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Ecology and Management of the Commercially Harvested American Matsutake Mushroom

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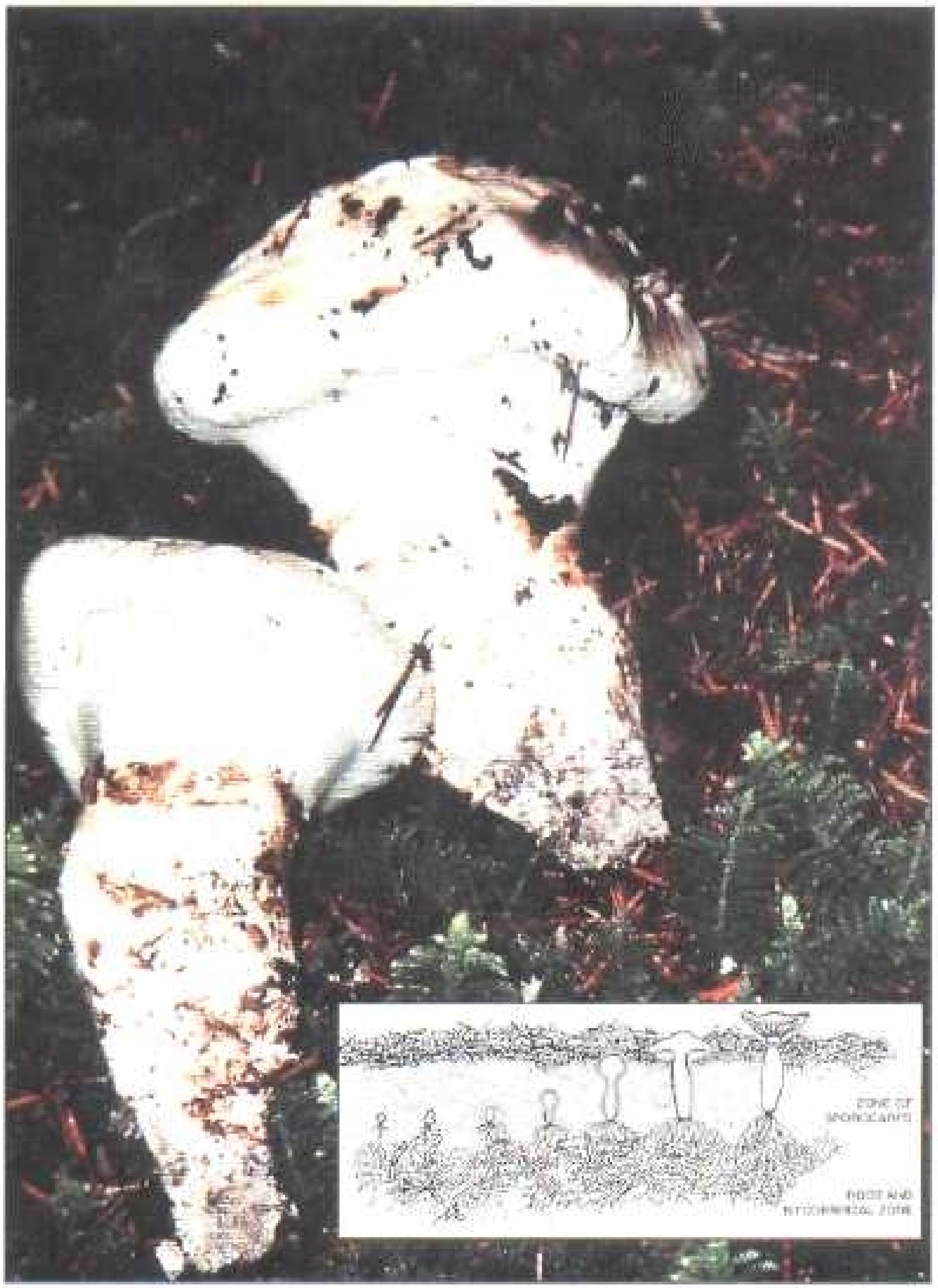

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Cover—En route to retail markets, young mushrooms retain their freshness better than older ones. Before the veil between the cap and the stem breaks, they are considered "buttons," and if there is no other physical or insect damage, they are graded as "number 1's," and command the highest price at buying stations. The large, young American matsutake shown in the photograph are just beginning to lose value. The veils on these specimens are starting to separate from the cap and they might be demoted to grade 2, depending on market conditions and the discretion of the buyer. In areas that experience intensive harvesting, the financial incentive to collect immature mushrooms is the basis for concern about diminished reproductive success due to decreased spore dispersal. To address this concern, mushroom harvesters often intentionally disperse the spores of commercially defective mushrooms, land managers limit collection to certain times or areas, and scientists are studying the reproductive biology of the *Tricholoma magnivelare.* The inset drawing shows mushroom development and relative position to mycorrhizae in a soil profile (Hosford and Ohara 1990).

Abstract

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The commercial harvest of American matsutake *(Tricholoma magnivelare)* from forests in the Pacific Northwest has increased dramatically in the last decade. The similarity of this mushroom to the Japanese matsutake *(T. matsutake)* has prompted its harvest to meet increasing demands for matsutake in Japan. The American matsutake is likely to remain a sustainable forest product in North America if its harvest and forest habitats are managed appropriately.

This summary paper begins by reviewing the historical importance of the Japanese matsutake, its declining production and harvest in Japan, the taxonomy of matsutake species worldwide, ecological research pioneered by the Japanese, and how Japanese forests are managed for matsutake production. Our discussion of the American matsutake begins with descriptions of its distribution, tree hosts, and commercially important habitats, which is followed by a case study of its ecology in central Washington. Next, we examine the social and economic context of its harvest in North America, as well as the biological, ecological and forest management issues that land managers must address to sustain its harvest. We conclude by discussing current matsutake research and monitoring activities in the Pacific Northwest and explaining the relevance of these activities for integrating the harvest of the American matsutake into forest ecosystem management plans.

Keywords: Matsutake (American), mushroom, forest management, mycology, fungi, mycorrhiza, special forest products, nonwood forest products.

Contents

Introduction

The commercial harvest of special forest products has emerged as a major industry in the Pacific Northwest, employing over 10,000 people and contributing over $100 million to the regional economy (Schlosser and Blatner 1995) (color plates 1-3 [in center of paper]). Its emergence comes at a critical time for the region, in both economic benefits and changing attitudes toward forest management. With the decline in Federal timber supply, the harvest of special forest products provides significant economic diversification for forest-associated communities. Public land agencies also have embraced a more comprehensive philosophy of land stewardship, called ecosystem management. In this approach, all forest organisms and processes are valued for their contribution to the healthy functioning of the forest, and management decisions focus on maintaining this biological diversity and functional complexity, while encouraging sustainable commodity production. This new management paradigm requires expanded knowledge of how forests function and uses an adaptive management strategy that modifies forest management plans as new knowledge is incorporated. Thus, the opportunity is at hand for integrating the wise harvest of special forest products into evolving ecosystem management scenarios (see Pilz and others 1996 for more details).

Japanese terminology

The Japanese term "matsu-take" literally translates as "pine-mushroom," and originally it referred collectively to *Tricholoma matsutake* and closely related Asian species Japanese-Americans used it for the American species *T magnivelare* when they began substituting this mushroom for matsutake species found in their native homelands (Redhead 1997) *Tricholoma magnivelare* is variously called (North) American matsutake, white matsutake, pine mushroom, or tanoak mushroom (plates 4 and 5) *Tricholoma magnivelare* grows in association with a wide variety of tree hosts, so we prefer the genera] and inclusive common name "American matsutake " By contrast, we will use "Japanese matsutake" to refer to *T matsutake* (plate 6)

Use of the term "matsutake" can be confusing, and it is used inconsistently in published literature Some authors capitalize it, as if referring to an individual, others do not We will not, and will instead follow common practice for "morel" or "chanterelle" mushrooms More importantly, "matsutake" is both **singular** and **plural** Also, it is variously used to refer to **any** *Tricholoma* species that is marketed as matsutake, collectively to **all** the species marketed as matsutake, to **individuals** of the matsutake fungus (that is, genetically unique colonies in the soil), or to the fruiting bodies **(mushrooms)** that an individual matsutake fungus produces We avoid the bilingually redundant term "matsutake mushroom," even though it is used in the literature Scientific names are used to distinguish among *Tricholoma* species References to matsutake habitat, management, monitoring, or resource imply either species or populations Matsutake fruiting refers to the fungus (either individually or as populations of individuals) Matsutake production refers to numbers of mushrooms or weight of a crop of mushrooms Matsutake harvesting, collecting, or marketing refers to the mushrooms (singular or plural)

Another commonly used Japanese term in matsutake literature is "shiro " As a Japanese noun, it means castle or domain (fruiting place) of a mushroom As an adjective, it means white More specifically, a shiro is the dense mat of fungal filaments ("hyphae" or collectively "mycelium") that matsutake species form in the soil It is also used to refer to locations where the matsutake fungus fruits (that is, mushroom patches in the forest) In this sense, a typical shiro consists of mushrooms growing in a linear arc, like incomplete (or occasionally complete) "fairy rings " Shiro morphology and ecology are discussed later in greater detail Both "shiro" and "shiros" are used for the plural of this term in the literature For clarity, we will use "shiros" as the plural

Wild, edible forest mushrooms are a relatively new crop among special forest products, but their harvest has quickly expanded into a multimillion dollar industry in the Pacific Northwest Several mushroom species are harvested (Molina and others 1993, Amaranthus and Pilz 1996) but the most valuable, in fresh weight price paid to harvesters, is the American matsutake Considerable controversy surrounds the proper management of the American matsutake and its harvest, disagreement often stems from lack of knowledge about its ecology, productivity, proper harvesting techniques, and the effect of repeated harvesting on future production The objectives of this paper are to summarize existing knowledge about Japanese and American matsutake species and to discuss how land managers can incorporate this information into existing forest ecosystem management plans and practices to improve management of the matsutake resource

The American matsutake is commercially harvested from northern Canada to northern California, and more recently, in the mountains of central Mexico Unlike other harvested wild mushrooms, however, the market for American matsutake is almost entirely for export to Japan (70 percent) or for sale to Asian communities in the Pacific Northwest (21 percent) (Schlosser and Blatner 1995) The American matsutake resembles the Japanese matsutake in shape, odor, and flavor Demand for Japanese matsutake has increasingly exceeded supplies during the last 30 years owing to the decline of matsutake habitat in Japan and growing demand from a larger and wealthier consumer population Hence, Japanese entrepreneurs began importing similar mushrooms to supplement supply, especially since the mid-1980s

We begin our first chapter by examining ancient traditions regarding matsutake and events that have prompted importation of the Japanese matsutake and similar species Matsutake species develop symbiotic associations with the roots of forest trees, these are called mycorrhizae (literally fungus-roots) and are essential to the health of both symbionts (plate 7) The fungus explores the soil with its mycelium and directly provides nutrients to the roots In return, the plant provides carbohydrates (sugars) produced from photosynthesis that serve as the energy source for the fungus Japanese mycologists have extensively studied the ecology and physiology of the Japanese matsutake and its mycorrhizal relationship to host trees Together with professional foresters, they have developed forest management techniques aimed at sustaining and enhancing matsutake productivity by manipulating forest stands and soil surface conditions In essence, they manage pine forests with enhanced mushroom production as the primary objective We conclude our first chapter by reviewing the ecology and management of the Japanese matsutake because that knowledge is rich with possibilities and approaches for managing the American matsutake

Chapter 2 explores the ecology of the American matsutake, a fungus widely distributed throughout North America (Redhead 1989) and harvested from diverse forest habitats where it develops mycorrhizal associations with numerous tree species. Although the American and Japanese matsutake species share some common biological features, the American matsutake has a much larger geographic range and thus exhibits a broader range of local ecological adaptations and specific habitat requirements. Managing the American matsutake must take these ecotypic or strain differences into account. In this chapter, we also describe some of the habitats known to produce reliable commercial crops. We conclude this chapter by describing a pioneering biological and ecological study of American matsutake populations in central Washington.

Chapter 3 discusses the challenges managers face when integrating the commercial harvest of American matsutake into forest ecosystem management plans. We begin by describing the social and economic context of the matsutake harvest in North America and internationally. Then we analyze the biological, ecological, and forest management considerations managers must integrate to maintain both fungus populations and their habitat, and thus sustain mushroom productivity.

Implementing long-term monitoring programs for wild, edible mushrooms is a challenge for managers. Fungi are unique among forest organisms in their reproductive biology. Their fruiting bodies (mushrooms and truffles) are ephemeral and patchy in distribution, and the quantities produced differ greatly from year to year. Practical methods to measure mushroom productivity in a variety of habitats are mostly in early developmental stages. Survey and monitoring procedures developed for plants and animals need extensive modification to make them suitable for measuring fungal distributions and productivity. We summarize monitoring approaches and challenges and then describe current and future studies that will provide managers with pertinent information for better decisions. We conclude by explaining how matsutake management can be integrated into broader ecosystem management plans.

Our goal is to provide forest managers and the public with a summary of current knowledge about the matsutake. We believe this will help resource managers develop long-term matsutake monitoring projects at important harvest sites around the Pacific Northwest and, in conjunction with input from the interested public, develop effective and equitable plans for managing this valued resource.

Chapter 1: Matsutake: An Ancient Tradition

History of Matsutake

Matsutake have been used and revered by the Japanese people for more than a millennium and have become more than just a seasonal delicacy. They also symbolize fertility, and by extension, good fortune and happiness. A gift of matsutake is considered special and is cherished by those who receive it. According to Ohara (1994), one of the earliest records extolling its virtues is found in a 759 A.D. poem. Later references to matsutake often were related to activities of nobles and priests. Records from the 13th to 17th centuries indicate that nobility enjoyed mushrooming events and often sent matsutake as gifts, a tradition that persists today, especially in the corporate world. During the 11th century in the Imperial Court of Kyoto, women were prohibited from saying "matsutake" openly but instead were required to speak of it with the honorific marker "O," as O-Matsu. Until the 17th and 18th centuries, matsutake consumption was strictly limited to the imperial court. As matsutake consumption became more common among the public during these centuries, vulgar (phallic symbolism) and graphic short stories came into vogue, portraying comical characters attempting to conceal their matsutake picking areas and indulging in risque talk about the mushroom. It was in this same period that the first stirrings of scientific interest were recorded: A Buddhist priest in Kyoto recorded the annual productivity of matsutake (that is, mushroom numbers) in a mountain forest (Kinkakuji-yama). Later, based on the priest's diary, Professor M. Hamada of Kyoto University was able to approximate the seasonal precipitation, temperature conditions, age and ecological status of the mountain forest from 1636 to 1667 (Ohara 1994).

The Decline of the Japanese Matsutake

Matsutake shiros were once widespread and common in mixed pine forests of Japan from Hokkaido in the north to Kyushu in the south After World War II, they became increasingly scarce, in spite of efforts to enhance productivity in local forests By 1981, productivity had declined to one-tenth of the pre-War levels, and imports of Japanese matsutake, especially from South Korea, increased greatly to meet demand (Kawal and Ogawa 1981) The quantity imported today differs from season to season but can exceed 60 percent of the total retail market (EAITC 1990) Imported matsutake, especially species other than *T matsutake,* are generally perceived as lacking freshness, proper color, taste, and fragrance and therefore are considered lower in quality and value Whether or not this perception is true, improved grading, handling, and marketing strategies, coupled with a continuing decline of Japan's matsutake production, will certainly improve the image and market value of imported mushrooms

Since 1905, the matsutake forests of Japan have been plagued by the pine nematode or pine weevil [1] The nematode is transmitted to living pines by the Japanese pine sawyer, a longhorn beetle Invasion of vascular tissue by the nematode results in wilt and rapid death (Futai 1979, 1980a, 1980b, 1980c, Futai and Furuno 1979) Most host pines of matsutake, including the Japanese black and red pines, are very susceptible to this devastating pathogen Since the introduction of the nematode at the start of the 20th century on the southern island of Kyushu, it has steadily spread north-eastward The current blight is the fourth in a series of epidemics since 1905 The third epidemic lasted a decade, peaked in 1979, and caused an estimated loss of 2 4 million cubic meters of pine wood The current epidemic began in 1990, and killed enough trees in one year to build 50,000 houses Recent reports indicate that the disease has also spread to forests of Okinawa, Taiwan, South Korea, North Korea, and China A combination of climatic, socio-economic, and biological factors in Japan tends to increase the magnitude of the blight Pine mortality from the nematode often increases after prolonged drought and high temperatures, which weaken the resistance of the pines to the parasite

A change in the way communities use local forests also has adversely affected the health of pine forests and, indirectly, matsutake productivity For at least a millennium, routine harvesting of understory shrubs and oak trees for charcoal favored growth of shade-intolerant pines and the matsutake associated with them In post-World War II years, traditional charcoal- and wood-burning stoves were replaced by natural gas burners, and the removal of woody shrubs for charcoal diminished Trees and shrubs that do not form matsutake mycorrhizae have consequently formed dense, brushy understones that block sunlight needed by pine seedlings While mature pines die from nematode attacks, new pine seedlings find themselves at a competitive disadvantage and have difficulty becoming established, hence, matsutake shiros disappear along with their pine hosts as other tree species become dominant

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[1] Scientific names for all species are in the appendix

Essentially, the red and black pines introduced from the Korean Peninsula flourished in the past under conditions no longer existing in Japan Although the Japanese have developed many silvicultural strategies to manage matsutake forests (discussed below), matsutake production has disappeared from the vast stretches of mountain pine forests that die each year Indeed, Japan's temples and public parks may eventually become the last refuge for matsutake pine forests, as suggested by a respected Kyoto gardener, Mr Shiro Nakane (c 1992)

> *To me, this already seems to be the case When I was a kid, I'd walk on the paths right up there and gather matsutake from the many, many red pine trees Now I sometimes go up to the mountain with my two boys and my dog, but the forest there has changed The trees I remember are gone Still, different trees are appearing, and maybe this is nature's way*

Other Species

Other Species of Matsutake

Two species of matsutake are recognized in Japan *Tricholoma matsutake* and *T bakamatsutake* The first is the principle Asian species and grows widely in Japanese red pine (known as "aka-matsu") forests throughout Japan, South Korea, North Korea, northeastern China, and Primorsk Kray, Russia In Japan, *T matsutake* also associates with Japanese black pine, Japanese stone pine, Japanese white pine, southern Japanese hemlock, northern Japanese hemlock, and Sakhalin spruce On the Korean Peninsula and in Manchuria, it associates with Korean pine, in Sakhalin with Maries fir, and in Taiwan and along the east coast of China, with Taiwan red pine (Hamada 1966, Ogawa 1982, Ohara 1981) It occurs in at least eight provinces of China under various pines (often mixed with oaks), but most often under Japanese red pine in the northeastern province of Jilin (Wang c 1982) *Tricholoma bakamatsutake* or "foolish pine mushroom," is less common and differs from *T matsutake* by its association with broadleaf trees, particularly Mongolian oak, serrated-leafed oak, edible Asian tanoak, and chinkapin species (Ogawa and Ohara 1978) It, too, ranges from Hokkaido to Kyushu in Japan, and is found in Taiwan, South Korea, North Korea and China It has the same general morphology and strong matsutake odor and taste of *T matsutake,* but it differs from the latter in being slightly smaller and more fragile, and in having cheilocystidia on the gills (Hongo 1974) Thus, the two can be easily confused morphologically and indeed may represent only ecotypes or variants of one "plastic" species

The principal North American counterpart of the Asian matsutake species is *Tricholoma magnivelare* It is similar in texture, taste, and odor to Asian species and has long been a favorite of Japanese-Americans and certain tribes of Native Americans Mushroom guides often refer to the American matsutake as either *T ponderosum* (Peck) Singer or *Armillaria Ponderosa* (Peck) Sacc The epithet "Ponderosa," meaning large and heavy, is descriptive of the species The earliest name applied to the American matsutake was *Agaricus magnivelare* "Magnivelare' also describes the species well, it refers to the large well-developed veil, which breaks or tears, leaving a membranous ring on the stalk In his 1984 review of the literature, Redhead determined that the nomenclaturally correct name is *T magnivelare* (Peck) Redhead The species is morphologically distinct from the Japanese species and is described by Smith and Weber (1980 127) as follows "This large white mushroom gradually develops cinnamon stains as it ages, and in age is quite discolored The cap may be up to 35 centimeters broad and covered with cinnamon colored patches of tissue The gills are white and slowly stain vinaceous cinnamon " Arora (1986 191) ventures the most intriguing description of its unique spicy odor as a "cross between redhots [spicy cinnamon candy] and dirty socks"

A rarer and consequently less well-known species of North American matsutake is *T caligatum,* or "booted" matsutake It occurs in North America, Europe, and northern Africa The species is generally smaller and more slender than *T magnivelare,* has a broad cap with dark vinaceous to cinnamon-brown scales or fibrillose (hairlike) patches, and has the same colors on the underside of the ring and the stalk below the ring or "boot" The stalk above the ring is white and the odor of the mushroom is quite variable As Smith and Weber (1980 127) write "One variety has an odor like that of *A ponderosa,* another has an odor somewhat like that of bitter almonds, and a third no odor at all The Japanese matsutake is one of the varieties of this collective species" Likely the variability in odor is geographic, specimens found in western North American smell more like the Japanese matsutake than those from eastern North American (Arora 1986, Smith 1979) *Tricholoma caligatum* may be found in pure coniferous stands, mixed coniferous and hardwood stands, and pure hardwood stands In general, *T caligatum* seems to be closely related in size, odor, and habitat to *T matsutake, T bakamatsutake,* and *T fulvocastaneum* of Japan

Kytovuon (1989) discusses the *T caligatum* group in Europe *T caligatum* and *T nauseosum* are species with overlapping ranges in Europe and northern Africa After examining many specimens, he asserts that *T nauseosum* of Europe is synonymous with *T matsutake* of Asia, and because *T nauseosum* was named first, it is therefore the valid name Specimens originally described as *T nauseosum* and *T matsutake* came from opposite sides of the Eurasian continent, hence, this claim likely will require further verification (perhaps genetic comparisons) before it is widely accepted It would, however, be ironic if one of the most highly prized mushrooms in the world ends up with the specific epithet "nauseosum" due to the priority rule of the International Code of Botanical Nomenclature (Greuter 1994), which states that the first name validly published for a species is the correct name Kytovuon (1989) also discusses the affinities between *T nauseosum* and *T magnivelare* He further asserts that the *T caligatum* of Europe is distinct from both *T nauseosum* and the *T caligatum* of North America

The global taxonomy of wide-ranging species like matsutake can be confusing even for experts To further complicate matters, commercial collectors and retailers often make odor, taste, and value distinctions among specimens of the same matsutake species collected from different areas Species distinctions often are based on descriptions of physical characteristics, and many of these have a range of gradations With the advent of easy global communication and techniques for genetic analysis, taxonomists have powerful tools for distinguishing between actual species and local ecotypic variation within a species Readers are referred to Wang and others (in press) for further discussion of the global distribution of closely related matsutake species

Look-Alikes

Tricholoma zelleri is another North American species related to *T magnivelare* It is not considered a matsutake and has no commercial value, but it is often abundant and is commonly found near shiros of *T magnivelare,* hence, it may be considered an indicator species (Hosford and Ohara 1990) This species resembles *T magnivelare* in shape, texture, and occurrence but usually is smaller and different in color, odor, and taste The cap is viscid at first but soon dries and cracks into small scales The cap ranges from yellow to orange and often develops distinct olive tones in spots The stem below the well-developed ring has colors similar to the cap The odor and taste of *T zelleri* is similar to freshly ground meal (farinaceous), with an added pungent metallic taste *Tricholoma zelleri* fruits prolifically at about the same time as other matsutakes in the coniferous forests of the Pacific Northwest and the Great Lakes area It is closely related or identical to *T locale* of Europe and *T robustum* of Japan

The "imperial mushroom" *(Catathelasma imperiale)* is a species sometimes mistaken for the American matsutake by novice collectors Although typically larger and lacking the distinctive odor of the American matsutake, the imperial mushroom otherwise has a similar appearance It is edible and collected commercially

Deadly *Amanita* mushrooms are distinctive from matsutake, but they can fruit within meters of each other (Pilz, personal observation), and poisonings from mistaking *Amanita smithiana* for matsutake have occured (Benjamin 1995, Leatham and others 1997, Tullos and Lindgren 1992) *Amanita* mushrooms have a brittle texture, whereas matsutake have a fibrous texture (they can be peeled like string cheese) The matsutake odor is also distinctive, when one is familiar with it The usual caveats apply **always** make sure of your identification before eating any mushroom, and then start with small quantities

Ecology of the Japanese Matsutake

The roots of ecological knowledge stem from ancient tradition During the Edo Period (1603-1867), a number of books contained descriptions (including habitat) and illustrations of matsutake (fig 1) The book Honcho Shokkan (1697) was the first to recognize the symbiotic relationship between matsutake and pine and to promote matsutake cultivation by transplanting soil from matsutake shiros [2] No data on either the success or failure of transplanting is mentioned Early research[3] by Inoue in 1930, Kaneyuki in Hiroshima in 1955, Senbara in Kyoto in 1937, and Asada (1937) added greatly to our knowledge of matsutake biology and ecology and promoted further study Senbara focused ecological research on the shiro and its management and developed techniques later refined by Professor M Hamada at Kyoto University His principal graduate students, M Ogawa, H Ohara, N Sagara, and K Kinugawa, contributed information on matsutake mycorrhizae, microbial interactions in the shiro, chemical treatment of the shiro, and effects of temperature on formation of the mushrooms The research of Hamada (1950), his students and others, such as Tominaga (1963, 1973, 1978), is embodied in the following discussion of matsutake shiros and forest management

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[2] Author and place of publication unknown The book is discussed by Ohara (1994 22)

[3] In the matsutake literature the work of these pioneer researchers has been cited incompletely The information available to us is listed here so that readers serious about pursuing old references have a starting point Kaneyuki 1955 *Hiketsu Kokai Matsutake Zoshoku Ho* Inoue M 1930 *Nihon Matsutake Jinko Saibaiho* Senbara 1937 *Yama No Sachi*

菌譜の中の松茸（国会図書館所蔵）

Figure 1—An early description of matsutake and its ecology published in an 1834, KINFU (= Fungal Notes Ohara 1994 23) (Original text of KINFU is held by the National Diet Library, Tokyo, call number 22)

Ohara (1994:29) defines a matsutake shiro as "...a subterranean biotic community where mycorrhizal development plays a leading part over the soil constituents, especially soil microbes." Ohara's definition emphasizes the key importance of the fungus-root association in a shiro. The annual growth of a matsutake shiro (initially located by the emergence of mushrooms) is typically followed by inserting bamboo or flag markers at the exact point of fruiting. A few seasons of such marking provide an accurate record of mushroom production and a map of the shiro's growth. The growth of the shiro is directly correlated to mycorrhizal development in the soil beneath the organic layer. Several zones are recognized in a soil profile of a shiro (fig. 2). Zone III, the currently active mycorrhizal zone (AMZ), contains the mycorrhizae directly below the mushroom. When fruiting occurs, the soil in this zone becomes strongly desiccated and the mycorrhizae begin to deteriorate. The AMZ contains about 10 times the number of fine rootlets (of Japanese red pine in this case) compared to the zones on either side of it. Zone II contains young, physiologically active mycorrhizae that will produce mushrooms the following season. The mycorrhizae of both zones II and III appear as broomlike clusters. Structurally, the mycorrhizae are classified as ectomycorrhizae but, unlike most ectomycorrhizae, have loose, soft mantles with poorly developed Hartig nets. Zone I contains mycelium and structural roots but no mycorrhizae. In zones IV and V (representing the previous two years of fruiting), the soil is still granular and desiccated and contains decayed mycorrhizae. Finally, in zone O, there is no mycelium, and zone VII shows complete recovery from the earlier effects of active mycorrhizae. All zones (O-VII) can be recognized in the field by variation in the color of the soil profile, as well as soil texture, relative moisture, and odor (the unique matsutake aroma). Ogawa and Hamada (1965), Ohara (1966), and Ohara and Hamada (1967) also report qualitative and quantitative differences in microbial populations for each zone, especially the AMZ. Fruiting bodies begin to develop in the AMZ when soil temperature falls below 19 °C. About 20 days after initiation, the cap of the fruiting bodies opens (Kinugawa 1963). Fruiting typically ceases when shiro temperatures fall below 10 °C. The species of plants and fungi present, their densities, health, age and ecological effects on shiro productivity have been carefully studied (Ogawa 1982, Ohara 1974). The results have been applied to forest management techniques intended to enhance matsutake production.

Enhancing Japanese Matsutake Production

The following sections summarize management techniques employed to enhance the production of matsutake (numbers and size of the mushrooms) in Japanese red pine forests. More complete discussions of the subject can be found in books (in Japanese) by Ogawa (1982) and Ogawa and Ito (1989) and papers by Ohara (1994) and Sagara and Hamada (1965). Although this discussion pertains to research with the Japanese matsutake, many of the techniques may prove applicable to the American matsutake.

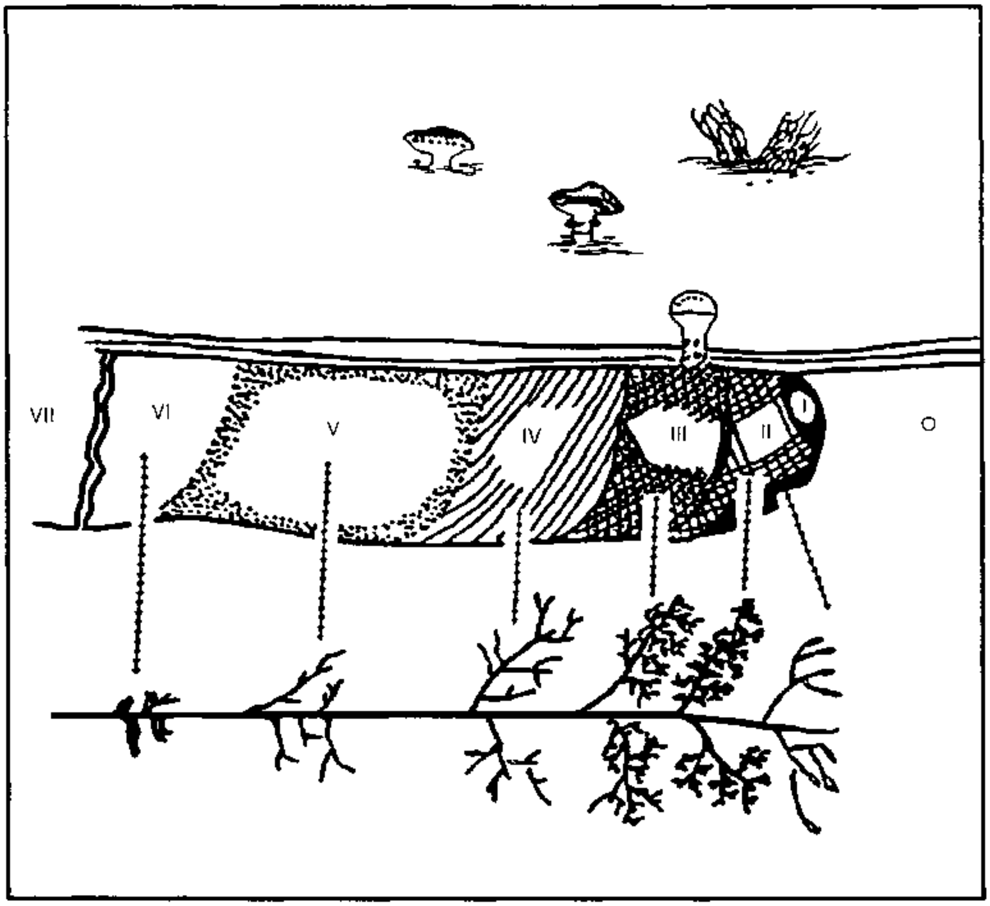

Figure 2—Soil profile of the shiro of *Tricholoma matsutake* (Ohara 1981)
O = zone of roots free from mycorrhizal infection
I = zone of mycelium
II = zone of physiologically active mycorrhizae (next season's AMZ or "active mycorrhizal zone")
III = zone of mycorrhizae for fruiting (AMZ)
IV = zone of decaying mycorrhizae
V = zone of decayed mycorrhizae
VI = zone of sloughed mycorrhizae
VII = zone of soil recovered from mycorrhizal effect

Site Selection and Vegetation Management

Important criteria for site selection include age of the pine trees; composition, density, and stratification of tree species, canopy coverage; slope; and soil characteristics, including moisture and temperature. Pines 40 to 50 years old are best for matsutake production, but those over 50 exhibit declining production. Forests consisting predominantly of pines, with few other tree and shrub species, are most favorable for matsutake production Ideal conditions also include an open canopy that allows light to penetrate to a sparsely vegetated forest floor, and warm, well-drained soils with thin litter and organic layers Pine forests positioned on southwestern slopes and ridgetops tend to be most suitable. Unfortunately, few sites are naturally optimal for matsutake production.

Forest management treatments employed for enhancement of matsutake production differ from those used to maximize timber production The primary objective is to alter tree species composition, stand density, and soil conditions to encourage shiro development Ogawa (1982) has designed a schedule of silvicultural treatments that produces ideal conditions for the establishment, growth, and fruiting of matsutake shiros in a 30-year-old Japanese red pine forest A similar set of treatments also may be applied to younger stands over a longer period This management regime produces an open canopy and forest floor that is warm, dry, and free of excessive debris and organic material Under these conditions, pine roots proliferate near the soil surface while many nonhost roots, bacteria, and saprobic and other mycorrhizal fungi decline In an experimental forest near Kyoto, these management procedures increased the number of shiros from 12 to 73 over 15 years (Ogawa 1982).

The first year includes thinning of pines and other competing tree species, removal of shrubs, herbs, dead branches, and damaged or diseased trees The increased light penetration and air circulation reduce soil moisture and increase soil temperature

Vegetation management during the second year includes removal of new sprouts, weeding, and tree trimming Soils with excess accumulation of litter and organic matter are raked to expose the mineral soil In effect, this eliminates pine roots and pests, which tend to accumulate in the litter layer, decreases soil moisture, and increases soil temperature to levels conducive to mushroom production On the other hand, if needed, a bare forest soil may be mulched with rice straw, to increase moisture and lower temperature to levels again more conducive to the matsutake The third year of treatment is much the same as the second, but may include another thinning of pine and pruning of nondominant trees New sprouts, weeds, and excess litter are again removed By autumn of the third year, matsutake shiros usually appear and marking of mushrooms begins

After the third year, management consists of annual inspection and cleanup of the forest floor, removal of dead trees, and biannual pruning of understory vegetation Vigorous growth and gradual increase in numbers of shiros usually occurs between the fifth and tenth years of treatment. After the tenth year, production of mushrooms drops as the growth rate of maturing red pines declines

Fruiting Enhancement

Several techniques, other than those discussed above, have been used to stimulate the formation of matsutake primordia (small "protomushrooms" with the potential to develop), increase the number of mushrooms that actually develop from the primordia, or increase the eventual size and weight of the mushroom Most of these techniques operate by controlling humidity and temperature

The "Hiroshima tunnel" (plate 8) is one such method, where a tunnelike construction is placed over the physiologically active mycorrhizal zone (AMZ II-III) The tunnel roof is formed with fine-mesh netting or screening (as used in greenhouses) stretched over wire wickets arching to a height of 30 centimeters and spanning up to 1 meter in width The length of the tunnel differs with the length of the active shiro front The tunnel shades and cools the soil to 20 °C or less for 4 to 5 days to initiate the development of primordia The tunnel netting also maintains soil moisture levels and may control some insects

Tominaga (1975) and other Japanese have reported success with this method Tominaga (1975, 1978) compared two shiros over 3 years by using variable treatments, including artificial sprinkling of water, air-conditioning, and ice, beneath the tunnel to control moisture and temperature Some treatment combinations resulted in two to six times greater mushroom production and 12 to 20 days earlier production than without a tunnel

On a smaller scale, the size of individual mushrooms and their rate of maturation may be increased by covering them with damp soil or a small cup as they begin to emerge, thus maintaining higher humidity and preventing the stunting of their growth through desiccation (Lee 1989a) Plastic cups also may reduce insect damage by acting as a barrier

In the previous section, we described how foresters open forest stands to allow sunlight to warm the forest floor, and in this section we describe techniques for cooling the mycelium and sustaining high humidity Although these activities may appear contradictory, the vegetation management is intended to promote the establishment and growth of shiros and the formation of matsutake mycorrhizae with selected host trees, whereas the cooling and humidity control are more localized treatments to enhance fruiting

Inoculation

In addition to fruiting enhancement, various inoculation or "seeding" methods have been tried over the years in attempts to establish and spread matsutake shiros to new areas Methods include inoculating seedling roots before transplanting, transferring soil from the active mycorrhizal zone of established shiros, and spreading spores into new forest sites

Seedling roots have been successfully inoculated in both field and laboratory Field inoculation involves planting mycorrhiza-free seedlings in active shiros to form matsutake mycorrhizae, and subsequently (usually the next year) transplanting them into appropriate habitat lacking matsutake shiros Laboratory inoculation involves isolating a sterile culture of matsutake from the aseptic interior of a mushroom, growing it on Hamada's medium (Hamada 1964), and placing it in contact with mycorrhiza-free seedling roots New matsutake shiros, unfortunately, have not yet been successfully produced by planting inoculated seedlings Soil transfers from active shiros to likely habitats also have been attempted without success at establishing new shiros For further information on these techniques, refer to Ogawa 1982, Ogawa and Ito 1989, and Lee 1989b

The simplest inoculation method is to cut a fully opened mushroom cap from its stem and bury it near host plant roots or place it on the soil surface within a young pine stand Litter and organic layers should be removed from the soil to improve the chance that spores will come into contact with appropriate host roots Spore suspensions also may be created by mixing spore prints or macerated gills in water Spore suspensions are then poured into holes in the soil near pine roots or mixed with soil placed around the roots Japanese matsutake spores are short-lived and few apparently germinate Repeated application as close as possible to young, noncolonized host roots often is necessary The use of spore dissemination to establish new matsutake shiros has had a long history Those who claim success are those who cleaned the forest floor of excess organic material and sowed spores frequently over 5 years or more (Ogawa 1982)

Although attempts to establish new matsutake shiros have not yet yielded much success, plantation establishment and management for matsutake production holds the greatest promise for artificial cultivation. The high value of matsutake suggests this approach may be economically feasible. Many of the techniques for truffle (*Tuber* species) cultivation in plantations established with inoculated seedlings may be adapted eventually to create matsutake plantations. Progress with this approach has been demonstrated recently with chanterelle mushrooms (Danell 1994, Danell and Camacho 1997). Even if the technology to do this is developed, success will depend on using appropriate host trees, selecting adaptable matsutake strains, and establishing the plantations in appropriate habitat (especially proper soils). Artificially established matsutake plantations are unlikely to be developed on Federal lands in the United States because other species would be displaced, an effect that would conflict with management goals for preserving biological diversity and multiple use. Managing natural stands (through activities such as thinning or controlled burns) that already have matsutake populations does hold promise, however, for enhancing fruiting within the context of Federal ecosystem management goals. Plantations for American matsutake production may eventually become economically attractive for private land owners.

Pure Culture Production

Growing matsutake in pure culture and inducing it to fruit (without its mycorrhizal tree symbionts) has been a goal of researchers and commercial interests for many years. Unlike saprobic fungi that decompose organic matter, symbiotic mycorrhizal fungi have complex biochemical interactions with their plant hosts. Although most mycorrhizal fungi can be grown in pure culture, only a few have been induced to fruit without colonizing the roots of a host plant (Ohta 1994; Pantidou 1961, 1962, 1964). Both Japanese and American matsutake grow very slowly on nutrient media alone, and innovative biotechnology developments will likely be needed to induce matsutake to fruit in the absence of its tree partners.

Chapter 2: The American Matsutake

Distribution and Tree Hosts

The distribution of American matsutake has been documented by several researchers. Zeller and Togashi (1934) published the first comprehensive treatment of Japanese and American matsutake species, noting tree associates and occurrence in North America. Ohara (1977), Kinugawa and Goto (1978), Ogawa (1979), Smith (1979), Redhead (1984, 1989), Villarreal and Perez-Moreno (1989), and Villarreal (1994) provide additional information.

The distribution of the American matsutake coincides with the northern coniferous forest belt (or taiga), running east-west across Canada, and temperate conifer forests extending southward along the Appalachian, Rocky, Cascade and Pacific Coast mountain ranges. It is found under a variety of conifers with which it forms mycorrhizae. Among the reported tree associates are Douglas-fir, western hemlock, grand fir, Shasta red fir, Pacific silver fir, Engelmann spruce, white spruce, jack pine, red pine, sugar pine, ponderosa pine, inland lodgepole pine, and coastal shore pine. In southwestern Oregon and along the coast of northern California, it often associates with tanoak. Inland, the distribution continues south through the Rocky Mountains into high-elevation pine and fir forests in the mountains of México.

Tricholoma caligatum is much more sporadic in occurrence but generally follows the same distribution pattern. It also grows in pure coniferous stands, mixed stands of conifers and hardwoods, and in pure hardwood stands (the latter common in the Appalachian Mountains). In central Washington and Oregon, it most often is found in mixed stands of conifers containing Douglas-fir and western hemlock

Commercially Important Habitats

Although matsutake occurs and is commercially collected throughout much of the coniferous forest zone of North America, certain areas are especially productive and heavily harvested. We are most familiar with commercial harvesting in the Pacific Northwest United States but include general habitat descriptions for areas of commercial harvesting in Canada and Mexico as well Harvesters are secretive about where they collect, and new areas of profitable matsutake harvesting are still being discovered This section reflects our current knowledge but is subject to change as new areas become widely known, harvesters shift their activities, and public land managers become aware of the trends

Canadian Habitats

The American matsutake fruits abundantly in the coniferous forests of Canada British Columbia currently experiences the largest harvest, where fruiting occurs in at least 10 biogeoclimatic zones (de Geus 1995a, Meidinger and Pojar 1991) Figure 3 illustrates areas of known harvesting. It was compiled through consultation with forest district staff and from discussions among industry participants at a series of public meetings (de Geus and others 1992, de Geus 1995b) Commercial harvesting in this province is favored by relative proximity to Japanese markets and a harvest season that starts early and lasts for several months as fruiting progresses from north to south, high to low elevation, and inland to coastal areas.

The American matsutake also fruits across Canada in northern Alberta, Saskatchewan, Manitoba, Ontario, and Québec In Québec and Ontario, it is especially associated with jack pine forests growing on long mounds of well-drained glacial till called eskers (Miron 1994) In this zone, matsutake fruits in August and September as trees become dormant in response to shortening photoperiods The season can be brief, because killing frosts soon follow Although crops can be huge, the commercial harvest is only beginning to grow as the industry learns to cope with the short season, large areas of unroaded habitat, a limited transportation infrastructure, and a small labor force [1]

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[1] Personal communication J Andre Fortin, Institut Recherche Biologie Vegetale, Universite de Montreal, 4101, rue Sherbrooke est, Montreal, PQ HIX 2B2

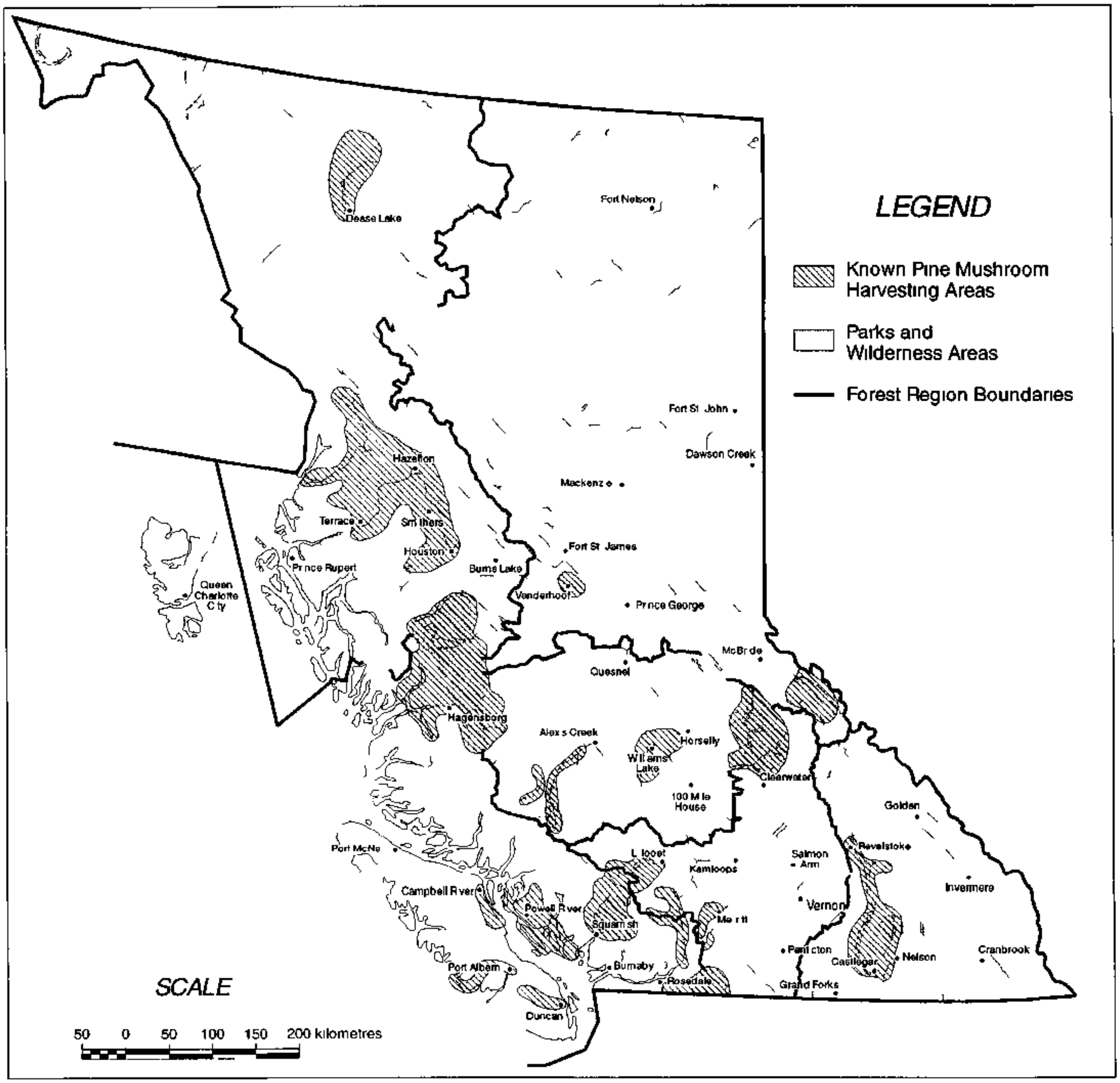

Figure 3—Known commercial pine mushroom harvesting areas in British Columbia (reprinted with permission from de Geus 1995a)

United States Habitats

Figure 4 shows areas in the Pacific Northwest were matsutake fruits consistently and commercial harvesting is concentrated. In Washington State, the American matsutake is harvested commercially on the Olympic Peninsula near Shelton and on both sides of Stevens Pass in the Cascade Range south to the Columbia River. Soils near Shelton and in central Washington are derived from well-drained glacial tills and, at higher elevations in the Cascade Range, consist of tephra deposits from Mount Rainier, Mount Adams, and Mount St. Helens. Matsutake typically fruits from 300 to 1200 meters in elevation in a variety of forest types, including:

- Douglas-fir, western hemlock/salal/sword-fern—Near Shelton on the Olympic Peninsula and in the valleys of the western slopes of the Cascade Range, the forest stands are typically composed of Douglas-fir, western hemlock, and western redcedar with salal and sword-fern in the understory.
- Mixed conifer/ericaceous shrubs—At higher elevations, on both east and west slopes of the Cascade Range, other trees intermingle with Douglas-fir and western hemlock to create mixed-conifer stands; the predominant species are Pacific silver fir, noble fir, grand fir, lodgepole pine, western white pine, and Ponderosa pine. These forests often have ericacious shrubs in their understory. In all these habitat types, the candy stick plant is common where matsutake fruits (plate 9).

The sand dunes of the central Oregon coast contain three major habitat types where matsutake consistently fruits.[2]

- Shore pine/hairy manzanita/kinnikinnic—This habitat type is found on dry, naturally stabilized dune landforms. The dominant tree in these areas is shore pine, 35 to 80 years old, with younger pines colonizing along the perimeter of the stand. Brush understory is composed of hairy manzanita and kinnikinnic with patches of salal, evergreen huckleberry, and Pacific rhododendron. Herbaceous ground cover is generally lacking, with occasional candy stick and pinesap plants scattered throughout. The abundance and diversity of lichens is conspicuous. Duff and litter layers may be absent or up to 8 centimeters deep. Some areas contain a well-developed moss layer up to 20 centimeters deep. Elevation ranges from 3 to 100 meters. Slope and aspect vary.
- Shore pine/evergreen huckleberry—This habitat type is found on higher portions of naturally stabilized dune landforms. Arboreal overstory vegetation consists of shore pine, 35 to 80 years old, with some Sitka spruce and western hemlock beginning to colonize. Brush understory may be moderate to dense, composed of predominately evergreen huckleberry, salal, and Pacific rhododendron. Herbaceous ground cover is generally lacking with occasional candy stick and gnome-plant present. Duff and litter layers usually range from 2 to 8 centimeters deep with moss growing in open areas. Elevation ranges from 10 to 100 meters. Slope and aspect vary (plate 10). (American matsutake also fruits in similar habitat on the coast of northern California near Eureka.)

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[2] Information on commercially important dunes habitat contributed by Dan Segotta, Siuslaw National Forest, Waldport, OR 97394, and Jeanne McFarland, Humboldt State University, Arcada, CA 95521.

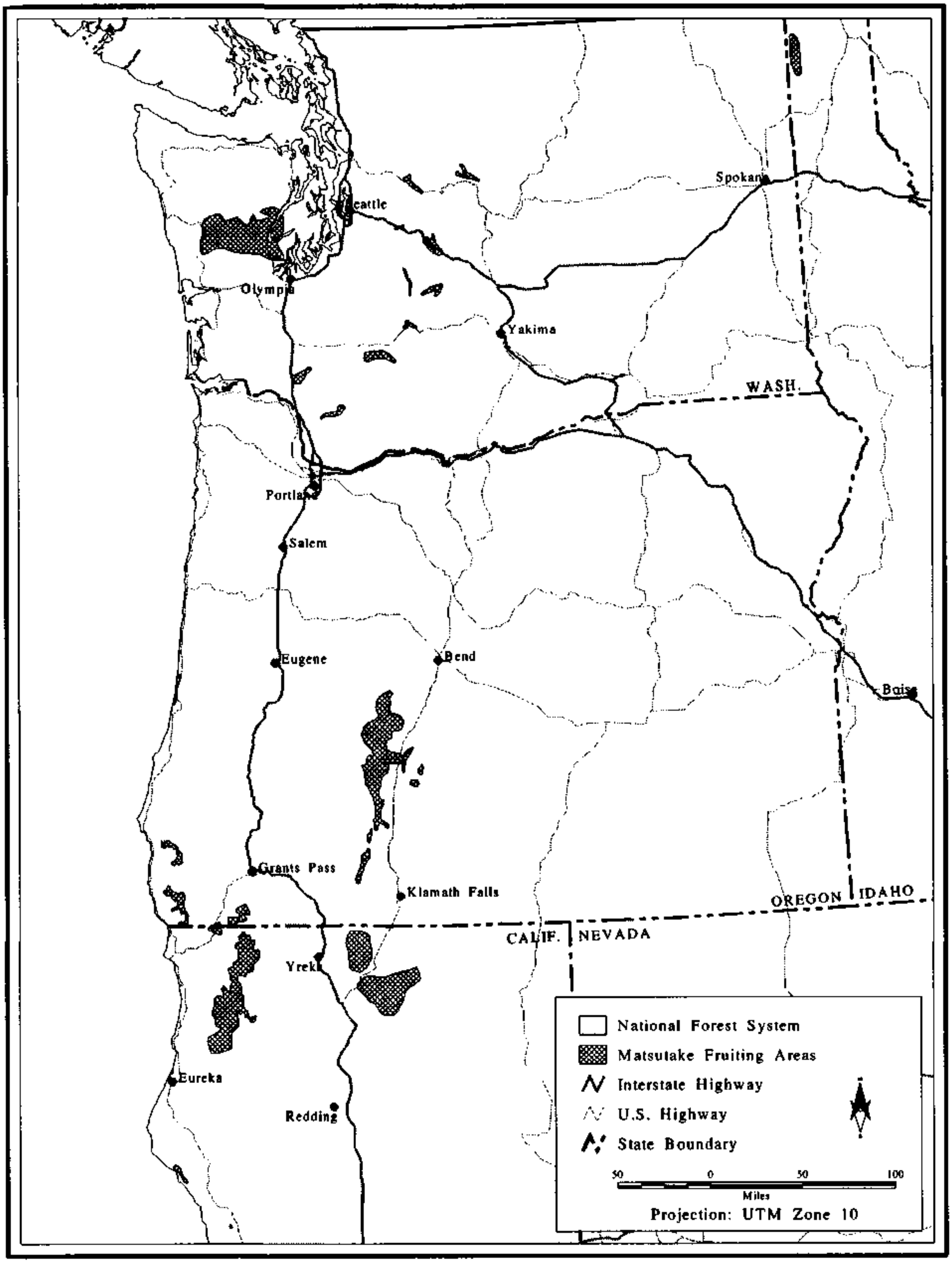

Figure 4—Known commercial matsutake harvesting areas in the Pacific Northwest. (Map created by Cary Lorimor, GIS analyst, Pacific Northwest Region, U.S. Department of Agriculture, Forest Service.)

- Shore pine plantations—This habitat type is found on dry dunes stabilized through management actions Almost all plantations where matsutake fruits are at least 35 years old The shore pines have an understory of Scot's broom and remnant patches of European beachgrass Several native species have begun to colonize the now-stabilized dune area including Sitka spruce, evergreen huckleberry, pearly everlasting, yarrow, and kinnikinnic Candy stick is present in older plantations Duff and litter layers are typically 5 to 10 centimeters deep Many areas contain well-developed moss layers Elevation ranges from 3 to 100 meters Slope and aspect vary

Three general habitat types occur in the southern Cascade Range where matsutake consistently fruits[3] Large quantities are regularly harvested from the Diamond Lake Ranger District of the Umpqua National Forest, the Crescent Ranger District of the Deschutes National Forest, the Chemult Ranger District of the Winema National Forest, the Goosenest Ranger District of the Klamath National Forest, and the McCloud Ranger District of the Shasta-Trinity National Forest

- Mixed conifer/snowbrush, manzanita—The presence of Shasta red fir (an important matsutake host) distinguishes this habitat from the mixed-conifer habitat in the Washington Cascade Range Shasta red fir grows in association with Pacific silver fir, white fir, and mountain hemlock on the eastern to northern aspects and at higher elevations On southern or western exposures and at lower elevations it grows with sugar pine and ponderosa pine Snowbrush and green-leaf manzanita dominate on the southern exposures or in disturbed areas Creeping snowberry and mahala mat are common in mesic areas, whereas bitterbrush and sage species prevail at lower elevations or in xeric environments *Phacelia* species, goldenweed, strawberry, western needlegrass, Ross's sedge, and bottlebrush squirreltail are common herbaceous associates As this habitat grades into northern California (as far south as the area around Mount Shasta) ponderosa pine, white fir, and incense-cedar become more common The sparse forest floor vegetation often includes dusky horkelia, western prince's pine, little prince's pine, mountain sweetcicily, white hawkweed, and heart-leafed arnica Soils are air-laid pumice over lava colluvium, cinders, and tuff Organic litter layers average 2 to 12 centimeters deep Elevation ranges from 1350 to 1650 meters in the north and 1450 to 1850 meters in the south (plate 11)

- Lodgepole pine/bitterbrush/needlegrass—The dominant overstory is lodgepole pine, 60 to 120 years old Brush understory is predominately bitterbrush with rabbitbrush, needlegrass, and sedges less common This habitat type is found on coarse sand to loamy sand or pumice soils Litter averages 2 to 8 centimeters deep Elevation ranges from 1600 to 2000 meters Slope position is generally flat or concave (plate 12)

[3] Information on commercially important habitats in the southern Cascade Range contributed by Gerry Smith Winema National Forest Chemult OR 97731 and Max Creasy Klamath National Forest Orleans, CA 95556

- Lodgepole pine/manzanita—Lodgepole pine is the predominant species with Shasta red fir, white fir, or white pine present depending on slope position The common understory species are pinemat manzanita, green-leaf manzanita, and western needlegrass, with some scattered bitterbrush The soils consist of air-laid pumice and loamy coarse sand Litter layers range from 2 to 8 centimeters deep Elevation ranges from 1550 to 1850 meters Slope position is generally flat or convex

The Klamath Mountains of southwestern Oregon and northern California contain three habitat types where matsutake consistently fruits [4]

- Tanoak, Douglas-fir, madrone/huckleberry, rhododendron—This habitat type is found in closed-canopy tanoak stands (50 to 150 years old) with scattered Douglas-fir, madrone, and knobcone pine Brush understory often consists of evergreen huckleberry, manzanita, and Pacific rhododendron Herbaceous ground cover is generally lacking and fruiting occurs in a duff layer of hardwood leaves 2 to 12 centimeters deep Soils are derived from schists, conglomerates, metasediments, and sandstones Elevation ranges from 300 to 800 meters Slope and aspect vary but ridges and south to southeast exposures are most productive Matsutake fruits in this habitat in Oregon between the Windchuck and Rogue River drainages in a band 15 to 40 kilometers inland from the Pacific Ocean In California, it fruits in this habitat on the Hupa Indian Reservation, in the Orleans, Gasquet, and Lower Trinity Ranger Districts of the Six Rivers National Forest, and further south in the King Range National Conservation Area to at least Laytonville
- Tanoak, Douglas-fir, golden chinkapin/Oregon grape, poison oak—This habitat type is found in closed-canopy tanoak stands (50 to 150 years old) with Douglas-fir, golden chinkapin, madrone, and sugar pine scattered in the overstory The understory vegetation typically consists of smaller tanoak, golden chinkapin, and madrone, in addition to canyon live oak, white fir, poison oak, and vine maple Herbaceous ground cover is generally light and contains dwarf Oregon grape, salal, twinflower, candy stick, and sword-fern Matsutake fruits in a duff layer of hardwood leaves 2 to 12 centimeters deep Soils are derived from metasediments, metavolcanic, igneous intrusive, and granitic parent materials Elevation ranges from 550 to 900 meters, slope and aspect are variable, but ridges and north to northeast exposures have the most consistent production In Oregon, matsutake fruits in this habitat in the Illinois Valley west from the Elk Creek drainage and east to the Deer Creek drainage Isolated fruiting occurs in the Applegate River watershed in similar habitats In California, fruiting occurs in portions of the Ukonom and Happy Camp Ranger Districts of the Klamath National Forest, along the Klamath River from the mouth of the Salmon River north to Indian Creek, and along the Salmon River from the mouth upstream to the Forks of the Salmon (plate 13)

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[4] Information on commercially important Klamath Mountains habitat contributed by Max Creasy Klamath National Forest Orleans CA 95556 and Jeanne McFarland Humboldt State Univeristy Arcada CA 95521

- Douglas-fir, canyon live oak/poison oak, red bud/hairy honeysuckle—Canopy layers range from predominately canyon live oak to a mix of live oak and Douglas-fir. Madrone and California black oak are typical hardwood associates. Common shrubs are poison oak, California red bud, and hairy honeysuckle Soils are shallow to deep, well drained, and derived mostly from shists and metasediments with some igneous intrusives Elevation ranges from 300 to 1050 meters Although this plant community is commonly associated with south and west aspects, matsutake predominantly fruits where it occurs on east and north aspects that have steep slopes and soils with high rock content This habitat is common along the Klamath River from the mouth of the Trinity River to Happy Camp and along the Salmon River from the mouth upstream to the Forks of the Salmon

Méxican Habitats

The distribution and harvest of the American matsutake in Mexico is limited to temperate montane forests at relatively high elevations (greater than 1500-2000 meters) [5] These forests are biologically diverse; México has more pine species than any other country. The American matsutake likely grows in association with various tree species, especially pine, fir, and evergreen oaks The taxonomic identity of mushrooms collected as matsutake in México is unclear, some specialists feel there are distinct species or ecotypes in México and, given the diversity of habitats and arboreal associates in México, this is possible (plate 14) Affinities of Méxican ecotypes or species with Eurasian and other North American species still need study, genetic analyses will be revealing The range of locations (fig 5) where matsutake is harvested coincides fairly closely with the distribution of the teocote pine, a matsutake host (plate 15) Commercial harvesting has occurred since 1985, principally in the States of Hidalgo, Mexico, Michoacán, Pueblo, and Veracruz (Villarreal and Perez-Moreno 1989) Although matsutake frequently fruits in remote areas with rugged topography, harvesters and mushroom companies are developing the means to quickly transport the mushrooms to their markets in Japan, thereby expanding their activities in México The fruiting season in Mexico is early, it ranges from late July through October, depending on the specific locale and elevation The southernmost extent of the range of the American matsutake is still unclear. Some harvesters are currently bioprospecting for new populations in Chiapas, México, and in Guatemala

[5] Information on commercially important habitats in Mexico derived from personal communications with Ignacio Chapela (Oaxaca, Mexico), University of California at Berkeley, California, and Luis Villarreal, Colegio de Postgraduados, Institucion de Enseñanza e Investigacion en Ciencias Agncolas Programa Forestal Montecillo, Mexico

Figure 5—The range of the teocote pine in Mexico (Critchfield and Little 1966). Although matsutake are associated with many pine, fir, and evergreen oak species in Mexico, the range of teocote pine approximates the locations where matsutake are collected commercially.

A Case Study of Shiro Ecology in Central Washington

In autumn 1985, Hosford and Ohara (1986, 1990, 1995) began the first matsutake shiro studies in North America in central Washington. Using the basic approach of Japanese investigators, they mapped shiros and characterized the topography, climate, soil type and vegetation. Each year, from late August through mid-November, each site was monitored one to three times per week for appearance of matsutake and other mushrooms. Matsutake were counted and their position in the shiro marked by flags color coded by year. From these markings, the relative position of mycelia and host roots (mycorrhizae) were determined and annual growth mapped. Soil temperature and moisture, fungal species, bacteria populations, and other biotic factors also have been examined.

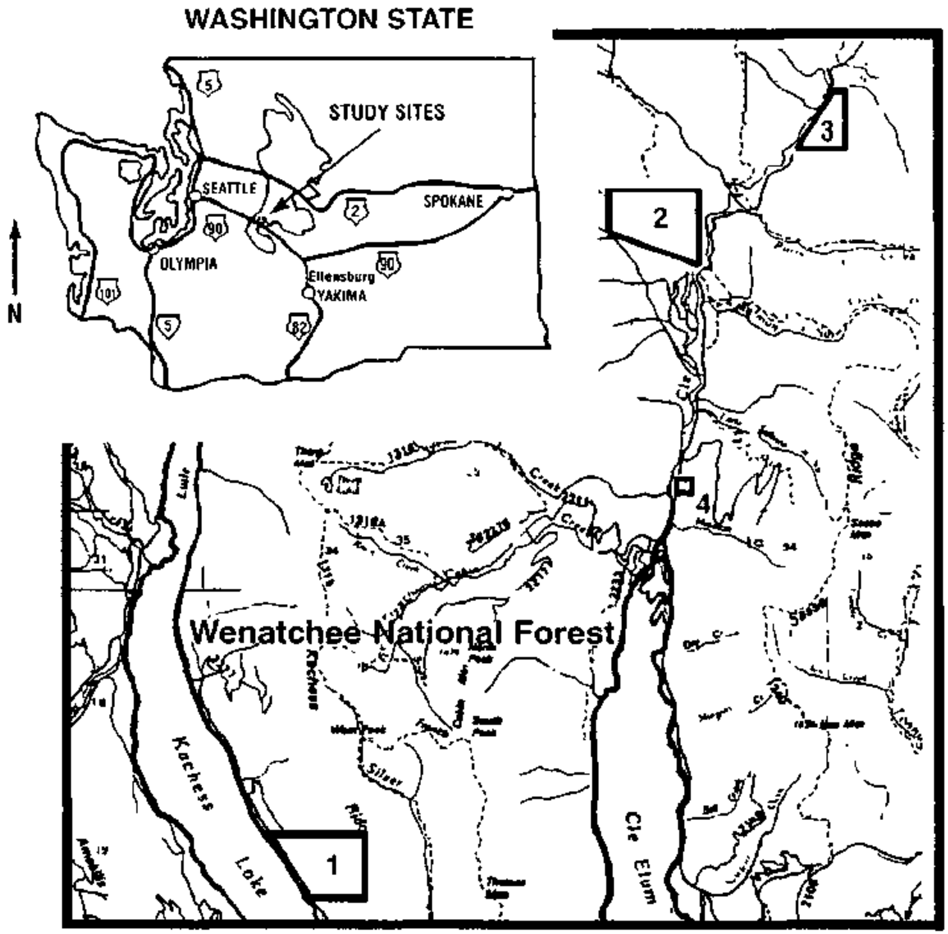

Figure 6—Study areas in central Washington (Hosford and Ohara 1990). Original shiro number for each site in parentheses; loss due to logging.

Sites	No. of shiros
1 = Lake Kachess	0(2)
2 = Salmon La Sac	3(10)
3 = Fish Lake	3 (4)
4 = Howson Creek	3 (3)
Total shiros	9(19)

Study Sites

Nineteen shiros were identified and mapped at four sites (fig. 6). Subsequent logging on private forests reduced the study to nine shiros on three sites. The sites occur in warm, moderately dry forest, on the east slope of the Cascade Range on both private and public land. The shiros were found on gentle, southwest-facing slopes and benches between 700 and 900 meters elevation. Summers are hot and dry, and most precipitation occurs between November and April as snow. The fruiting period for matsutake is relatively short, usually 2 to 3 weeks, and coincides with increasing rainfall from October through early November.

The study sites occur in several forest types—lodgepole pine (site 3), grand fir (site 2), and western hemlock (sites 1 and 4) that range from relatively dry to wet, respectively. All sites, except for site 4 (a climax stand), are mid- to late-seral stands from 80 to 200 years old. Grand fir is a minor overstory species at all four sites but common in the understory. Douglas-fir is present at all sites, dominant at sites 1-3, and codominant with western hemlock at site 4.

Shrub and surface vegetation is generally sparse in shiros. In the most productive shiros, vine maple and several ericaceous plants often are present. These plants and several other species, especially those in the Caprifoliaceae, were used as indicators for locating new shiros. In addition, the ectomycorrhizal fungi *Tricholoma zelleri, Gomphidius, Suillus, Cantharellus subalbidus* (the white chanterelle), and *Rhizopogon parksii* were found in or near shiros at the time of matsutake fruiting. Table 1 lists plant and fungus species documented at these research sites.

Table 1—Plant and fungal species typically found in an *Abies grandis/Acer circinatum/ Chimaphila umbellata/Tricholoma magnivelare* forest association in central Washington

Species[a]	Family
Tree overstory layer:	
*Abies grandis**+	Pinaceae
Pinus contorta v. *latifolia*	Pinaceae
Larix occidentalis	Pinaceae
*Pseudotsuga menziesii**+	Pinaceae
*Tsuga heterophylla**+	Pinaceae
Thuja plicata	Cupressaceae
Tree understory layer:	
*Abies grandis**+	Pinaceae
*Tsuga heterophylla**+	Pinaceae
Thuja plicata	Cupressaceae
Shrubs and subshrubs:	
*Acer circinatum**	Aceraceae
Berberis nervosa	Berberidaceae
Corylus cornuta	Betulaceae
*Linnea borealis**	Caprifoliacea
*Symphoricarpos oreophilus**	Caprifoliacea
*Pachystima myrsinites**	Celastracea
Cornus canadensis	Cornaceae
*Arctostaphylos uva-ursi**	Ericaceae
*Chimaphila umbellata**	Ericaceae
Gaultheria shallon	Ericaceae
*Pyrola asarifolia**	Ericaceae
*Pyrola picta**	Ericaceae
Pyrola secunda	Ericaceae
*Vaccinium membranaceum**	Ericaceae
Vaccinium parvifolium	Ericaceae
Rubus ursinus	Rosaceae
Rosa woodsia v. *ultramontana**	Rosaceae

Table 1—Plant and fungal species typically found in an *Abies grandis/Acer circinatum/ Chimaphila umbellata/Tricholoma magnivelare* forest association in central Washington (continued)

Species[a]	Family
Herbs	
Achlys triphylla	Berbendaceae
*Hieracium scouleri**	Compositae
Trillium ovatum	Liliaceae
*Goodyera oblongifolia**	Orchidaceae
Trientalis latifolia	Primulaceae
Pteridium aquilinum	Polypodiacea
Mushrooms	
*Tricholoma zelleri** (= *Tricholoma focale?)*	Agaricales
Tricholoma flavovirens	Agaricales
Tricholoma virgatum	Agaricales
*Gomphidius subroseus**	Agaricales
Gomphidius glutinosus	Agaricales
Gomphidius smithii	Agaricales
Gomphidius oregonensis	Agaricales
R*ussula cascadensis**	Agaricales
Russula (emetica complex)	Agaricales
Cystoderma granulosum	Agaricales
Inocybe lilacina	Agaricales
Dermocybe species	Agaricales
Cortinarius montanus	Agaricales
Cortinarius species	Agaricales
Lepiota clypeolaria	Agaricales
Hebeloma crustiliniforme	Agaricales
Suillus species	Boletales
*Suillus brevipes**	Boletales
*Cantharellus subalbidus**	Cantharellales
Gomphus floccosus	Cantharellales
*Rhizopogon parksii**	Hymenogastrales
Rhizopogon ellenae	Hymenogastrales

[a] * = indicator species, + = suspected mycorrhizal host
Source Hosford and Ohara 1990

PROFILE

Duff (0): 2 to 7 cm thick needles, leaves and twigs

Surface Soil (E): 0 2 to 7 5 cm thick light gray loose sand and loamy sand

(EB) 0 to 25 cm thick, grayish brown to strong brown, firm to very triable loam or loamy sand, 15 to 35 percent gravel

SubSoil (B): 25 to 1 75 cm thick brown fnable, sandy loam or loamy sand, 10 to 50 percent gravel

Substratum: 75 to 300 cm thick,very firm (compacted), sandy loam or loamy sand, 15 to 65 percent gravel and cobbles

CHARACTERISTICS

Parent material: glacial till

Drainage class: well to moderately well drained

Typical landform: valley bottom and sideslopes Valleys generally have characteristic U-shape Slopes range from 3 to 40 percent

Depth of Bedrock: generally >360 cm, but some rock outcrops occur

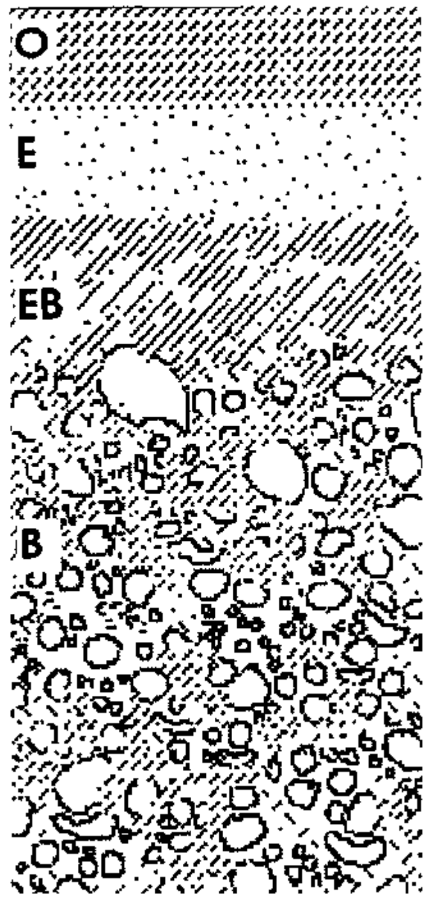

Figure 7—Soil profile and characteristics at central Washington study sites (Hosford and Ohara 1990).

Soils are typically spodosols, originate from glacially deposited parent material, have less than 25 percent organic matter, and are thin, sandy and well drained. In profile they have a shallow, but distinct, ashy E-horizon and a reddish B-horizon enriched with iron and organic matter. A relatively thin duff layer, 0.5 to 4 centimeters thick, overlies the E-horizon (fig. 7).

Mushroom primordia developed in the ashy E-honzon, whereas the ectomycorrhizae developed below, in the transitional grayish-brown EB-horizon. Development from primordia initiation to fully opened specimens took about 10 to 20 days depending on soil temperature and moisture. As the primordia absorbed moisture they expanded upward through the ashy E-layer Fully expanded mature specimens often just barely reached or broke through the duff layer, so lateral spore dissemination was restricted [cover insert]

Shiro Description

American matsutake fruited more abundantly in mixed stands of Douglas-fir and western hemlock (for example, site 4) than in other forest types Although density of fruiting was relatively high, distribution of the mushrooms was unevenly scattered This is similar to the Japanese matsutake in mixed stands of northern Japanese hemlock (Ohara 1981). Perfect mycehal rings were uncommon and the shape of the ring often appeared fragmented or as separated arcs (fig 8) When the fragments or arcs were connected by lines, the shiro typically took the shape of a semicircle. Figure 9 shows the profile of a shiro that had a diameter of about 6 meters and expanded about 4 centimeters per year on average The physiologically active mycorrhizal zone (AMZ) (II-III) was relatively wide and deep with abundant blackish, branched mycorrhizae The ectomycorrhizae examined were structurally similar to those formed by the Japanese matsutake in that they lacked well-defined Hartig nets The epidermis was sloughed when infected by the fungus and the hyphae invaded the intercellular spaces of the root cortex [6] Preliminary studies also indicated that the AMZ had a simplified bacterial flora similar to that of the Japanese matsutake shiro The boundary between the decaying mycorrhizae and decayed mycorrhizae, zones IV and V, could not be visibly distinguished

Shiro Productivity

Each study site and all shiros were monitored one to three times per week from September to November 15 Mushrooms were marked and recorded, but for uniformity, only counts from the two most productive shiros per site are presented for comparison Ambient temperature and precipitation data, recorded as monthly averages and accumulative values, respectively, were obtained from a nearby weather station at Lake Cle Elum

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[6] Considerable disagreement exists about the trophic character of the matsutake fungus Various researchers have reported characteristics of saprobic, parasitic, and mycorrhizal fungi Aggressively invasive hyphae and a weakly developed mantle are cited as evidence that species of matsutake fungi may be somewhat parasitic Other researchers have been unable to substantiate these claims, rather they find typical mycorrhiza morphologies Likely these discrepancies are the result of examining mycorrhizae in various stages of infection and senescence That matsutake fungi may vary on a spectrum of mutualism to parasitism (Johnson and others, in press) is certainly possible Likewise, many mycorrhizal fungi have some saprobic (decompositional) abilities, and often these abilities are enhanced by surplus carbohydrates the fungus obtains from its photosynthetic plant host (Durall and others 1994, Miller 1995) The dense mycelial mat of the matsutake shiro suggests that it may be capable of aggressively weathering mineral soil through organic acid exudates that alter soil chemistry and shift microbial populations (Griffiths and Caldwell 1992)

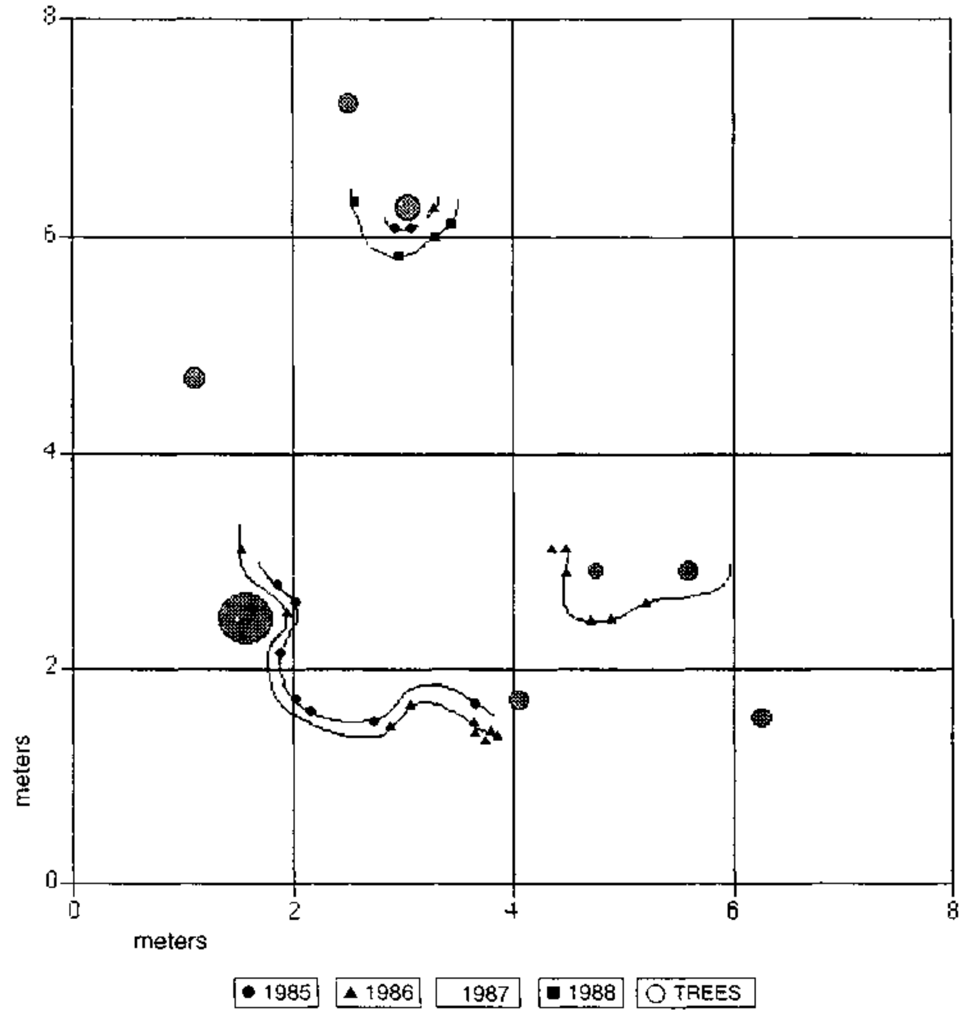


Figure 8—Mushroom map for *Tricholoma magnivelare* at site 1, shiro 1, 1985-88 (Hosford and Ohara 1990).

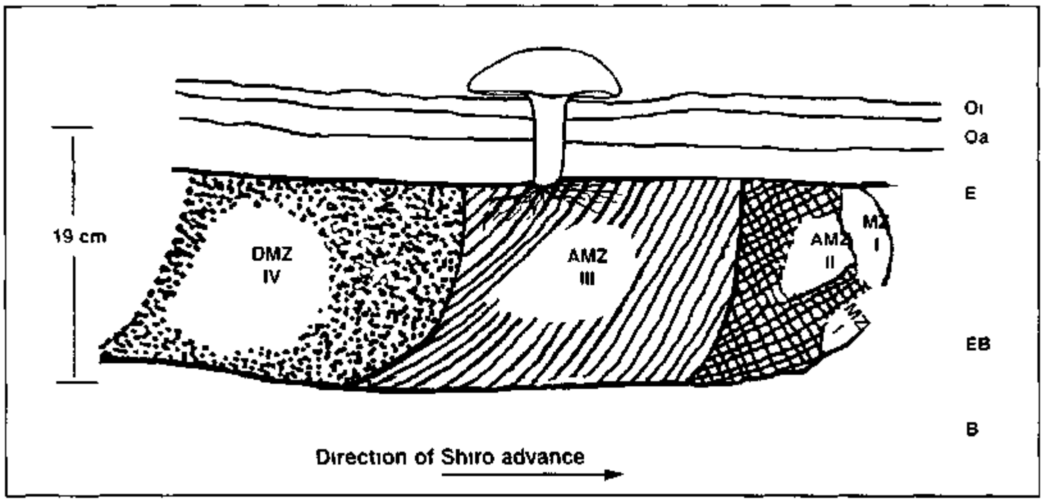


Figure 9—The shiro profile of a *Tricholoma magnivelare* shiro at site 1, a western hemlock forest type with Douglas-fir and true fir species (Hosford 1995).
MZI = leading edge of mycelium
AMZ = physiologically active mycorrhizal zone
AMZ - II = next season's fruiting
AMZ - III = present fruiting zone
DMZ - IV = decaying mycorrhizal zone
Oi = organic, slightly decomposed (duff) layer
Oa = organic, highly decomposed layer
E = soil horizon of maximum eluviation
EB = thin transition layer
B = soil horizon of maximum illuviation

Figures 10 through 13 compare the sites over four seasons. Cumulatively, Site 1 (Lake Kachess, western hemlock site) was the most productive, producing 48 mushrooms. Site 2 (Salmon La Sac, grand fir site) and site 3 (Fish Lake, lodgepole pine site) each produced 32. Site 4 (Howson Creek, western hemlock/Douglas-fir site) produced 37. Higher production at Lake Kachess and Howson Creek (sites 1 and 4) may have been related to slightly wetter and warmer conditions, as indicated by the relative abundance of western hemlock. Both sites also have an understory of vine maple and a variety of encaceous plants, which seem to be associated with shiros in this area. The Salmon La Sac and Fish Lake sites (sites 2 and 3), on the other hand, are higher in elevation and drier. Both contain lodgepole pine, western larch, and a sparse ground cover of species such as Oregon grape.

On a combined yearly basis (sites 1 through 3 only), 1988 production was the highest with 51 mushrooms over 18 days; 1985 was second with 39 over 16 days; 1986 was third with 22 (zero at site 3) over 11 days; and 1987 had none (note: these figures represent counts from only two of the most productive shiros at each site). Differences in seasonal length and production are related directly to rainfall and temperature. In 1985, 1986, and 1988, fruiting occurred when accumulative rainfall reached 14 centimeters and continued until accumulation reached 35 centimeters or more. At the same time, average temperatures were mild and above 5 °C. In 1987, a year of no mushroom production, temperatures were mild and above 5 °C through mid-November, but only 16 centimeters of rain fell during the same period. A pattern similar to 1987 has occurred several times since; these were some of the driest and warmest years recorded in the area.

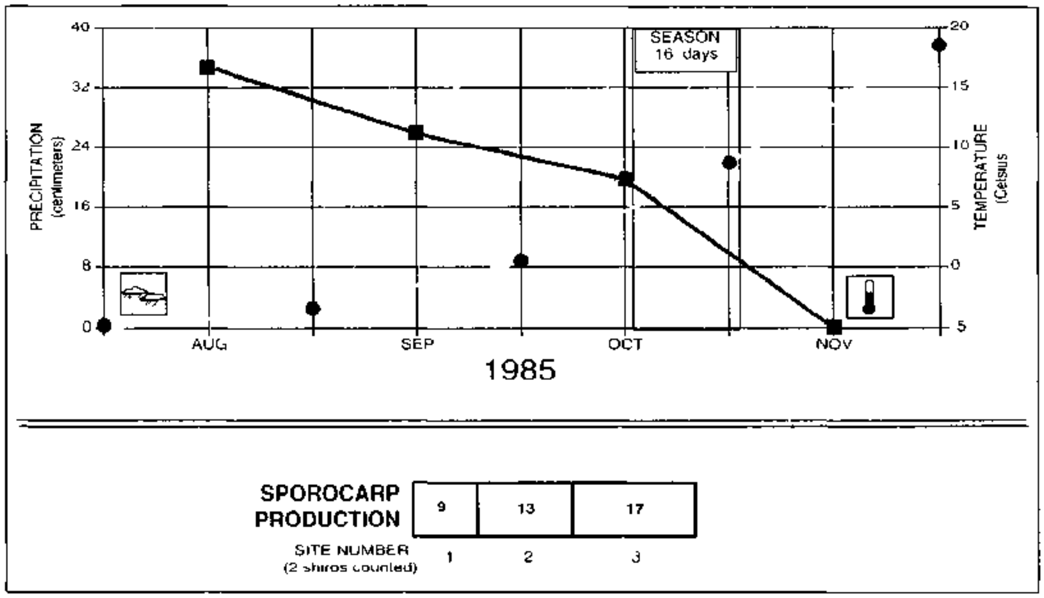


Figure 10—Matsutake production, 1985 season in central Washington (Hosford and Ohara 1990).

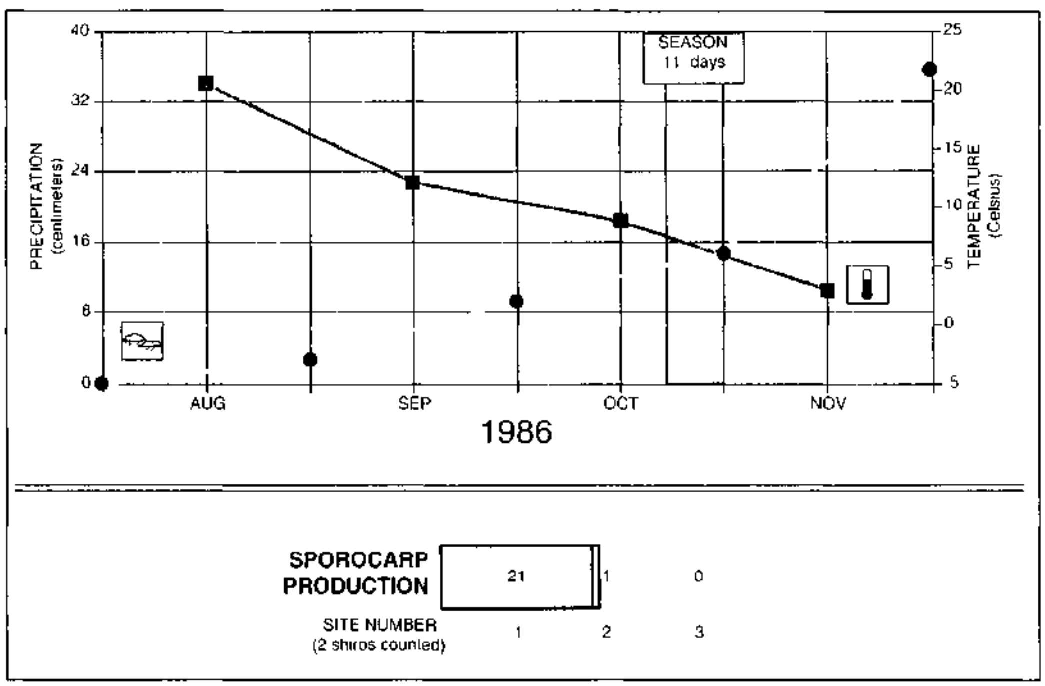


Figure 11—Matsutake production, 1986 season in central Washington (Hosford and Ohara 1990).

Plate 1—Mushroom buyers establish temporary buying stations in local communities during the harvestseason

Plate 2—American matsutake collected near Chemult, Oregon

Plate 3—Matsutake collection baskets lined up for sale at a buying station. Sales often occur in the evening after a long day of harvesting

Plate 4—Mature Americanmatsutake specimens.

Plate 5—Young American matsutake specimens.

Plate 6—Japanese matsutake

Plate 7— A tanoak mycorrhizae excavated from immediately underneath a matsutake.

Plate 8—A "Hiroshima tunnel" for enhancing the fruiting of Japanese matsutakes.

Plate 9—*Allottropa virgata*, the candy stick plant, obtains all its food from mycorrhizal fungi, because it lacks chlorophyll and has rudimentary mycorrhizal roots. It is frequently found adjacent to matsutake and is thought to be a symbiont of the fungus.

Plate 10—Matsutake habitat at the Oregon dunes. Sixty-year-old shore pines are in the background, pine seedlings are becoming established in the midpround, and European beachgrass is colonizing the sand dunes in the foreground.

Plato 11— Matsutake fruiting is closely assorted with the large Shasta red tirs that are common dominant species in the mixed conifer/snowbrush-manzanita habitat in the southern Oregon and northern California Cascade Range.

Plate 12—Lodegepole pine often grows so dense that understory brush is shaded to exclusion, and malsutake are easy to find.

Plate 13—Matsutake habitals in the Klamath Mountains of southwest Oregon and northern Clailfornia typically contain a mixture of tree species, age classes, and canopy layers. Grand tir can be seen in the background. Douglas-tirs are the larger conifers in the foreground. The light-barked hardwoods in the lower foreground are Pacific madrone. Surrounding shrubs consist of young tanoak regenerating from stump sprouts.

Plate 14-Melsulake corded in a Pinus teocole forest, Cofre de Perote, Veracruz, México State, México. Note the brown color in contrast to the whiter *T. magnivelare* found elsewhere n North America

Plale 15— *Pinus teocole* forest habitat Cofre de Perote, Veracruz Mexico State, México. Harvester in the foreground

Plate 16—Blue tarps often indicate temporary camps of travelling mushroom harvesters Forest managers are increasingly designating special sites for mushroom harvester camps and providing services.

Plate 17—A matsutake button emerging from tanoak leaf litter, southwest Oregon.

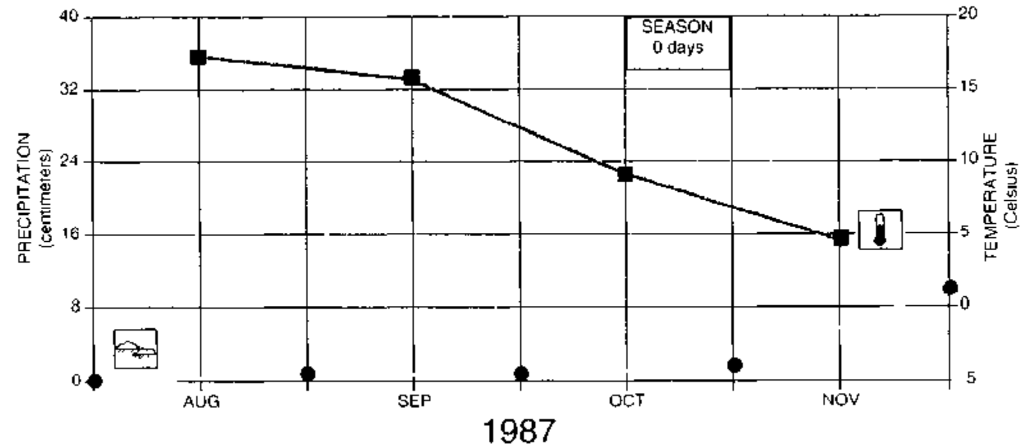
Plate 18—Siskiyou National Forest employee examining an area where tanoak leaves were raked downhill to search for matsutake buttons.

Plate 19—A matsutake button emerging from reindeer lichens on the Oregon dunes.

Plate 20-An example of litter raking to search for matsutake buttons in a state park, Oregon dunes

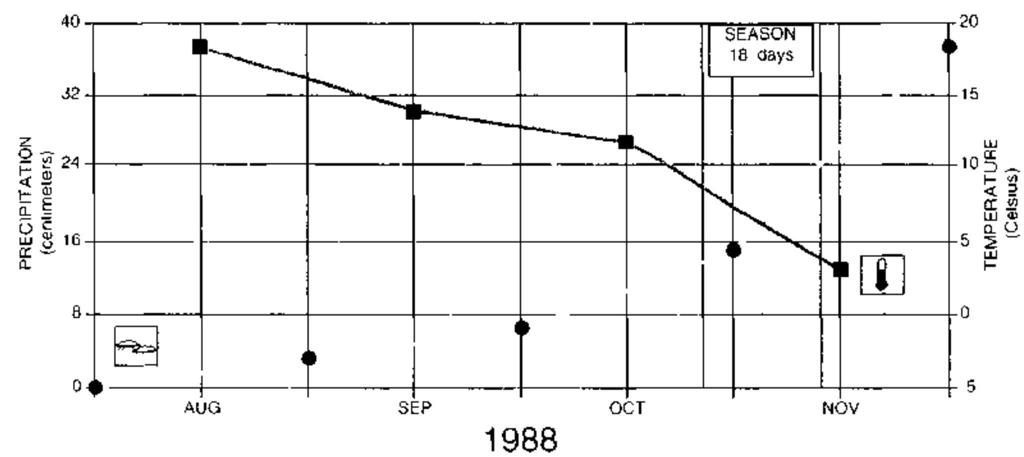
Plate 21—A deep rake treatment applied to a study shiro near Diamond Lake, Oregon Flags mark where matsutake grew in the prior year.

Plate 22—A soil plug collected underneath a matsutake to study the mychorrhizae. Note the white spores on the needles under the mushroom.



SPOROCARP PRODUCTION	0	0	0
SITE NUMBER (2 shiros counted)	1	2	3

Figure 12—Matsutake production, 1987 season in central Washington (Hosford and Ohara 1990)



SPOROCARP PRODUCTION	18	18	15	37
SITE NUMBER (2 shiros counted)	1	2	3	4

Figure 13—Matsutake production, 1988 season in central Washington (Hosford and Ohara 1990)

Continuing Research

In spring 1995, we began daily monitoring of soil temperature at site 4 (Howson Creek) In future years, soil moisture will be monitored weekly from mid-August through November Measurement of mycelial and mushroom growth and productivity will continue at Howson Creek only Meanwhile, we will follow fungal and plant succession at Lake Kachess (site 1), which was logged in 1992 Dr Ohara will analyze soil microbes in the AMZ and examine mycorrhizae Spore germination and cultural studies of American matsutake will be conducted in cooperation with colleagues From additional ecological data we hope to refine our geographic information system (GIS) map of potential matsutake habitats in the Wenatchee National Forest

Chapter 3: Managing the Matsutake Harvest

Social and Economic Context

Japan started importing matsutake in 1975, but a large portion of the import consists of *T. matsutake* from North and South Korea and China (EAITC 1990). Imports of *T. magnivelare* from North America also began in the mid 1970s but have increased a thousand-fold since the mid 1980s. Imports from North America (Canada, the United States, and México) now average 500 metric tonnes (500 000 kilograms) per year and constitute about 15 percent of worldwide imports (fig. 14). Redhead (1996) provides a history of the commercial matsutake harvest in Canada and the United States, including an extensive bibliography. Bandala and others (1997) discuss recent matsutake harvesting in México, including issues of communal land tenure and harvest sustainability. We summarize features of the harvest that pertain to the management of forest ecosystems and the individuals who obtain income from harvesting these mushrooms.

The largest harvest of American matsutake typically occurs in interior British Columbia. De Geus and Berch (1997) summarize the social, economic and managerial issues generated by Canadian harvest. They report that by the early 1980s, large volumes were being collected. Many of they harvest areas are inaccessible by road, but the mushrooms are valuable enough to justify transporting harvesters and mushrooms by helicopter.

Washington, Oregon, and California experience most of the matsutake harvesting in the United States (with lesser quantities from the coniferous forests of the intermountain West). Schlosser and Blatner (1995) provide the only published survey of matsutake harvest quantities and values; in this case, from Oregon, Washington, and Idaho.

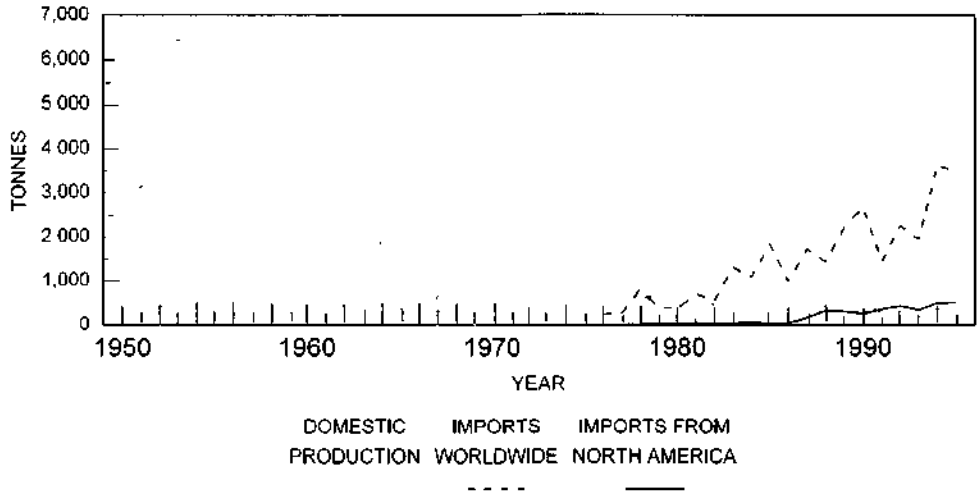


Figure 14—Matsutake production and imports, 1950-95. (Graph by Jim Weigand, USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon; sources: Japan Ministry of Agriculture, Forests, and Fisheries and Japan Tariff Association.)

Mushroom brokers have recently employed scouts to arrange matsutake harvests from the mountainous regions of México. Limited accessibility to international airports has hindered rapid transport of fresh Méxican mushrooms to Japanese markets, but export quantities are likely to increase as harvest permission and transport arrangements are established.

Harvest in these three North American countries is strongly influenced by land ownership patterns. On Federal and private lands, harvesters typically operate independently. They sell the mushrooms they collect to the highest bidder, usually representatives of mushroom processing and brokerage companies purchasing mushrooms at local, temporary buying stations. By contrast, tribes of indigenous Americans in the three countries are attempting to derive communal benefits from harvests on their lands. Richards[1] reports on the traditional role of matsutake harvesting in the culture of the Karuk Tribe of northern California. Chapela and Palm (1996) summarize a discussion session about the relation of matsutake harvests to the potential for sustainable community development in forested regions of México, the United States, and Canada.

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[1] Richards, B. [In review]. Native American ethnoecology and ecosystem management: Karuk harvesting of matsutake (tanoak) mushrooms.

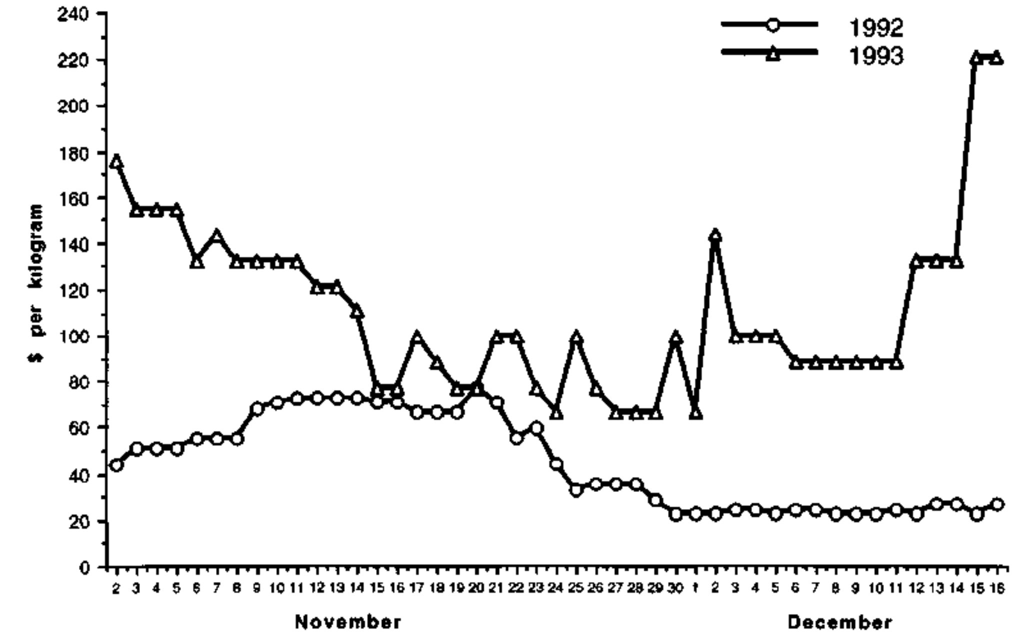

Figure 15—Price fluctuations for grade 1 matsutake during the 1992 and 1993 fruiting seasons in the Illinois Valley, southwest Oregon

Because of the international nature of matsutake harvest and commerce, the price paid to harvesters in each location depends on fluctuations in quantities collected elsewhere (fig. 15). To date, little has been published regarding international commerce in matsutake. Mushroom brokers typically consider their activities proprietary information, thereby hindering efforts to summarize regional or national harvest and sales information. Efforts to study market price structures and factors influencing commerce in matsutake are needed to place harvest management plans in perspective. Research efforts aimed at cultivating matsutake in managed plantations of appropriate mycorrhizal host trees or in pure culture without host trees are not likely to produce large quantities in the next decade or two but may eventually impact the level of harvesting from forests.

Harvesters can earn hundreds of dollars a day if high-quality mushrooms are abundant and the prices are high Buyers pay in cash and often handle tens of thousands of dollars each day. Mushroom buying arguably represents the largest, legal, cash-based commerce remaining in U.S. society. Communities benefit from the income of local harvesters, and businesses profit from waves of migrant harvesters who shop for supplies, unlike timber, local communities do not obtain any harvest tax revenues.

Mushroom hunters are well known for secretive and protective attitudes towards "their" mushroom patches. Some individuals have picked in the same spots for decades. The recent decline in timber industry employment, increasing demand for matsutake, and high value for mushrooms encouraged more people to pick commercially than in the past. This has led to conflicts with individuals who traditionally have harvested matsutake. The most salient example is commercial harvesters entering Native American tribal picking grounds; but other citizens also become upset when they find "newcomers" or "outsiders" in areas they have traditionally harvested. Tensions heighten when the newcomers are migrant harvesters who often follow the progression of matsutake fruiting from north to south along the west coast. Local and traditional pickers (for both personal and commercial use) complain that migrant harvesters have no vested interest in returning to the same patch of mushrooms year after year, and therefore use search and harvest techniques that may damage mycelial beds through raking or removal of organic layers of the soil. Conflict among harvesters also can result from prejudice toward other ethnic groups.

Migrant harvesters account for a large portion of the commercial work force and thus are important for providing a reliable supply of matsutake to buyers and brokers. This is particularly important in regions where local labor is insufficient to collect the available crop. Large and sudden influxes of migrant pickers, however, can catch public land agencies and local communities unprepared to provide adequate lodging, camping, sanitation, and garbage facilities (plate 16). Large numbers of people in the woods can create other problems, including increased litter, noise, fire danger, traffic hazards, disturbance of wildlife, conflicts with big game hunters, and the need for search and rescue operations. Federal agencies are facing these difficult challenges by developing new regulations and educational programs.

Managers must understand the diversity of backgrounds of the harvester groups if they are to effectively communicate harvest regulations and anticipate potential conflicts. Sociological surveys are needed to characterize various ethnic groups, their demographics, the role of mushroom harvesting in their household economies, their educational background, language constraints, cultural beliefs, and attitudes towards the forest. Sound ecosystem management must incorporate an understanding of these factors, because humans are an integral part of forest ecosystems (Daniels and others 1994, Pilz and others 1996, Richards and Creasy 1996).

Because the demand for and value of matsutake vary widely (within and between seasons), land owners or managers have difficulty calculating fair market value and reasonable compensation for the harvest from their forests. Managers also find it difficult to calculate the quantities of mushrooms collected from their lands. Harvesters often cross ownership boundaries in their search for mushrooms and sell to buyers of their choosing. Federal mushroom permits are not currently based on a percentage of the market value of the crop, as permits are for many other products. Higher permit fees are problematic because harvesters may not be able to predict if they can cover the expense.

Harvest regulations and permits differ widely among countries, land owners, and administrative units. The lack of uniformity confuses and frustrates both commercial and recreational harvesters. National Forests in the United States typically issue inexpensive or free permits for personal use and more expensive commercial permits for individuals who intend to sell their mushrooms. Personal use permits often specify a small allowable quantity, so that commercial harvesters find it more difficult to surreptitiously use the less expensive personal-use permit during collection and then sell the mushrooms anyway. Other National Forests or Ranger Districts require that matsutake collected for personal use be immediately sliced in a manner that destroys their commercial value. Law enforcement officers face new circumstances when patrolling mushroom harvesters. For instance, because matsutake are so valuable, some unscrupulous hunters use flashlights at night to avoid picking limits or to enter restricted areas. Many harvesters also carry firearms for signaling or defense, although the popular press has exaggerated the theme of "mushroom wars" (Lipske 1994, McRae 1993).

In 1988, Washington adopted legislation requiring buyers to report quantities of mushrooms purchased by county. This law was revised in 1991 but expired in June 1994 (State of Washington 1988, 1991). Oregon and Washington both have passed laws regulating the transportation of special forest products by requiring evidence of landowner permission for collection (State of Oregon 1993; State of Washington 1992, 1995). Neither state has regulated the sale or purchase of mushrooms yet. The dispersed and transient nature of mushroom collection and sales makes registration, licensing, and taxation difficult. Buyers may go elsewhere (wild mushroom harvesting is a global enterprise) to purchase mushrooms if local regulations become too burdensome for the participants.

Some forested areas have been set aside as inappropriate for matsutake harvesting. Crater Lake National Park has this policy. Commercial harvests are not allowed in designated Federal wilderness areas. Research areas, botanically sensitive areas, and areas where commercial or recreational picking may present other conflicts also are being designated as off-limits. Some managers are considering rotation of harvest areas or specifying restricted seasons. All these restrictions have been difficult to enforce, but as harvest pressures increase, managers are likely to develop more regulations to protect the resource. Improved matsutake production as a result of research may partially offset harvest restrictions.

As managers develop regulations governing the harvest of matsutake and other mushrooms, they must bear in mind that, at least on public lands, these resources belong to all citizens. Open communication and accurate information will be essential to ensure the fairness and efficacy of matsutake harvesting programs.

Biology, Ecology, and Forest Management

Sustainable management of the matsutake harvest requires improved understanding of the life history, reproductive mechanisms, population genetics, and ecology of the fungus. Estimating annual and long-term production, assessing the impact of harvesting and picking techniques on future production, and examining means of enhancing production are important considerations.

The American matsutake is adapted to a wide variety of soils, climates, host trees, and fungal competitors. Unlike the Japanese matsutake that predominantly occurs in young, early successional stands of pines, the American matsutake also fruits abundantly in stands that are uneven aged, have many canopy layers, and consist of multiple tree species. The applicability of Japanese matsutake research to management of the American matsutake therefore may be limited. Likewise, information about American matsutake in one location may not apply to other habitats. Productivity differs from site to site, and many of the factors influencing this variation are unknown, although age and species of host trees probably are important. The life histories and reproductive mechanisms likely differ less than productivity or ecotypic adaptations among various populations of the American matsutake, but differences may exist. For example, mycophagy (animal consumption of the mushroom) may be an important spore dispersal mechanism in some locations but not in others. An understanding of genetic variation among populations will allow managers to ascertain the importance of conserving local colonies by determining how unique or rare they may be and how much interbreeding occurs over various distances. Knowing the longevity and persistence of individual colonies under varied environmental conditions will give us clues to the factors influencing how colonies become established, grow, compete, decline, and die.

The potential interactions between forest management and matsutake production are numerous, complex, and site-specific. Clearcutting is efficient for timber harvest, but it removes the photosynthetic host and energy source on which the matsutake colony depends. Spores or mycelium of the matsutake may persist in the soil and colonize young trees, or the new stand may be inoculated with spores from nearby populations, but matsutake rarely fruit in stands less than 30 years old. On the other hand, matsutake may fruit more abundantly in young and middle-age stands that develop after logging or fire than in some undisturbed or old-growth forests.

Japanese foresters clear understory growth, reduce litter depth, and thin trees to increase matsutake production; so mild controlled burns or density management may improve American matsutake fruiting conditions. Changes in matsutake production may depend greatly on how the litter removal or thinning is conducted. Tree species selection, thinning intensity and patterns, soil compaction and movement, and slash disposal all may significantly affect matsutake production. As in Japan, the value of matsutake could be an important factor in design of thinning operations. Silviculturists may choose to plant favorable host species, or seedlings inoculated with the fungus, into known matsutake habitat. Irrigation, where practical, may be another effective technique for enhancing production (Amaranthus and others, in press).

American foresters, however, are likely to view the Japanese methods for enhancing matsutake production in a different context. Japan has been densely settled by people for millennia and has few remaining native forests, so original forest conditions are less important than desired future conditions. The area of matsutake habitat is much larger in western North America than in Japan, and forest management goals differ greatly. The preservation of biodiversity and healthy native ecosystems are important management goals on public lands in North America. Introducing new matsutake colonies into previously noncolonized habitats raises questions about potentially harmful side effects, such as displacing other sensitive fungal species.

A variety of animals consume matsutake If it is an important food source for wildlife, then human competition for these mushrooms may affect certain wildlife populations One forester has asked whether matsutake harvesting should be restricted near northern spotted owl nest sites on the supposition that northern flying squirrels (a main item of the spotted owl diet) might feed on the mushrooms Conversely, mycophagy by indigenous wildlife species might be an important spore dispersal mechanism in certain locales In southwest Oregon, for example, commercial collectors claim that shiros often are associated with dusky-footed wood rat nests and speculate that new shiros are formed through dispersal of spores in the wood rat feces Deer, elk, and bear actively seek matsutake and may consume large quantities, but the importance of this mushroom in their diet is unknown Many mushroom species contain concentrations of mineral salts and so may function as a natural salt lick for wildlife

Harvesting impacts may vary, for example, matsutake harvesting in the Oregon Dunes National Recreation Area may be threatened by the impact of people walking on the highly erosive sandy soils Moving freshly fallen leaves to look for matsutake buttons (immature mushrooms) in the Siskiyou Mountains of southwestern Oregon may have less impact than removing slow-growing moss from the sandy soils of coastal dunes (plates 17-20)

Concern for other organisms may also influence management decisions about harvesting A legal appeal[2] of commercial matsutake harvesting in the Klamath National Forest, northern California, was based on fears that matsutake harvesting would increase the likelihood that Port-Orford root rot would rapidly and widely spread to uninfected tree populations through soil movement on harvesters' boots or the tires of their vehicles Human trampling of locally endemic sensitive plant or fungal species is another concern

Ecosystem management issues surrounding the commercial harvest of matsutake and sustaining the resource are numerous and complex Although it is unlikely that the resource is in immediate danger from mushroom harvesting, long-term impacts from forest management and matsutake harvesting are less certain Much in the way of research and long-term monitoring remains to be done, if managers intend to sustain or improve the matsutake supply for human use while maintaining the biological role of the fungus in healthy forest ecosystems

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[2] October 28 1993 correspondence by Stephen H Suagee Attorney at Law to Barbara Holder Forest Supervisor Klamath National Forest in reference to the Karuk Tribes Notice of Appeal and Request for Stay of the October 20 1993 Decision Notice and Finding of No Significant Impact (FONSI) for [Tanoak] Mushroom Management by district rangers George R Harper and Sam Wilbanks for the Happy Camp and Ukonom Ranger Districts Klamath National Forest CA respectively On file with Klamath National Forest 1312 Fairlane Road Yreka CA 96097

Monitoring

Monitoring is essential to effectively regulate the matsutake harvest. On federal forests in the United States, Federal laws (U S Laws, Statutes, etc 1960, 1969, 1973, 1976a, 1976b) and derivative regulations require the monitoring of land management activities, the consequences of those activities, and the validity of management assumptions. Similar laws require resource monitoring on state lands The recently completed Northwest Forest Plan for Federal lands within the range of the northern spotted owl emphasizes that successful ecosystem management requires extensive monitoring (USDA and USDI 1994a, 1994b)

Types of Monitoring

Monitoring can be defined as the repeated recording or sampling of information for comparison with a reference The monitoring purpose determines what information is collected and what comparisons are made. Monitoring disturbance from matsutake harvesting activities, for example, can be as simple as observing or photographing a site before and after picking. It can be as complex as a regional experiment designed to investigate effects of forest practices on productivity of matsutake in various habitats. Two features are critical, however, regardless of the simplicity or complexity of a monitoring project First, observations must be repeated, and second, the observations must be compared to an established reference (the first observation, assumptions, anticipated results) Federal land management agencies have defined monitoring in various ways. Managers refer to implementation, effectiveness, and validation monitoring when they wish to assess the results of their management choices We discuss types of monitoring that are especially pertinent to understanding the matsutake resource and the impacts of its harvest

"Detection" monitoring entails surveys of occurrence or inventories of abundance that are repeated to detect trends Examples of detection monitoring questions include, Is matsutake present in a given location and how regularly does it fruit[7] How many matsutake are produced in a given area, and how much does production fluctuate during the course of a season and from year to year? How does this differ by plant association, seral stage, and habitat[7] How many are harvested and by whom[7] How will these factors vary over time and under different management scenarios[7]

"Evaluation" monitoring examines correlations or cause-and-effect relations between the sampled object and potentially related variables such as management activities Evaluation monitoring is triggered by concern over sustainability of management practices or trends discerned from detection monitoring For instance, the declining yield of matsutake in Japanese forests in recent decades has increased interest in "evaluating" the effects of our forest management activities on the American matsutake Evaluation monitoring assesses the effects of mushroom harvesting, timber harvesting, site disturbance and changes in forest structure and composition on mushroom productivity Evaluation monitoring also can include studies on mushroom harvesting impacts or strategies for increasing the production of matsutake

"Research" monitoring consists of long-term, intensive investigations of basic biological, ecological, and ecosystem management questions For example, managers will have difficulty determining long-term impacts of timber harvesting regimes on survival and health of matsutake populations over time until the genetic structure, dispersal mechanisms, and reproductive strategies of the fungus are better understood Specific topics include shiro development and senescence, mycorrhiza formation, character, and function, primordium initiation and determinants of mushroom growth, and spore maturation and modes of dispersal These studies should be conducted in various habitats and geographic locations to examine similarities and differences among locally adapted populations The role of the American matsutake in forest ecosystem processes also needs investigation What role does matsutake play in forest nutrient cycling, tree resistance to moisture stress, or food webs for wildlife species? What are the habitat requirements for matsutake? Are these ecosystem processes affected by mushroom harvesting[7]

Monitoring Challenges

Matsutake vary greatly in occurrence, abundance, and distribution from year to year Numerous factors influence fruiting of matsutake, such as rainfall and temperature patterns (Hosford and Ohara 1995) and other biotic and abiotic factors Poorly documented historical levels of production, ephemeral fruiting, and weather-dependent variations in fruiting all complicate efforts to characterize typical productivity Matsutake fruits in clustered patterns and is associated with specific trees and substrates The distribution of shiros also can differ from a few scattered groups to concentrated clusters This spatial and temporal variability in fruiting complicates sampling schemes (Amaranthus and Pilz 1996, Amaranthus and others, in press, Vogt and others 1992)

All types of monitoring and research are threatened by unplanned commercial and recreational harvest This is particularly acute for matsutake because of their high value Few sites are both convenient and secure Locked gates, obscure locations, and frequent visits by law enforcement personnel and researchers can reduce unauthorized harvesting Research plots should be clearly designated Agency personnel issuing permits should emphasize the importance of research results for maintaining commercial harvesting programs and then solicit harvester cooperation in protecting the sites

Predicting or modeling future mushroom productivity must be based on multiyear data sets, hence long-term access to secure sites is critical Many years or even decades of monitoring will likely be needed to quantify annual variations in production, determine the effects of management activities, and investigate the biological and ecological roles of the American matsutake in our ecosystems Matsutake monitoring shares many of the challenges inherent in sampling forest fungi in general Pilz and Molina (1996) provide a synopsis of these issues in a paper summarizing presentations and audience discussion at a conference on ecosystem management of forest fungi specifically convened to address this topic

Current Monitoring

Matsutake monitoring in the Pacific Northwest has evolved a multipurpose, decentralized approach Interested researchers from state and Federal institutions in Canada, the United States, and México have begun collaborating with land managers who experience heavy demand for matsutake harvesting on their properties Commercial harvesters and private mycological groups also have become involved. Land managers have questions specific to their ownership, but many monitoring questions are shared.

Following pioneering work on matsutake shiro ecology in central Washington, researchers from the USDA Forest Service, Pacific Northwest (PNW) Research Station, began to develop methods for estimating matsutake productivity in habitats reputedly ideal for reliable and abundant matsutake fruiting. A design with randomly oriented 2- by 50-meter strip plots, spaced to avoid overlap, was borrowed from fungus diversity surveys (O'Dell and others 1992) to sample matsutake production in representative habitats on lands administered by the Illinois Valley Ranger District, Siskiyou National Forest, the Medford District, Bureau of Land Management, in the Siskiyou Mountains of southwestern Oregon, and in the Chemult Ranger District, Winema National Forest, along the east side of the Cascade Range in south-central Oregon Installation of the permanent strip plots proved very expensive and labor intensive, and the sample area was inadequate to develop good estimates of production when fruiting was sparse Difficulties with trespass, drought, and inadequate sample area convinced researchers to abandon the strip plots in the Siskiyou Mountains Fruiting was more abundant and consistent at the Chemult sites, where productivity data have been collected with this sampling design since 1993 These plots also were designed to provide information on wildlife use, spatial association with potential mycorrhizal host plants, and correlations between fruiting and weather.

Productivity per unit of area has been determined by various methods in other habitats as well. In most cases, productivity was measured rather than estimated, because it was easier to discourage unauthorized harvesting in study areas by picking every matsutake almost daily. Figure 16 summarizes productivity per unit of area in several Oregon habitats known for their commercial harvesting popularity. It also illustrates the variability in annual levels of fruiting.

As noted previously, if matsutake harvesters are inexperienced or unfamiliar with an area, they may rake or move forest floor litter to locate the valuable buttons before others find them, or before the mushrooms lose value as their veils separate from the stem in maturity. Evidence of raking or digging has caused concern that subsequent matsutake fruiting in these areas might be diminished or destroyed. A study is underway at five sites[3] in Oregon to evaluate the effects of matsutake harvesting and searching techniques on matsutake production and commercial value. Treatments are as follows.

1. Control; no mushroom harvest. (Mushroom size is measured, and weight is estimated from size-weight regressions developed from harvested mushrooms.)

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[3] Diamond Lake Ranger District, Umpqua National Forest, Idleyld Park, OR 97447, Oregon Dunes National Recreation Area, Siuslaw National Forest, Reedsport, OR 97467, Chemult Ranger District, Winema National Forest, Chemult, OR 97731, Medford District, Bureau of Land Management, Medford, OR 97504, and Boswell Mine, Cave Junction, OR 97523

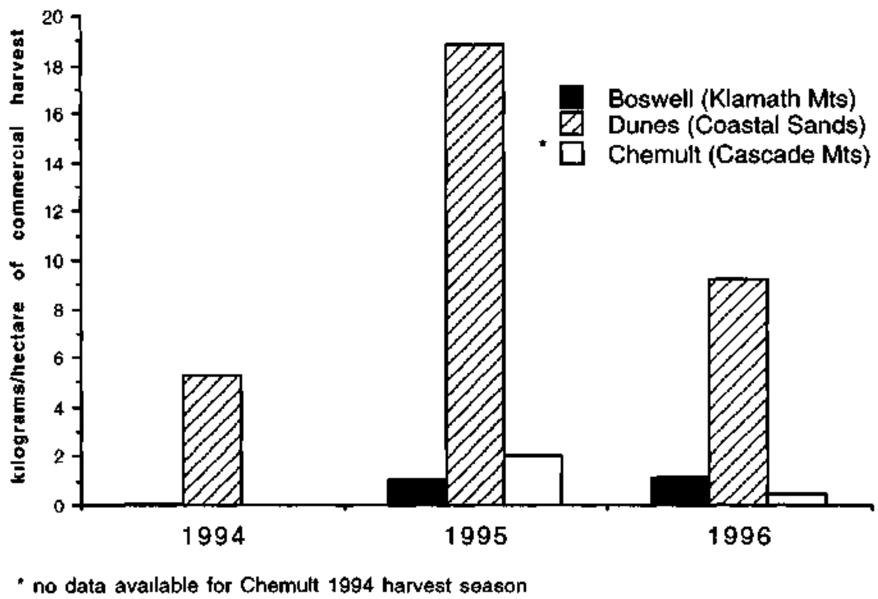

Figure 16—Matsutake production (kilograms per hectare) commercially harvested from experimental sites in Oregon

2. Harvest with minimal disturbance; that is, gentle rocking and pulling. (Mushrooms are counted and weighed.)

3. Total removal of the litter and duff layer with a rake down to the surface of the mycelial layer and no replacement of the duff. (Mushrooms are harvested, counted, and weighed)

4. Same as treatment 3, but the duff is replaced. (Mushrooms are harvested, counted and weighed.)

5. Raking through the duff and into the mycelial layer with no replacement of the duff. (Mushrooms are harvested, counted, and weighed.)

6. Same as treatment 5, but the duff and soil are replaced. (Mushrooms are harvested, counted, and weighed.)

These treatments are being applied to clusters of mushrooms (roughly corresponding to Japanese shiros) mapped in the first season at each site (plate 21). Productivity will be tracked for several years to monitor potential damage and subsequent recovery from the treatments. Mapped shiros not selected for this study can be used for other research. For instance, in an effort to explore means of enhancing production, irrigation trials have been started at several shiros in the Diamond Lake Ranger District, Umpqua National Forest (Amaranthus and others, in press).

In conjunction with the harvest impact studies, cooperating commercial harvesters have been measuring their harvests from surrounding areas and keeping track of the daily value of the mushrooms by commercial quality grade Their observations of environmental and ecological conditions associated with fruiting have proven invaluable for refining monitoring goals, strategies, and procedures Their familiarity with selling mushrooms (prices, competition among buyers, marketing strategies, and so forth) will be essential to characterize the local economics of matsutake harvesting

Other research in North America includes genetic studies of population variability and species relatedness in Mexico, the United States, and Canada,[4] detailed descriptions of *T magnivelare* mycorrhiza morphology on a variety of tree hosts[5] (plate 22), and studies of fungus diversity in coniferous forests that have documented the occurrence and productivity of *Tricholoma* species in a large variety of habitats.[6] Commercial and recreational harvesters of matsutake also have a wealth of personal knowledge about the fungus, unfortunately, this information is seldom collected, verified, or published

In spite of the notable matsutake research effort in recent years, several important questions still need answers. Managers wishing to predict matsutake production on watershed, landscape, and regional scales need good productivity estimates for many habitat types. This will require development of more efficient sampling methods and regional monitoring programs. For future reference, the precise location of identified shiros may be recorded with portable receivers that access Global Positioning System (GPS) satellites.

Research also is needed on the life cycle and reproduction of matsutake. Only by determining how the matsutake fungus typically reproduces and disperses into new habitat can we begin to understand the impacts of land management practices on long-term viability of the fungus and the sustainability of harvesting it

Last, but not least, social and economic studies of matsutake harvesters and commerce in matsutake would help managers develop fair harvest regulations and supply agency personnel and lawmakers in local, county, state, province, and Federal governments with the information needed to develop equitable, nonintrusive, and effective policies supporting and regulating the industry.

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[4] Researchers working on population variability and species relatedness are Carol Carter, Portland State University Portland, OR Ignacio Chapela (Oaxaca Mexico) University of California, Berkeley, CA, Charles LeFevre, Oregon State University Corvallis, OR, and Shannon Berch, Research Branch Laboratory Ministry of Forests, Victoria, BC

[5] Researchers working on American matsutake mycorrhiza morphology are Charles LeFevre, Oregon State University, Corvallis, OR, and Fidel Fogerty and Shannon Berch, Research Branch Laboratory, Ministry of Forests, Victoria, BC

[6] Researchers working on the occurrence and productivity of American matsutake are Scott Redhead, Centre for Land and Biological Resources Research, Agriculture and Agri-Food Canada, Ottawa, ON, Thorn O'Dell, USDA Forest Service, Pacific Northwest Research Station, Corvallis, OR, Dan Luoma, Oregon State University, Corvallis, OR, David Largent, Humboldt State University, Arcata, CA and Luis Villarreal, Colegio de Postgraduados Institucion de Enseñanza e Investigacion en Ciencias Agricolas Programa Forestal Montecillo Mexico

Matsutake and Ecosystem Management

Tenets of Ecosystem Management

The American matsutake occurs on lands administered by a wide variety of organizations, all of which are experiencing significant changes in their forestry practices Concerns about old-growth forests, endangered species, biodiversity, anadromous fish habitat, forest health, and sustainability have prompted the adoption of ecosystem management as a guiding philosophy for Federal lands in the United States Many other forestry organizations are adopting similar approaches to managing their lands The basic tenets of this concept include

- Using the best available ecological knowledge to conserve biological diversity and maintain healthy ecosystems while providing sustainable benefits for society
- Recognizing that ecosystems encompass dynamic processes that occur on many scales and that they overlap ownership boundaries and management jurisdictions
- Conducting periodic resource monitoring to address management concerns, determining the validity of management assumptions, and tracking the consequences of management activities, then adapting management plans to integrate the new information
- Soliciting the active participation of interested individuals and organizations in monitoring and management activities

These tenets provide a strategy for managing matsutake and their harvest despite significant gaps in our knowledge of their occurrence, biology, and ecology

Adaptive Management

Adaptive management may be considered the means for implementing ecosystem management It refers to the process of basing timely management decisions on the best available knowledge and revising those decisions as better information becomes available Application of this process entails continuously updating priorities, collecting information, testing assumptions, and revising management decisions Data collection efforts should be commensurate with potential impacts of selected management options

Modeling

Modeling is a systematic procedure for predicting the future results of complex management decisions A conceptual model of the factors influencing an outcome we wish to predict is developed by investigators familiar with the subject The most important factors and interactions are noted, and areas of critically needed information are identified These areas then receive priority for research and monitoring efforts As new information is acquired, estimates derived from various components of the model are tested and refined, thus improving the model

As an example, let us say a manager would like to predict how a timber management plan will affect availability of matsutake harvesting areas over time A model might include factors such as distribution of matsutake habitat types, matsutake productivity in each habitat type or forest stand age class, and how these factors will change with selected timber management scenarios The influence of timber management regimes on habitat characteristics such as vegetation communities and forest growth may be well understood, but the response of matsutake fruiting to these variables may be a critical area of needed information Monitoring would provide the data required to improve the model predictions

Modeling differs from common sense decisionmaking in its systematic approach and documentation Decisionmaking within an ecosystem management context involves so many variables and interactions that computer simulations of models are frequently necessary The very process of developing and testing models is useful for clarifying relations among components and determining the relative importance of factors affecting the prediction

Cooperative Investigations

Cooperative investigations are the final element of an adaptive ecosystem management strategy Before the early 1990s, most matsutake research in North America was conducted by individual researchers who obtained their own funding and pursued small, local projects of interest Although valuable, these studies typically were constrained by limited resources, the information frequently was not widely disseminated to managers, and the results from one study location were not necessarily applicable to other habitats The burgeoning mushroom industry has created a need for definitive, statistically sound, regionally based studies so that managers can develop justifiable regulatory decisions Most land management organizations, however, have not devoted substantial resources to mushroom research Federal research institutions, universities, mycological societies and clubs, the mushroom industry, and individual collectors also have various levels of interests in matsutake research, even though they may not manage lands directly Coordinated research efforts can ensure geographically broad-based investigations with definitive results, while keeping the expense for any one group to a minimum Many individuals involved in matsutake research in North America have already begun to cooperate and share information informally, our understanding and management of the resource will benefit further from institutional support of these efforts

Closing Remarks

It is no dream
Matsutake are growing
On the belly of the mountain

Shigetaka[1]

Exports of matsutake from North American to Japan exemplify the greatly expanded trade among Pacific Rim countries. As more people become involved in the North American harvest of matsutake, western society also is learning to appreciate this unique fungus. Development of commercial matsutake harvesting coincides with recent efforts to diversify the products we obtain from our native forests. The potential for developing a sustainable harvest of these mushrooms is great.

The American matsutake has evolved over millennia as a component of diverse and complex natural forest ecosystems. Managers cannot manage it in isolation from the plant communities and ecosystems to which it is ecologically adapted. Just as the forest invests tremendous capital in the form of photosynthates to maintain mycorrhizae and fuel the production of wild edible mushrooms, so too we must invest time and expertise to conserve this ephemeral, valuable, and poorly understood resource. Immediate management decisions must be based on the best available information, and this publication is our effort to summarize current knowledge. Adaptive ecosystem management relies on monitoring to improve decisions. Expanding the knowledge base will be a good investment and is an essential part of maintaining continuous production of the valuable matsutake for future generations. Providing managers and harvesters with a greater understanding of the matsutake will enable them to develop the most appropriate regulations and optimize use of the resource for the benefit of all.

' As quoted by Arora 1991.

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English Equivalents

When you know:	Multiply by:	To find:
centimeters	2.540	inches
meters	3.281	feet
cubic meters	35.32	cubic feet
kilometers	0.62	miles
Celsius	1.8, then add 32	Fahrenheit

Literature Cited

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

Amaranthus, M.; Pilz, D.; Abbott, R.; Moore, A.; Luoma, D. [In press]. Function, diversity and commercial production of American matsutake across spatial and temporal scales. Gen. Tech. Rep. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.

Arora, D. 1986. Mushrooms demystified: a comprehensive guide to the fleshy fungi. Berkeley, CA: Ten Speed Press. 959 p.

Arora, D. 1991. All that the rain promises and more...a hip pocket guide to western mushrooms. Berkeley, CA: Ten Speed Press. 265 p.

Asada. 1937. Increasing the number of matsutake. Take Rui No Kenkyu. 3: 22-31. (In Japanese).

Bandala, V.M.; Montoya, L.; Chapela, I.H. 1997. Wild edible mushrooms in México: a challenge and opportunity for sustainable development. In: Chapela, I.H.; Palm, M.E., eds. Mycology in sustainable development: expanding concepts, vanishing borders. Boone, NC: Parkway Publishers: 76-90.

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

Chapela, I.H.; Palm, M.E. 1997. Mycology in sustainable development: expanding concepts, vanishing borders. Boone, NC: Parkway Publishers. 150 p.

Critchfield, W.B.; Little, Jr., E.L. 1966. Geographic distribution of pines of the world Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service.

Danell, E. 1994. Formation and growth of the ectomycorrhiza of *Cantharellus cibarius.* Mycorrhiza. 5: 89-97

Danell, E.; Camacho, F.J. 1997. Successful cultivation of the golden chanterelle. Nature. 385: 303

Daniels, S.E.; Walker, G.B.; Boeder, J.R.; Means, J.E. 1994. Managing ecosystems and social conflict. In: Jensen, M.E.; Bourgeron, P.S., tech eds Volume IT Ecosystem management: principles and applications. Gen. Tech. Rep. PNW-GTR-318. Portland, OR U.S Department of Agriculture, Forest Service, Pacific Northwest Research Station: 327-339. (Everett, Richard L, assessment team leader; Eastside forest ecosystem health assessment).

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

de Geus, P.M.J. 1995b. Summary of public response pine mushroom task force recommendations. Victoria, BC: Integrated Resources Branch, British Columbia Ministry of Forests. 19 p

de Geus, P.M.J.; Berch, S. 1997. The pine mushroom industry in British Columbia. In Chapela, I.H.; Palm, M.E., eds. Mycology in sustainable development: expanding concepts, vanishing borders. Boone, NC: Parkway Publishers: 55-67.

de Geus, P.M.J.; Redhead, S.; Callan, B. 1992. Wild mushroom harvesting discussion session minutes; 1992 March 3; Victoria, BC. Victoria, BC: Integrated Resources Branch, British Columbia Ministry of Forests. 45 p.

Durall, D.M.; Todd, A.W.; Trappe, J.M. 1994. Decomposition of ^{14}C-labeled substrates by ectomycorrhizal fungi in association with Douglas-fir. New Phytologist. 127 725-729.

External Affairs and International Trade Canada [EAITC]. 1990. The mushroom market. Export Opportunities in Japan Series. Ottawa, ON: Japan Trade Development Division. 26 p.

Futai, K. 1979. Responses of two species of *Bursaphelenchus* to the extracts from pine segments and to the segments immersed in different solvents. Japanese Journal of Nematology. 9: 54-59.

Futai, K. 1980a. Developmental rate and population growth of *Bursaphelenchus lignicolous* (Nematoda: Aphelenchoididae) and *B. mucronatus.* Applied Entomology and Zoology. 15(2): 115-122.

Futai, K. 1980b. Host preferences of *Bursaphelenchus lignicolous* (Nematoda: Aphelenchoididae) and *B. mucronatus* shown by their aggregation to pine saps. Applied Entomology and Zoology. 15(3): 193-197.

Futai, K. 1980c. Population dynamics of *Bursaphelenchus lignicolous* (Nematoda. Aphelenchoididae) and *B mucronatus* in pine seedlings Applied Entomology and Zoology. 15(4): 458-464.

Futai, K.; Furuno, T. 1979. The variety of resistances among pine species to pine wood nematode *Bursaphelenchus lignicolous* Bulletin of the Kyoto University Forests 51 23-36

Greuter, W., ed. 1994. International code of botanical nomenclature (Tokyo code) Adopted by the 15th international botanical congress, 1993 Aug -Sept, Yokohama, Japan Konigstein, Germany Koeltz Scientific Books 389 p

Griffiths, R.P.; Caldwell, B.A. 1992. Mycorrhizal mat communities in forest soils In Read, D J , Lewis, D H , Fitter, A H , Alexander, I J eds Mycorrhizas in ecosystems Wallingford, United Kingdom CAB International, University Press 98-105

Hamada, M. 1950. Physiology and ecology of *Armillaria matsutake* The Botanic Magazine 63 40-41 In Japanese

Hamada, M. 1964. Method of pure culture of the mycelia of Armillaria matsutake and of its allies In Matsutake Research Association, ed Matsutake *(Tricholoma matsutake* Singer) Kyoto, Japan 97-100

Hamada, M. 1966. Studies on the physiology and ecology of *Armillana matsutake* report of studies conducted under special agriculture, forestry and fisheries grant Kyoto, Japan Kyoto University Publication

Hongo, T. 1974. Study on the mushrooms from Japan The Botanic Magazine 49 294-305 In Japanese

Hosford, D.; Ohara, H. 1986. Shiro analysis of mycorrhizal fungi [Abstract] In Roots in forest soils biology and symbioses Meeting of the IUFRO working party on root physiology and symbioses (S2 01-13), 1986 Aug 4-8, Victoria, BC Victoria, BC [Publisher unknown]

Hosford, D.; Ohara, H. 1990. Ecological characterization of American matsutake In Abstracts International congress on bacteriology and mycology, 1990 September 20, Osaka, Japan Strasbourg, France International Union of Microbiological Societies

Hosford, D.; Ohara, H. 1995. Ecological study of *Tricholoma magnivelare* shiros in central Washington In Schnepf, C , comp , ed Dancing with the elephant Proceedings The business and science of special forest products—a conference and exposition, 1994 Jan 26-27, Hillsboro, OR [Place of publication unknown] University of Idaho Extension Service 111-116 Sponsored by Northwest Forest Products Association, Western Forestry and Conservation Association

Johnson, N.C.; Graham, J.H.; Smith, F.A. [In press]. Functioning of mycorrhizal association along the mutualism-parasitism continuum New Phytologist

Kawai, M.; Ogawa, M. 1981. Some approaches to the cultivation of a mycorrhizal fungus, *Tricholoma matsutake* (Ito et Imai) Sing In Mushroom science XI, part 2 Proceedings of 11th international scientific congress on the cultivation of edible fungi, 1981 [day and month unknown], Sydney, Australia [Location of publisher unknown], [Publisher unknown] 869-883

Kinugawa, K. 1963. Biological studies related to fruiting of matsutake Bulletin, University of Osaka Prefecture (Series B) 14 27-60

Kinugawa, K.; Goto, T. 1978. Preliminary survey on the "matsutake" *(Armillaria ponderosa*) of North America. Transactions of the Mycological Society of Japan. 19: 91-101.

Kytövuori, I. 1989. The *Tricholoma caligatum* group in Europe and North Africa. Karstenia. 28: 65-77.

Leatham, A.M.; Chan, V.R.; Kroeger, P.D. 1997. Renal failure caused by mushroom poisoning. Clinical Toxicology 35(1): 67-75.

Lee, T.S. 1989a. Increasing yields and promoting quality of the pine mushroom by cap-covering or soil-covering. In: Mahadevan, A.; Raman, N.; Natarajan, K., eds. Mycorrhizae for a green Asia: Proceedings of the 1st Asian conference on mycorrhizae; 1988 Jan. 29-31; Madras, India. Royapettah, Madras, India: Alamu Printing Works: 224-230.

Lee, T.S. 1989b. Status of mycorrhizal research in Korea. In: Mahadevan, A.; Raman, N.; Natarajan, K., eds. Mycorrhizae for a green Asia: Proceedings of the first Asian conference on mycorrhizae; 1988 Jan. 29-31; Madras, India. Royapettah, Madras, India: Alamu Printing Works: 16.

Lipske, M. 1994. A new gold rush packs the woods in central Oregon. Smithsonian. 25: 35-46.

McRae, M. 1993. Mushrooms, guns, and money. Outside. 18: 64-69, 151-154.

Meidinger, D.; Pojar, J., eds. 1991. Ecosystems of British Columbia. Spec. Rep. Series 6. Victoria, BC: Research Branch, British Columbia Ministry of Forests, Crown Publications. 330 p.

Miller, S. L. 1995. Functional diversity in fungi. Canadian Journal of Botany 73, Supplement 1: 50-57.

Miron, F. 1994. Woodland mushrooms: harvesting and marketing, project 4050. Sainte-Foy, PQ: Natural Resources Canada, Canadian Forest Service. 56 p.

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

Nakane, Shiro. c. 1992. The Daily Yomiuri. [Date unknown]. Tokyo, Japan.

O'Dell, T.E.; Luoma, D.L.; Molina, R.J. 1992. Ectomycorrhizal fungal communities in young, managed and old growth Douglas-fir stands. Northwest Environmental Journal. 8: 166-168.

Ogawa, M. 1979. Microbial ecology of "shiro" in *Tricholoma matsutake* and its allied species. IX: *Tricholoma ponderosum* in *Pseudotsuga menziesii-Tsuga heterophylla* and *Pinus contorta* forests. Transactions of the Mycological Society of Japan. 20: 370-382.

Ogawa, M. 1982. How to produce matsutake mushroom. Nara, Japan: Matsutake Research and Consultation Office, Forest Service Research Station. 158 p.

Ogawa, M.; Hamada, M. 1965. Microbial ecology of shiro in *Tricholoma matsutake* (S. Ito et Imai) Sing, and its allied species. Transactions of the Mycological Society of Japan. 6: 67-71. In Japanese; English summary.

Ogawa, M.; Ito, I. 1989. Is it possible to cultivate matsutake. Tokyo: Sou Shin Press. In Japanese.

Ogawa, M.; Ohara, H. 1978. Microbial ecology of shiro in *Tricholoma matsutake* (S. Ito et Imai) Sing, and its allied species: VIM *Tricholoma bakamatsutake* Hongo in *Quercus mongolica* var. *grosserrata* forest and *Q. serrata* forests. Transactions of the Mycological Society of Japan. 19: 391-405. In Japanese; English summary.

Ohara, H. 1966. Antibacterial activity of mycorrhiza of *Pinus densiflora* formed by *Tricholoma matsutake.* Proceedings, Japan Academy, Series B, Physical and Biological Sciences. 42(5): 503-506.

Ohara, H. 1974. Bacterial behavior in the rhizosphere of *Pinus densiflora* infected by *Tricholoma matsutake.* Proceedings, International Association of Microbiological Societies 2: 445-450.

Ohara, H. 1977. Ecology of *Tricholoma matsutake* and its allied species with special reference to their hosts. Annual Report of Studies, Doshisha Joshi Daigaku. 11: 16-20.

Ohara, H. 1981. A note on *Armillaria Ponderosa* in North America. Annual Report of Studies, Doshisha Joshi Daigaku. 15: 39-50.

Ohara, H. 1994. A history of the trial and error in artificial production of matsutake fruitings. Annual Report of Studies, Doshisha Joshi Daigaku. 27: 20-30.

Ohara, H.; Hamada, M. 1967. Disappearance of bacteria from the zone of active mycorrhizas in *Tricholoma matsutake* (Ito et Imai) Singer. Nature. 213: 528-529.

Ohta, A. 1994. Production of fruit-bodies of a mycorrhizal fungus, *Lyophyllum shimeji,* in pure culture. Mycoscience. 35: 147-51

Pantidou, M.E. 1961. Carpophores of *Phlebopus sulphureus* in culture. Canadian Journal of Botany. 39: 1163-1167.

Pantidou, M.E. 1962. Cultural studies of Boletaceae—carpophores of *Phlebopus lignicola* in culture. Canadian Journal of Botany. 40: 1313-1319.

Pantidou, M.E. 1964. Cultural studies of Boletaceae: carpophores of *Xerocomus badius* and *Xerocomus illudens* in culture. Canadian Journal of Botany. 42: 1147-1149.

Pilz, D.; Molina, R. 1996. Managing forest ecosystems to conserve fungus diversity and sustain wild mushroom harvests. Gen. Tech. Rep. PNW-GTR-371. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 104 p.

Pilz, D.; Molina, R.; Amaranthus, M. [and others]. 1996. Forest fungi and ecosystem management. In: Pilz, D.; Molina, R., eds. Managing forest ecosystems to conserve fungus diversity and sustain wild mushroom harvests. Gen. Tech. Rep. PNW-GTR-371. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 86-103.

Redhead, S. 1989. A biogeographical overview of the Canadian mushroom flora. Canadian Journal of Botany. 67: 3003-3062

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

Redhead, S.A. 1984. Mycological observations 13-14: on *Hypsizygus* and *Tricholoma.* Transactions of the Mycological Society of Japan. 25: 1-9.

Richards, B.; Creasy, M. 1996. Ethnic diversity, resource values, and ecosystem management: matsutake mushroom harvesting in the Klamath bioregion. Society and Natural Resources. 9: 359-374

Sagara, N.; Hamada, M. 1965. Responses of higher fungi to some chemical treatments of forest ground. Transactions of the Mycological Society of Japan. 6(3): 72-74.

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

Smith, A.H. 1979. The stirps *Caligata* of *Armillaria* in North America. Sydowia Beiheft. 7: 368-377.

Smith, A.H.; Weber, N.S. 1980. The mushroom hunter's field guide. Ann Arbor, MI: The University of Michigan Press. 316 p.

State of Oregon. 1993. An act relating to the theft of forest products, creating new provisions, amending ORS 164.813, 164.828, 164.835, 164.845, and 164.855; and declaring an emergency, Oregon Laws and Resolutions, Chap. 167, Sect. 1-7. Effective June 24, 1993.

State of Washington. 1988. "Wild mushrooms." Revised code of Washington. Chap. 230, Sect. 1-10. Effective June 10, 1988.

State of Washington. 1991. "Wild mushroom harvesting." Revised code of Washington. Chap. 15.90. Sect. 010-901. Effective June 7, 1990.

State of Washington. 1992. "An act relating to wild mushrooms." Revised code of Washington. Chap. 184. Sect. 76.48.020, 76.48.060, and 76.48.070. Effective June 11, 1992.

State of Washington. 1995. "Special forest product permits." Revised code of Washington. Chap. 366. Sect. 78.48. Effective July 23, 1995.

Tominaga, Y. 1963. Studies on the life history of Japanese pine mushroom, *Armillaria matsutake* (Ito et Imai.) Bulletin of the Hiroshima Agricultural College. 2: 105-145. In Japanese; English summary.

Tominaga, Y. 1973. Studies on the mycorrhiza of "fairy rings" of *Armillaria matsutake* Ito et Imai. Bulletin of the Hiroshima Agricultural College. 4: 294-298. In Japanese; English summary.

Tominaga, Y. 1975. Studies on the tunnel cultivation, the so-called Hiroshima method of *Tricholoma matsutake* (Ito et Imai) Sing. I: On the forcing culture of *Tricholoma matsutake* in the year 1974. Bulletin of the Hiroshima Agricultural College. 5. 165-180. In Japanese.

Tominaga, Y. 1978. *Tricholoma matsutake* In Chang, S T.; Hayes, W.A , eds The biology and cultivation of edible mushrooms. New York Academic Press 683-697

Tullos, R.E.; Lindgren, J.E. 1992. Amanita smithiana—taxonomy, distribution and poisonings Mycotaxon 45 373-387.

U.S. Department of Agriculture, Forest Service; U.S. Department of the Interior, Bureau of Land Management. 1994a. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. [Place of publication unknown]. 2 vol.

U.S. Department of Agriculture, Forest Service; U.S. Department of the Interior, Bureau of Land Management. 1994b. Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl. [Place of publication unknown]. 74 p. [plus Attachment A standards and guidelines].

U.S. Laws, Statutes, etc. 1960. Multiple Use-Sustained Yield Act. Act of June 12, 1960 16 USC 528-531

U.S. Laws, Statutes, etc. 1969. Public Law 91-190. [S. 1075], National Environmental Policy Act. Act of Jan. 1, 1970. 42 USC 4321-4370a (1982 and Supplement. V 1987)

U.S. Laws, Statutes, etc. 1973. Endangered Species Act (as amended) 16 USC 1531-1543

U.S. Laws, Statutes, etc. 1976a. Federal Land Policy and Management Act. Act of Oct. 21, 1976 43 USC. 1701 (note).

U.S. Laws, Statutes, etc. 1976b. National Forest Management Act Act of Oct 22, 1976. Public Law 94-588 16 USC 1600 (1976)

Villarreal, L. 1994. Analisis ecologico-silvicola de la productividad natural de hongos comestibles silvestres en los bosques del cofre de perote, Veracruz. = Ecological and silvicultural analysis of the natural production of edible forest mushrooms in the forests of Cofre de Perote, Veracruz. Montecillo, México Colegio de Postgraduados, Institución de Enseñanza e Investigación en Ciencias Agricolas, Programa Forestal. M S. thesis.

Villarreal, L.; Perez-Moreno, J. 1989. Aprovechamiento y conservacion del "Matsutake Americano" (*Tricholoma magnivelare)* en los bosques de Mexico = Conservation and use of the "American matsutake" *(Tricholoma magnivelare)* in the Mexican forests. Veracruz, Mexico: Instituto de Micologia Neotropical Aphcada 2- 131-144

Vogt, K.A.; Bloomfield, J.; Ammirati, J.F.; Ammirati, S.R. 1992. Sporocarp production by Basidiomycetes, with emphasis on forest ecosystems In Carroll, G C , Wicklow, D.T., eds. The fungal community, its organization and role in the ecosystem 2d ed New York Marcel Dekker, Inc 563-582

Wang, C. (c. **1982).** An investigation research on *Tricholoma matsutake* ecology in Jilin Province of China. Jilin City, Jilin Province, China: Jilin Forestry Institute. 18 p. In Chinese.

Wang, Y.; Hall, I.R.; Evans, L.A. [In press]. Ectomycorrhizal fungi with edible fruiting bodies. 1: *Tricholoma matsutake* and related fungi. Economic Botany.

Zeller, S.M.; Togashi, K. 1934. The American and Japanese matsu-take. Mycologia. 26: 544-558.

Appendix: Common and Scientific Names

Fungi and Lichens[1]

Common name	Scientific name
Tricholoma species:	
foolish pine mushroom	*Tricholoma bakamatsutake* Hongo
booted or brown matsutake	*Tricholoma caligatum* (Viv.) Ricken
man on horseback	*Tricholoma flavovirens* (Pers. ex Fr.) Lundell
(none)	*Tricholoma focale* (Fr.) Ricken of Europe
(none)	*Tricholoma fulvocastaneum* Hongo
American matsutake, pine mushroom, tanoak mushroom, white matsutake—	*Tricholoma magnivelare* (Peck) Redhead
Prior synonym	*Tricholoma ponderosum* (Peck) Singer
Prior synonym	*Armillaria ponderosa* (Peck) Sacc.
Japanese matsutake	*Tricholoma matsutake* (S. Ito et Imai) Sing,
(none)	*Tricholoma nauseosum* (Blytt) Kytövuori
(none)	*Tricholoma robustum* (A. & S. ex Fr.) Ricken
(none)	*Tricholoma virgatum* (Fr.:Fr.) Kummer
(none)	*Tricholoma zelleri* (Stuntz & Smith) Ovrebro & Tylutki
Other fungal and lichen species:	
Amanitas	*Amanita* species Pers. ex S.F. Gray
(none)	*Amanita smithiana* Bas.
chanterelle	*Cantharellus* species Fr.
white chanterelle	*Cantharellus subalbidus* Smith & Morse
imperial mushroom	*Catathelasma imperiale* (Fr. apud Lund) Sing,
reindeer lichen	*Cladina portentosa* (Duf.) Follm. ssp. *pacifica* (Ahti) Ahti
(none)	*Cortinarius* species Fr.

[1] Alphabetical by scientific name.

Common name	Scientific name
(none)	*Cortinarius montanus* Kauff
(none)	*Cystoderma granulosum* (Fr) Fayod
(none)	*Dermocybe* species (Fr) Wunsche
(none)	*Gomphidius* species Fr
rosy *Gomphidius*	*Gomphidius* subroseus Kauff
glutinous *Gomphidius*	*Gomphidius* glutinosus Fr
(none)	*Gomphidius smithii* Sing
insidious *Gomphidius*	*Gomphidius oregonensis* Pk
scaly or woolly chanterelle	*Gomphus floccosus* (Schw) Sing
poison pie	*Hebeloma crustilniforme* (Bull) Quel
lilac *Inocybe*	*Inocybe lilacma* (Gill) Kauff
shaggy-stalked parasol	*Lepiota clypeolana* (Bull Fr) Kummer
Port-Orford root rot	*Phytophthora lateralis* Tucker & Milbrath
pogy	*Rhizopogon ellenae* A H Smith
pogy	*Rhizopogon parksii* A H Smith
cascade *Russula*	*Russula cascadensis* Schaffer
emetic *Russula*	*Russula emetica* (Fr) Pers (species complex)
slippery jack	*Suillus* species Gray
short-stemmed slippery jack	*Suillus brevipes* (Pk) Kuntze

Plants[2]

Common Name	Scientific name
Asian trees	
chinkapin	*Castanopsis* Spach species
edible Asian tanoak[3]	*Lithocarpus (Pasania) edulis* (Mak) Nakai
Japanese black pine	*Pinus thunbergn* Parl
Japanese red pine	*Pinus densiflora* Siebold & Zuccarini
Japanese stone pine	*Pinus pumila* (Pall) Regel
Japanese white pine	*Pinus parviflora* Siebold & Zuccarini
Korean pine	*Pinus koraiensis* Siebold & Zuccanni
Maries fir	*Abies manesii* Masters
Mongolian oak	*Quercus mongolica* Fisch & Turcz
northern Japanese hemlock	*T diversifolia* (Maxim) Masters
Sakhalin spruce	*Picea glehnii* (Fr Schmidt) Masters
serrated-leafed oak (see footnote 3)	*Quercus serrata* Thunb
southern Japanese hemlock	*Tsuga sieboldii* Carr
Taiwan red pine	*Pinus taiwanensis* Hayata
American trees	
California black oak	*Quercus kelloggn* Newb
canyon live oak	*Quercus chrysolepis* Liebm
golden chinkapin	*Castanopsis chrysophylla* (Dougl) A DC
Douglas-fir	*Pseudotsuga menziesn* (Mirb) Franco
Engelmann spruce	*Picea engelmannu* Parry ex Engelm
grand fir	*Abies grandis* (Dougl) Lindl
incense-cedar	*Calocedrus decurrens* (Torrey) Florin

[2] Alphabetical by common name
[3] Common name derived from scientific name

Common Name	Scientific name
American trees	
jack pine	*Pinus banksiana* Lamb
knobcone pine	*Pinus attenuata* Lemm
lodgepole pine	*Pinus contorta* v *latifolia* Engelm
madrone	*Arbutus menziesii* Pursh
mountain hemlock	*Tsuga mertensiana* (Bong) Carr
noble fir	*Abies procera* Rehd
Pacific silver fir	*Abies amabilis* (Dougl) Forbes
Ponderosa pine	*Pinus Ponderosa* Dougl ex Loud
Port-Orford-cedar	*Chamaecypans lawsoniana* (A Murr) Parl
red pine	*Pinus resinosa* Ait
Shasta red fir	*Abies magnifica* Murr v *shastensis* Lemm
shore pine	*Pinus contorta* var *contorta* Dougl ex Loud
Sitka spruce	*Picea sitchensis* (Bong) Carr
sugar pine	*Pinus lambertiana* Dougl
tanoak	*Lithocarpus densiflorus* (Hook & Arn) Rehd
teocote pine	*Pinus teocote* Cham & Schlectend
western hemlock	*Tsuga heterophylla* (Raf) Sarg
western larch	*Larix occidentalis* Nutt
western redcedar	*Thuja plicata* Donn
western white pine	*Pinus monticola* Dougl ex D Don
white fir	*Abies concolor* (Gord & Glend) Lindl
white spruce	*Picea glauca* (Moench) Voss
Shrubs and subshrubs	
big huckleberry	*Vaccimum membranaceum* Dougl
bitterbrush	*Purshia tridentata* (Pursh) DC
bunchberry	*Cornus canadensis* L
California red bud	*Cercis occidentals* Torrey
creeping snowberry	*Symphoricarpos mollis* Nutt
dwarf Oregon grape	*Berberis nervosa* Pursh
evergreen huckleberry	*Vaccimum ovatum* Pursh
green-leaf manzanita	*Arctostaphylos patula* Greene
hairy honeysuckle	*Lonicera hispidula* (Lindl) Dougl ex T & G
hairy manzanita	*Arctostaphylos columbiana* Piper
hazelnut, filbert	*Corylus cornuta* L
kinnikinnic	*Arctostaphylos uva-ursi* (L) Spreng
leafless pyrola	*Pyrola asanfolia* Michx
little prince's pine	*Chimaphila menziesu* (R Br) Spreng
mahala mat	*Ceanothus prostratus* Benth
mountain, myrtle, or Oregon boxwood	*Pachystima myrsinites* (Pursh) Raf
mountain snowberry	*Symphoncarpos oreophilus* Gray
Pacific blackberry	*Rubus ursinus* Cham & Schlecht
Pacific rhododendron	*Rhododendron macrophyllum* G Don
pearhip rose	*Rosa woodsia* v *ultramontana* (Wats) Jeps
pinemat manzanita	*Arctostaphylos nevadensis* Gray
poison oak	*Rhus diversiloba* T & G
rabbitbrush	*Chrysothamnus nauseousus* (Pall) Britt

	Common Name	Scientific name
	Shrubs and subshrubs:	
	red huckleberry	*Vaccinium parvifolium* Smith
	sage	*Artemesia* L.
	salal	*Gaultheria shallon* Pursch
	Scot's broom	*Cytisus scoparius* (L.) Link
	sidebells pyrola	*Pyrola secunda* L.
	snowbrush	*Ceanothus velutinus* Dougl. ex Hook,
	twinflower	*Linnaea borealis* L.
	vine maple	*Acer circinatum* Pursh
	western prince's pine	*Chimaphila umbellata* (L.) Bart,
	white vein pyrola	*Pyrola picta* Smith
	Herbs:	
	braken fern	*Pteridium aquilinum* (L) Kuhn.
	candy stick	*Allotropa virgata* T. & G. ex Gray
	dusky horkelia	*Horkelia fusca* Lindl.
	gnome-plant	*Hemitomes congestum* Gray
	goldenweed	*Haplopappus* Cass.
	heart-leafed arnica	*Arnica cordifolia* Hook,
	mountain sweet-cicily	*Osmorhiza chilensis* H. & A.
	pearly everlasting	*Anaphalis margaritacea* (L.) B. & H.
	Phacelia	*Phacelia* Juss.
	pinesap	*Hypopitys monotropa* Crantz.
	strawberry	*Fragaria* L
	sword-fern	*Polystichum munitum* (Kaulf.) Presl.
	vanillaleaf, deerfoot	*Achlys triphylla* (Smith) DC.
	western rattlesnake-plantain	*Goody era oblongifolia* Raf.
	western starflower	*Trientalis latifolia* Hook,
	western trillium	*Trillium ovatum* Pursh
	white hawkweed	*Hieracium albiflorum* Farr
	woolly hawkweed	*Hieracium scouleri* Hook,
	yarrow	*Achillea millefolium* L
	Grasses and sedges:	
	bottlebrush squirreltail	*Sitanion hystrix* (Nutt.) J.G. Smith
	European beachgrass	*Ammophila arenaria* (L) Link
	Ross's sedge	*Carex rossii* Boott
	western needlegrass	*Stipa occidentalis* Thurb. ex Wats.
Animals (see footnote 2)	Insects:	
	pine nematode, pine weevil	*Bursaphelenchus lignicolus*
	Japanese pine sawyer	*Monochamus alternates*
	Birds:	
	northern spotted owl	*Strix occidentalis caurina*
	Mammals:	
	bear	*Euarctos americanus*
	deer	*Odocoileus hemionus*
	dusky-footed wood rat	*Neotoma fuscipes*
	elk	*Cervus elaphus*
	northern flying squirrel	*Glaucomys sabrinus*

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

The commercial harvest of American matsutake *(Tricholoma magnivelare)* from forests in the Pacific Northwest has increased dramatically in the last decade. The similarity of this mushroom to the Japanese matsutake (T *matsutake)* has prompted its harvest to meet increasing demands for matsutake in Japan. The American matsutake is likely to remain a sustainable forest product in North America if its harvest and forest habitats are managed appropriately.

Keywords: Matsutake (American), mushroom, forest management, mycology, fungi, mycorrhiza, special forest products, nonwood forest products.

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