cultivation
 300 could ameliorate concerns about harvesting wild
 301 populations (Stamets, 1993).

302 2.3. Effects of forest management practices

303 Forest management activities affect habitat for
 304 edible mushrooms in many ways. Effects differ by
 305 the lifestyle and reproductive strategies of each fungal
 306 species, the forest types they inhabit, and management
 307 goals and activities associated with each forest type.
 308 Forest practices that can affect the occurrence, pro-
 309 ductivity and reproduction of mushrooms include
 310 silvicultural practices, logging methods, tree species
 311 selection, fire, fertilization, pesticide use, and grazing.

312 Clearcut harvesting, for instance, interrupts the
 313 fruiting of most edible ectomycorrhizal fungi for a
 314 decade or more while they become reestablished on
 315 new tree hosts and the trees grow large enough to
 316 provide the fungi with sufficient carbohydrates or
 317 appropriate metabolites to support fruiting. By con-
 318 trast, some of the tree hosts for ectomycorrhizal fungi
 319 are usually retained when stands are thinned. Thinning
 320 intensity influences to what degree and for how long
 321 fruiting is affected. Thinning also influences fruiting
 322 conditions by allowing rain and sunshine to penetrate
 323 the forest canopy more easily than in nonthinned
 324 stands, resulting in more rapid wetting and drying
 325 of the forest floor. Unpublished data from a thinning
 326 study on the Willamette National Forest in Oregon
 327 shows that heavy thinning (from 615 to 125 trees per
 328 ha) of Douglas-fir (*Pseudotsuga menziesii* (Mirb.)
 329 Franco) reduces chanterelle fruiting by 90% in the

330 following year. We do not yet know how quickly
 331 mushroom productivity will rebound as remaining
 332 trees reoccupy the site, but recovery rates are needed
 333 to understand the effects of thinning on total mush-
 334 room production during a timber rotation. Frequent
 335 light (few trees removed) thinning during a timber
 336 rotation might maintain mushroom productivity better
 337 than infrequent heavy thinning because the mycor-
 338 rhizal host trees would retain nearly full photosyn-
 339 thetic occupancy of the site. Conversely (depending on
 340 logging systems) frequent light thinning could also
 341 result in more soil compaction than infrequent heavy
 342 thinning, thus impairing mycelial growth of the fungi
 343 in the soil and reducing long-term mushroom produc-
 344 tion (Amaranthus et al., 1996).

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

362 Ectomycorrhizal fungi exhibit varying degrees of
 363 specificity for host tree genera (Molina et al., 1992),
 364 therefore tree species selection during planting or
 365 thinning influences mushroom occurrence and pro-
 366 duction. PNW-US tree genera, such as *Abies*, *Alnus*,
 367 *Arbutus*, *Castanopsis*, *Larix*, *Lithocarpus*, *Populus*,
 368 *Picea*, *Pinus*, *Pseudotsuga*, *Quercus*, and *Tsuga* form
 369 ectomycorrhizae with fungi that produce sporocarps,
 370 whereas other genera, such as *Acer*, *Calocedrus*,
 371 *Chamaecyparis*, *Sequoia*, *Sequoiadendron*, *Taxus*,
 372 and *Thuja* form a different type of mycorrhizae (arbus-
 373 cular mycorrhizae) with fungi that reproduce primar-
 374 ily with individual spores in the soil rather than
 375 sporocarps. Stand composition and dominance of
 376 ectomycorrhizal host trees relative to arbuscular
 377 mycorrhizal trees likely affects the quantity of carbo-

378 hydrates available to ectomycorrhizal fungi for fruit-
379 ing.

380 Fires that kill trees are known to shift the composi-
381 tion of ectomycorrhizal fungal communities (Visser,
382 1995; Horton et al., 1998; Barr et al., 1999). When soil
383 litter layers are consumed, the abundance of ectomy-
384 corrhizae at the interface of organic and mineral soil
385 layers is reduced (Stendell et al., 1999) but the effects
386 of less intense fires are not as dramatic (Jonsson et al.,
387 1999). Tree seedlings that establish in burned areas
388 can be colonized by ectomycorrhizal fungi through
389 persistent spores in the soil (Horton et al., 1998) wind
390 blown spores, or residual mycelia associated with
391 surviving trees or brush species (Amaranthus and
392 Perry, 1994). Little is known, however, about the
393 influence of forest fires on the productivity of edible
394 ectomycorrhizal mushrooms other than the fact that
395 stand replacement fires inhibit fruiting until a new
396 stand develops.

397 By contrast, some species of morels fruit prolifi-
398 cally for the first year or two following forest fires.
399 Other morel species fruit annually at moderate levels
400 in nondisturbed forests, but will produce large crops
401 when a forest is logged or killed by insect infestations.
402 Most morels are considered saprobic because they
403 grow rapidly in pure culture and can complete their
404 life-cycle without host trees, but some species can
405 form mycorrhizae (Buscot, 1994; Dahlstrom et al.,
406 2001). Thinning and prescribed burning are increas-
407 ingly being used in the montane forests of the inter-
408 mountain west to reduce wildfire danger, curtail
409 potential insect infestations, and produce timber.
410 Opportunities to increase the size, regularity, or fre-
411 quency of morel crops might be enhanced if managers
412 better understood how each morel species responded
413 to various disturbances.

414 Evidence from Europe suggests that nitrogen
415 deposition from air pollution inhibits the growth of
416 some ectomycorrhizal fungi and reduces the produc-
417 tivity of edible ectomycorrhizal mushrooms (Arnolds,
418 1991). This suggests that nitrogen fertilization of
419 forest soils has the potential to reduce edible mush-
420 room production. In general, trees allocate a lesser
421 portion of photosynthates to roots and mycorrhizae on
422 fertile sites than on infertile sites (Perry, 1994; Waring
423 and Running, 1998), but the total quantity of carbo-
424 hydrates available to edible mycorrhizal fungi for
425 fruiting also depends on many other factors.

We know of no studies investigating the relations 426
between pesticide applications and edible forest 427
mushroom production or consumption. Herbicides 428
are sometimes used to release newly planted conifers 429
from competition by broadleaf trees and shrubs, but 430
commercially harvested ectomycorrhizal mushrooms 431
usually begin fruiting 5–15 years later as the conifer 432
stand develops, so that only persistent compounds or 433
recent drift from nearby areas are potential hazards. 434
Aerial broadcasting of chemical insecticides would 435
pose a greater concern for human consumption of 436
mushrooms, especially if applied during the mush- 437
room fruiting season. Given that forest mushrooms are 438
often sold as natural, wild, or pure products, obvious 439
marketing implications exist for the desirability and 440
sales potential of mushrooms collected from forests 441
where pesticides are used. Currently, the source of 442
wild edible mushrooms is rarely identified in retail 443
sales, although this could change as certification of 444
NTFPs becomes more common. 445

We are not aware of any research investigating the 446
influence of grazing on edible mushroom production, 447
but if compaction becomes severe, hyphal growth near 448
the soil surface could be inhibited. In the PNW-US, 449
grazing occurs in drier forests where few edible mush- 450
rooms, other than morels, are commercially harvested. 451

2.4. Biology, ecology, and ecosystem functions of 452 fungi 453

Given the numerous mushroom species harvested, 454
the diversity of forest types they inhabit, and the wide 455
range of silvicultural systems that foresters use, many 456
opportunities remain to improve management of 457
mushrooms through better understanding of their 458
biology, ecology, and ecosystem functions. Additional 459
information is needed about sexual and asexual modes 460
of reproduction, spore dispersal mechanisms, and 461
factors influencing colony establishment, health, 462
growth, senescence, and death. Fungi have complex 463
breeding patterns that complicate their population 464
dynamics. Forest conditions that facilitate reproduc- 465
tion differ on time scales from days (favorable 466
weather) to centuries (episodic disturbance events 467
such as forest fires that create new habitats). Recent 468
research (Dahlberg and Stenlid, 1994; de la Bastide 469
et al., 1994; Bonello et al., 1998) is just beginning to 470
characterize ectomycorrhizal colony sizes, longevity, 471

472 and population structures, but species-specific investigations are needed to understand how colonies and
 473 populations of edible mushrooms will respond to
 474 forest management activities. Forest fungi, including
 475 edible mushrooms, contribute to healthy forests and
 476 food webs in ways too numerous to discuss here
 477 (Carroll and Wicklow, 1992; Molina et al., 1999; Read
 478 et al., 1992), and managers should consider these
 479 ecosystem roles and functions when developing mushroom
 480 harvest regulations or management plans.
 481

482 2.5. People management

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

491 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).

511 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 distur-

518 bance, pathogen dispersal, impacts on other sensitive
 519 species or archeological sites, and conflicts among
 520 user groups, such as recreational harvesters, commercial harvesters, and big game hunters.
 521

522 Complete ecosystem management plans must
 523 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.
 529

530 Supplies are not the only salient issue, however. The
 531 volatility of international commerce in edible forest
 532 mushrooms (Blatner and Alexander, 1998) results in
 533 unpredictable demand for mushrooms. For example,
 534 the vast majority of matsutake are sold to Japan, but
 535 the mushroom commands such high prices that it is
 536 considered a luxury item. Economic cycles or changes
 537 in monetary exchange rates can considerably alter
 538 prices paid to harvesters and their resulting incentive
 539 to collect. Harvest levels in other countries also vary
 540 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.
 548

549 As another example of economic issues, the value of
 550 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
 565

566 does timber harvesting, and many other NTFPs and
567 amenities are derived from any given forest.

568 3. Harvest regulations and resource conservation

569 Because federal forest lands are publicly owned, all
570 citizens and companies are entitled to equitable access
571 to commercial resources. Competitive auctions are
572 typically used for timber sales or products, such as
573 decorative boughs. This approach is problematic with
574 mushrooms, however, because quantities are difficult
575 to predict and individuals, rather than companies, do
576 the harvesting. For these reasons, most National For-
577 ests (USDA-FS) sell commercial harvest permits to
578 individuals at set prices. Permits usually allow unlim-
579 ited collection during a specified season because rules
580 limiting the quantities collected would be difficult to
581 enforce. In some cases the number of permits are
582 restricted. The Winema and Deschutes National For-
583 ests in Oregon set the number of available permits at
584 the capacity of nearby designated campgrounds (Pilz
585 et al., 1999). Matsutake fruiting in the Oregon Dunes
586 National Recreation Area is fairly reliable and har-
587 vesters can estimate how much they will be able to
588 collect in a season thus, a limited number of permits
589 are issued by sealed bid auction. The USDI-BLM sells
590 contracts for mushroom harvesting. Contracts stipu-
591 late the species that can be harvested, maximum
592 quantities for each, specified areas for harvesting,
593 and a limited time frame depending on the amount
594 sold and number of anticipated harvesters. The per
595 weight value of each species is determined by con-
596 tacting local mushroom buying sheds. Contract prices
597 are set at the maximum of either 10% of the wholesale
598 value or the calculated results of a formula that
599 includes items, such as shed price, purchaser's poten-
600 tial profit and risk, labor costs, transportation, and road
601 maintenance. Some districts have minimum contract
602 prices or quantities. All these methods have advan-
603 tages and disadvantages for both managers and har-
604 vesters, but equity and compliance are improving as
605 procedures are refined by experience and communica-
606 tion (Liegel, 1998).

607 A variety of measures have been adopted on federal
608 lands to ensure conservation of the resource until more
609 is known about the long-term impacts of intensive
610 commercial mushroom harvesting. For instance, in the

611 Winema and Deschutes National Forests, the com- 611
612 mercial matsutake harvest season begins in mid-Sep- 612
613 tember, after the first hard frost. Matsutake that fruit 613
614 earlier in the season are often riddled with insect 614
615 larvae and have little commercial value. This arrange- 615
616 ment allows the first flush to disseminate spores with- 616
617 out greatly reducing the potential value of the 617
618 commercial crop (Pilz et al., 1999). 618

619 Most federal forests also have areas off-limits to 619
620 commercial activities; these include wilderness areas, 620
621 research natural areas, mushroom research areas, 621
622 designated recreation areas, or other areas of special 622
623 environmental concern. All National Parks (USDI) in 623
624 the region prohibit commercial mushroom harvesting. 624
625 Some industrial and nonindustrial private forest land- 625
626 owners prohibit or restrict commercial harvesting on 626
627 their properties. Even in areas where commercial 627
628 activities are allowed, managers will sometimes rotate 628
629 areas where collection is permitted to provide fallow 629
630 periods. Adherence to various harvest restrictions is 630
631 not uniform; compliance is influenced by mushroom 631
632 prices, access difficulty, harvester attitudes about reg- 632
633 ulations, and enforcement. 633

634 Mushroom commerce is a global enterprise, and 634
635 potential impacts concern forest managers wherever 635
636 harvesting occurs. Regulations often are tailored to 636
637 local land tenure (Hardin, 1968; Bromely, 1991; Lund 637
638 et al., 1998) and traditions concerning access to 638
639 harvesting opportunities. For example, Bandala et al. 639
640 (1997) describe communally owned matsutake habitat 640
641 in Oaxaca, Mexico where native tribes participate in 641
642 matsutake harvesting, marketing, monitoring, conser- 642
643 vation, and forest management. In Sweden and else- 643
644 where in Europe there is a long tradition of access to 644
645 private property for collecting edibles, such as mush- 645
646 rooms. It is called "Allemansrätten", literally trans- 646
647 lated as every man's right. Egli et al. (1995) has 647
648 proposed standardizing regulations in Switzerland 648
649 because each canton stipulates differing days of the 649
650 week when mushrooms may be collected and indivi- 650
651 duals raid each other's cantons when they are prohib- 651
652 ited from collecting locally. 652

653 Many of the issues, concerns, and regulatory 653
654 approaches we have discussed also apply to the har- 654
655 vest of other NTFPs and affirm the utility of compre- 655
656 hensive and integrative approaches to management 656
657 (Molina et al., 1997). Monitoring and research are 657
658 essential components of management plans if deci- 658

659 sions and regulations are to be improved over time.
 660 However, fungi in general and ectomycorrhizal mush-
 661 rooms in particular pose some unique challenges for
 662 research and monitoring.

663 4. Sampling challenges and considerations

664 Most fungi are difficult to study in their native
 665 habitats because their thallus is microscopic, very
 666 delicate, diffuse, embedded in the substrate they have
 667 colonized, and intermixed with other soil fungi and
 668 microorganisms. Estimates of edible mushroom pro-
 669 ductivity do not necessarily reflect the extent or dom-
 670 inance of a species thallus in the soil or the number of
 671 ectomycorrhizae it forms relative to other species
 672 (Gardes and Bruns, 1996; Mehmman et al., 1995).
 673 Scientists have quantified morphological types of
 674 ectomycorrhizae extracted from soil cores, but until
 675 recently the fungal symbionts were identified only if
 676 the mycelium was distinctive. With the advent of
 677 molecular techniques of DNA analysis, fungi can be
 678 identified from ectomycorrhizal root tips (Goodman
 679 et al., 1996; Bruns et al., 1998) a development that is
 680 rapidly advancing ecological studies of ectomycor-
 681 rhizal fungi.

682 Because weather patterns can cause large annual
 683 variations in mushroom productivity, many years of
 684 sampling are needed to estimate the average or poten-
 685 tial productivity of a site or habitat over time (Luoma
 686 and Frenkel, 1991). Potential long-term productivity
 687 might be more precisely estimated if a covariate, such
 688 as the percentage of ectomycorrhizae colonized by the
 689 fungal species of interest, was also estimated. Proces-
 690 sing individual root tips for genetic analysis is time
 691 consuming and labor intensive but, if marker systems
 692 using monoclonal antibodies were developed, quick
 693 counts of how many ectomycorrhizae were formed by
 694 a targeted species of fungus could be obtained from
 695 soil cores. Currently estimates of mushroom produc-
 696 tivity are still derived from sampling the sporocarps.

697 Repeatedly-visited plots with fixed boundaries must
 698 be used to obtain total sporocarp production during the
 699 course of a fruiting season, because mushrooms
 700 recorded during a previous sampling visit must be
 701 marked or collected to avoid repeat sampling during
 702 subsequent visits. Selecting an optimal plot size for
 703 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 per-
 sonnel 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 prede-
 fined 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. Sub-
 sampling 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 appro-
 priately to unanticipated circumstances.

To be properly interpreted, reports of mushroom
 productivity must be explicit in describing sampling
 methods, sampling intervals, and minimum size cri-
 teria. Unlike trees or other vegetation, mushrooms
 appear, change in size, and disappear rapidly. Spor-
 ocarp longevity of each species constrains the max-

imum 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. Har-

vesters 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; Horsford 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 mea-

suring 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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936 regional mushroom harvests.

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