American Matsutake *(Tricholoma magnivelare*) across Spatial and Temporal Scales[1]

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Abstract

Thousands of people annually harvest American matsutake *(Tricholoma magnivelare* [Peck] Redhead) from private, State, and Federal lands. Yet, spatial and temporal uncertainties about matsutake ecology and production hinder efforts to manage this valuable resource on a sustained basis. Our studies indicate that production and value of American matsutake vary strongly over time, are spatially related to individual host plants, and can be enhanced by certain practices at various spatial scales. Managers wishing to predict matsutake production at individual shiro, stand, landscape, and regional scales need information for a wide variety of habitat types over the long term. Understanding local, regional, national, and international production and market factors will aid decision-making and policy-making. Biological, social, and economic influences function across many scales and are key to sustainable management of American matsutake.

Introduction

Current forest management decisions integrate increasingly complex and changing social, economic, and ecological values. The decision-making process requires in-depth knowledge of the function and abundance of organisms in forest ecosystems across various spatial and temporal scales. Usually, ectomycorrhizal fungi (EMF) have been overlooked when forest ecosystems are considered. However, foresters, ecologists, managers, and policymakers are beginning to recognize that EMF influence forest productivity, recovery, and wildlife food webs (Amaranthus and Perry 1987, 1989; Harley and Smith 1983; Waters and others 1995). This paper explores another EMF product of forest ecosystems: the expanding industry that harvests wild edible fungi.

Harvesting wild edible fungi in the Northern Hemisphere is a major industry, with sales estimated to exceed $1 billion (Hall and others [In press]). Interest in wild edible fungi stimulated early research on EMF (Frank 1885). Over the past century, we have developed a general understanding of the geographic range, host

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associations, and mycorrhizal characteristics of important edibles, such as *Boletus, Cantharellus, Tricholoma,* and *Tuber* species. However, we have poor understanding of their ecology and productivity (factors greatly influencing spatial and temporal variability) and their interaction with other forest vegetation and wildlife species. The decline of wild edible mushrooms in Europe and Japan (Arnolds 1991, Kawai and Ogawa 1981) has created the need to understand these EMF species over expanding temporal and spatial scales (*table 1).* This is particularly true of the American matsutake because the dramatic decline in Japanese matstuake production has created enormous market demand for related species.

Table 1—*Factors that influence matsutake production and harvest levels at various spatial scales.*

Spatial scale	Factor
Individual shiros 1-50 m^2	Mushroom harvest method Host presence Soil compaction/ripping Watering Host productivity
Stand and landscapes 1-100 km^2	Silvicultural method Temperature/rainfall Stand density/composition/age Plant community/seral stage Wildlife interactions
Regional and global >1,000 km^2	Market demand International production Socioeconomic forces Disturbance agents Policy and regulations Access to roads/airports

Individual Shiro Scale

The American matsutake and related species form a distinctive fungal colony in the soil called a “shiro,” the Japanese term for “white,” “castle,” or “place.” The shiro is a dense mass of mycelia that form a white to pale gray mat beginning just below the litter layer *(fig. 1)*. Across its range, American matsutake is an EMF symbiont with true firs, pines, hemlocks, Douglas-fir, and some hardwood species. Within a particular habitat type and when conditions are right, the matsutake mushroom will fruit in association with the mycorrhizae and hyphae of specific host plants in the shiro colony.

The American matsutake industry employs thousands of commercial harvesters from British Columbia to Mexico. Accelerated harvest of the mushroom has heightened concern that matsutake production may not be sustainable and that harvesting adversely impacts productivity of both plant host and matsutake. Government agencies operating in the Pacific Northwest, such as the USDI National Park Service, USDA Forest Service, and the State of Washington Department of Natural Resources, have recently restricted matsutake harvest in some areas because of uncertainties over production and environmental impacts. Many questions arise concerning the scale of the individual shiro. What are the spatial relationships to hosts or indicator plants? What are the impacts of litter removal, raking, and other mushroom harvest practices? What are the effects of harvesting mushrooms before spore maturation? Can shiro production of matsutake mushrooms be enhanced? Answers to these questions are needed by resource specialists, managers, and policymakers to make informed decisions about the sustainability of the resource and how it should be managed.

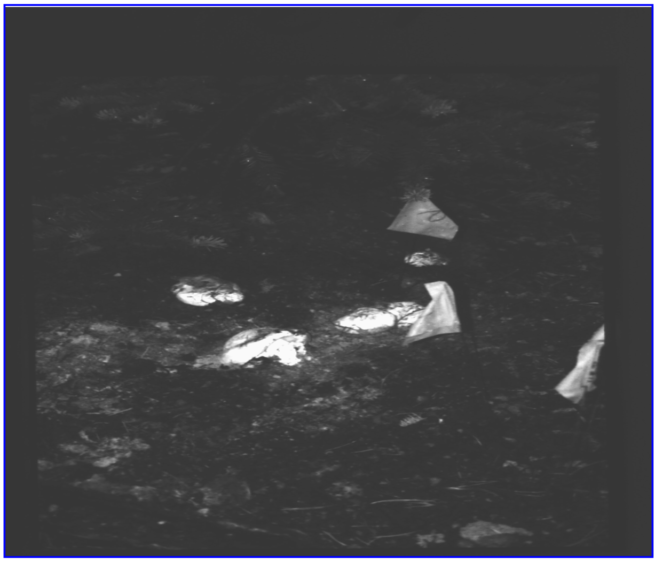

Figure 1—Raking exposes matsutake mushrooms and shiro-white mass of mycelia beneath the litter layer. Yellow flags indicate location of harvested matsutake mushrooms.

To study the spatial relationship between the American matsutake and individual plants, we established two study blocks within 5 km of each other in an area of known production. The study area occurs on the Diamond Lake Ranger District of the Umpqua National Forest in the southern Oregon Cascade Mountains. Soils are deep and derived from volcanic ash parent material. Block 1 is a north-facing slope and Block 2 is a west-facing slope. Slope steepness ranges from 0 to 5 percent on block 1 and from 10 to 45 percent on block 2. Block 1 occurs at a mean elevation of 1,450 m and block 2 at 1,370 m. In each block, a first point was randomly established. From this starting point, a 6 x 6 array of grid points (30-m spacing) was established.

In September and October 1995, each matsutake mushroom that fruited within the grid was located and marked by a wire engineering flag. In blocks 1 and 2, respectively, 86 and 82 matsutake mushrooms were located and flagged. For each matsutake, the distance to the base of the nearest Shasta red fir (*Abies magnifica* var. *shastensis*), mountain hemlock (*Tsuga mertensiana*), western white pine (*Pinus monticola*), candystick plant (*Allotropa virgata*; an achlorophyllous plant whose roots have been observed to be colonized by matsutake mycelium), and neighboring matsutake was measured to the nearest 0.1 m. Only trees that were of intermediate, codominant, or dominant crown class were used for measurements. The distance from each of the 36 grid points to the base of the nearest Shasta red fir, mountain hemlock, western white pine, candystick, and neighboring matsutake sporocarp was also measured to the nearest 0.1 m. Again, only trees that were of intermediate, codominant, or dominant crown class were measured. A Wilcoxon signed rank test was used in a nonparametric paired comparison of matsutake distances to random points, as represented by the grid points or other plants. A significant difference between the distance of the matsutake to a random point or to one of the trees—the candystick or another mushroom—indicated an association.

Results from this study indicate that at the Diamond Lake study site, American matsutake production is spatially related to the occurrence of individual Shasta red fir *(fig. 2),* candystick plants, and other matsutake mushrooms *(fig. 3)*. Matsutake were distributed spatially in proximity to Shasta red fir *(fig. 4)*. Matsutake are symbiotic and form mycorrhizae on the site with Shasta red fir—the Shasta red fir translocates tree carbohydrates to the matsutake fungus, and in return, the matsutake provides the Shasta red fir with the moisture and mineral nutrition absorbed from its filaments in the soil.

Figure 2—Open understory and Shasta red fir (*Abies magnifica* var. *shastensis*) from the Diamond Lake study area are indicators of productive matsutake habitat.

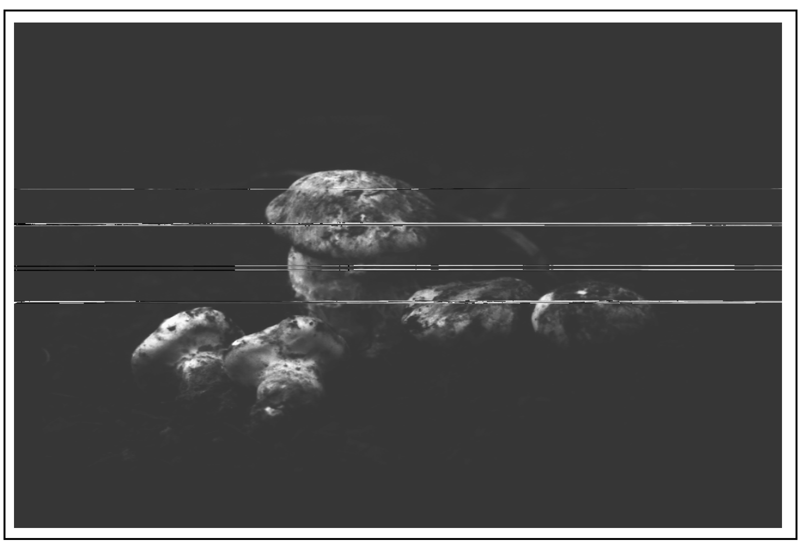

Figure 3—American matsutake (*Tricholoma magnivelare*) harvested from the Diamond Lake study area.

Matsutake were also distributed spatially in proximity to candystick (*Allotropa virgata*) *(fig. 4).* Although this species is often referred to as a saprophyte, candystick is a mycotroph that obtains nutrients and carbon compounds via a mycorrhizal fungus associated with its roots (Castellano and Trappe 1985). American matsutake has been observed to occupy the roots of candystick in Idaho (Lichthardt 1995), and it is likely that the Shasta red fir, matsutake, and candystick have a complex functional relationship in which compounds are transferred between all three partners.

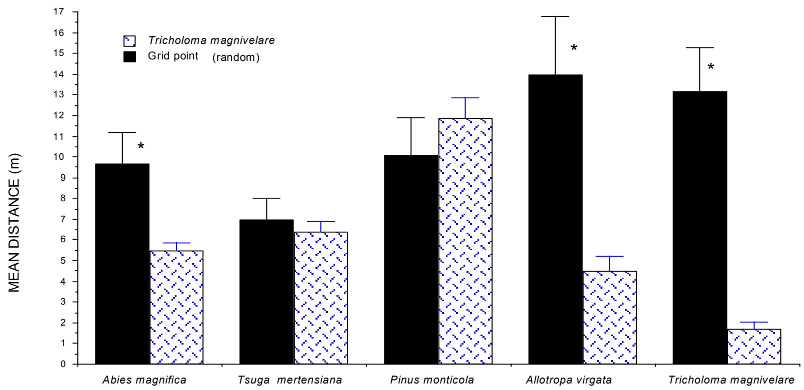

Figure 4—Comparison of distance from random points and individual *Tricholoma magnivelare* to nearest *Abies magnifica* var. *shastensis*, *Tsuga mertensiana*, *Pinus monticola, Allotropa virgata,* and neighboring *Tricholoma magnivelare.* Asterisk (*) indicates significantly closer to *Tricholoma magnivelare* than random point. Wilcoxon signed rank test $P \leq 0.05$.

The presence of Shasta red fir and candystick is an "indicator" of matsutake production that can be used by managers, researchers, and commercial and recreational harvesters for locating and managing matsutake in the southern Oregon Cascades. It is likely that other associations exist with specific trees and substrates in other areas of commercial production. For example, harvester activity is concentrated in tanoak (*Lithocarpus densiflorus*) areas in the Klamath Mountains of southwest Oregon and northwest California and in lodgepole pine (*Pinus contorta*) areas in the coastal dunes of the Oregon Coast. The significant spatial relation between American matsutake and other matsutake mushrooms reflects the clustering of fruiting-body production into the distinctive fungal colony or shiro. This clustered nature of production has implications for developing inventory and monitoring sampling designs for estimating matsutake production.

Research and monitoring of the effects of mushroom harvesting practices on sustainablilty of production is needed at this smaller scale. Activities such as litter removal, raking, compaction, timber harvest, and harvesting immature mushrooms before spore maturation may all influence matsutake production at the scale of the individual tree or cluster. A study is underway in four habitat types in Oregon to evaluate effects of various matsutake harvesting techniques on production (Pilz and others 1996). Research is also needed on the physiology, life cycle, and reproduction of shiros. Only by determining how matsutake typically grows, reproduces, and disperses into new habitat can we begin to understand the impacts of our land management practices on long-term viability of the fungus and its sporocarps.

There is also opportunity to enhance production at the scale of individual shiros. Near block 2 of the Diamond Lake study, we chose three pairs of matsutake clusters to determine whether watering would increase production. In September 1994, each matsutake mushroom was carefully located, flagged, harvested, and weighed. In summer 1995, pairs of matsutake mushroom clusters that had similar mushroom numbers and biomass production during the fall 1994 season were selected for treatment. One cluster in each pair was selected for treatment and 2.5 cm of water was sprinkled on each cluster once a week for 4 weeks, beginning August 3, 1995. Although the watered areas did not have an increase in the number of matsutake harvested, the average weight of individual mushrooms was greatly increased *(fig. 5)*. Although these results cannot be applied to all matsutake areas throughout its range, watering, where feasible, is a potential enhancement tool for increasing the biomass and value of individual clusters.

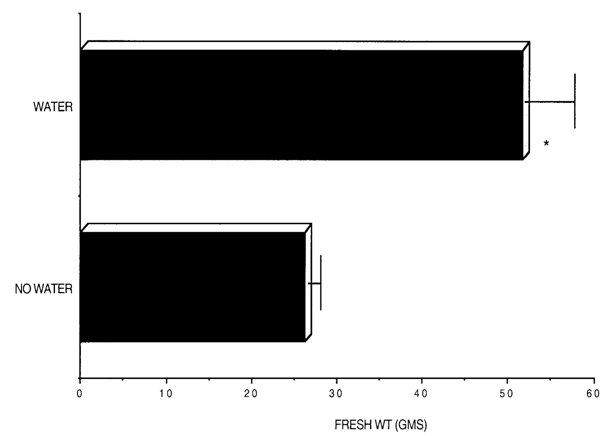

Figure 5—Average fresh weights of grade 1 *Tricholoma magnivelare* in watered and non-watered paired plots. Asterisk (*) indicates significantly greater fresh weight. Wilcoxon signed rank test $P \leq 0.05$

Stand and Landscape Scale

The potential interactions between matsutake, stand, landscape conditions, and management practices are numerous, complex, and site-specific. For example, clear-cutting is an efficient means of timber harvest, but it removes the photosynthetic host and energy source upon which the matsutake depends. Spores or mycelium of the matsutake may persist in the soil and colonize young trees, but fruiting typically ceases for at least two or three decades (Ogawa 1982). On the other hand, matsutake may fruit more abundantly in the middle-age stands that eventually develop with even-aged management than in late successional forests.

Japanese foresters utilize management techniques to increase or enhance the natural production of Japanese matsutake (*Tricholoma matsutake*) (Ogawa 1982). Pines 40 to 50 years old are most productive, whereas those more than 50 years in age decrease in productivity. Forests with a high density of pines and low density of other trees and shrub species are favored for matsutake stand-level treatments (Kawai and Ogawa 1981, Ogawa 1982). Foresters promote a pine canopy that allows light to penetrate to a sparsely vegetated or open forest floor. Forest practices in Japan include thinning of pines and other competing tree species and removal of shrubs, herbs, dead branches, and damaged and diseased trees. This allows the forest floor to dry and to receive more light with better air circulation. Soils that are relatively warm, well drained, and with thin litter and organic layers are favorable to the development of the Japanese matsutake mycelium. Pine forests positioned on southwestern slopes and ridgetops tend to be most suitable. Most sites lack optimal conditions for matsutake mushroom production.

Unfortunately, in North America, there is little analogous information on which to base forest management practices to enhance production of matsutake or any other EMF mushroom or truffle species. We are currently designing and implementing studies in Oregon to evaluate the influence of overstory and understory density and litter thickness on matsutake production. Manipulating overstory and understory vegetation and removing surface soil organic layers to improve matsutake production will result in a variety of other ecosystem effects related to changing forest structure and composition.

Our research indicates that tremendous variability in matsutake production can occur across stand and landscapes from year to year. Production records from 1992 to 1996 on our 160-hectare study site in tanoak/mixed conifer habitat in the Klamath Mountains of southwest Oregon exemplify this variation *(fig. 6)*. Commercial harvesters located and harvested matsutake daily during the fruiting season, and all sporocarps were tallied and weighed fresh. In 1992, the study area produced four times more matsutake by weight than in 1993 and 1995 and 620 times more than in 1994.

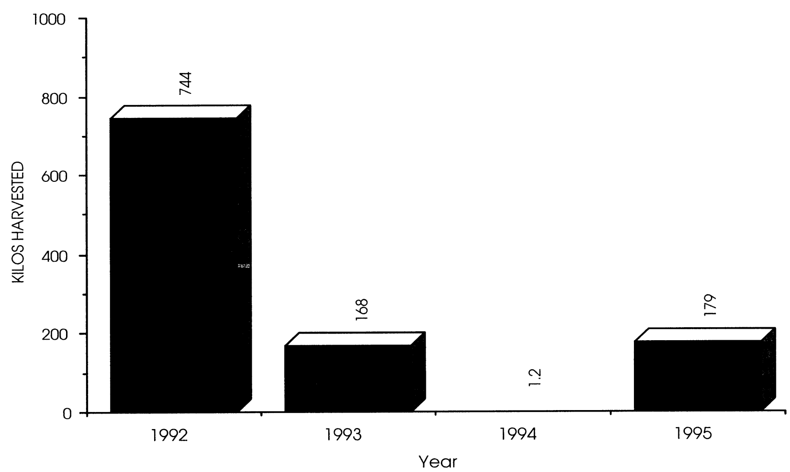

Figure 6—Total kilograms (fresh wt.) of *Tricholoma magnivelare* harvested from 160-hectare study area in the Klamath Mountains from 1992 to 1995.

Such dramatic swings in production from year to year have important implications for management and administration of the commercial harvest. Migrant harvesters account for a majority of the commercial work force and are important for providing a reliable supply of matsutakes to mushroom buyers and brokers. Large and sudden pulses of matsutake production lead to large and sudden influxes of migrant pickers that can catch public land agencies and local communities unprepared to provide adequate lodging, camping, sanitation, and garbage facilities. Influx of harvesters can stimulate rural economies but large numbers of people in the woods also can create problems: increased litter, noise, fire danger, traffic hazards, disturbance of wildlife, and conflicts with big-game hunters and recreational mushroom harvesters. Ongoing studies are improving our ability to predict the level of matsutake production in various habitats. The ability to predict the magnitude of matsutake production in advance would aid management and administration of the mushroom harvest.

Temporal variation in fruiting necessitates long-term monitoring to characterize abundance, distribution, and trends that are essential to the management of commercial harvest. Currently, poorly documented historical levels of production, ephemeral fruiting patterns, and natural variation in habitat are complicating efforts to provide reliable estimates of production at the stand and landscape scale.

Regional and Global Scale

The American matsutake is commercially harvested from the northern interior of British Columbia to Mexico. In British Columbia, the harvest begins in August and September, moving generally from north to south and from high to low elevations. In the Pacific Northwest, the harvest generally ends in January in the coastal areas of northern California. In 1992, nearly 1 million pounds of American matsutake were harvested. The mean price in 1992 was more than $8 per pound when averaged for all stages of development or "grades" (Schlosser and Blatner 1995). Grade 1 matsutake brings the highest price and is characterized by unopened caps in which the mushroom veil is still completely intact with the mushroom stem. Once the matsutake begins to open, it is downgraded to 2, 3, 4, 5, or 6, with the lowest grade reflecting a fully open matsutake that is often affected by insects or other damage agents. The average prices paid in 1992 for matsutake from the 160-hectare study site of tanoak/mixed conifer habitat in southwest Oregon was $20 for grade 1, compared to $1.50 for grade 5. For the period from 1992 to 1995, the price to harvesters ranged widely, from $0.25 to $100 per pound depending upon the grade and demand for the mushroom.

Unlike other harvested wild mushrooms, the market for the American matsutake is largely international, with most exported to Japan. The American matsutake closely resembles the Japanese matsutake (Redhead 1984) in shape, odor, and flavor. Demand for Japanese matsutake has increasingly exceeded supplies during the past 30 years because of the decline of Japan's matsutake habitat and growing demand from a larger and wealthier consumer population (Kawai and Ogawa 1981). Hence, Japanese entrepreneurs began importing similar mushrooms to supplement supply, especially during the past decade (Hosford and others [In press]). Japanese matsutake and related species are also harvested from China, North and South Korea, and Russia, but most studies of the Japanese matsutake have been conducted in a limited geographical area (Japan) and a narrow range of ideal habitats (red pine forest). By contrast, the American matsutake is widely distributed throughout North America and is harvested from diverse forest habitats where it develops mycorrhizal associations with numerous tree species.

Regional biological disturbance agents and climatic and socioeconomic forces can greatly influence production. Since 1905, the matsutake forests of Japan have been plagued by the pine short nematode (Hosford and others 1997). A combination of climatic, socioeconomic, and biological factors in Japan has increased the magnitude of the plague. Pine mortality from nematode disease often increases after a prolonged period of scarce rainfall and high temperatures. This apparently weakens the pines' resistance to the parasite. In addition, a change in the use of the forest has also had an adverse effect. Traditional harvesting of wood for charcoal from understory shrubs and trees, such as oaks, has historically favored the growth of shade intolerant pines. The conversion from wood burning stoves to natural gas burners has promoted conditions leading to pine mortality and the growth of the dense, brushy understory unfavorable to Japanese matsutake production. In contrast, matsutake production has increased dramatically in Korea where pine plantations of 40 to 50 years of age are widespread and prime for matsutake production. These pine plantations are a result of reforestation after the Korean war.

At the largest scale, a variety of global factors influence the demand for and value of matsutakes. Global weather patterns and fluctuating international trade creates large variations in local prices paid to pickers. Consequently, landowners or land managers in America have difficulty calculating fair market value and reasonable compensation for the harvest of matsutakes from their forests. Managers also have difficulty calculating the quantities of matsutakes collected from their lands. Harvesters often cross property boundaries in their search for mushrooms to sell to buyers of their choosing. Federal mushroom permits in the Pacific Northwest are not currently based on a percentage of the market value of the crop, as they are with many other products. Higher permit fees are problematic because harvesters may not be able to predict harvesting expense. Many factors determine harvester success, including fruiting abundance and density, competition from other harvesters, timing, price, and hunting and harvesting methods and conditions.

The monetary value of this relatively new, special forest crop and the conflict over its proper use have brought attention to and underscore the need to understand the American matsutake at both regional and global scales. Regional, social, and economic studies of matsutake harvesting and commerce would help managers develop fair harvest regulations and supply agency personnel and lawmakers in local, county, State, Provincial, and Federal governments with necessary information.

Conclusions

Today, tens of thousands of harvesters pick matsutake from private, State, and Federal lands in many countries across the world. Yet, uncertainty regarding managing matsutake hinders efforts to manage this valuable resource on a sustained basis. At the center of the management issue is a lack of information regarding productivity and management across a variety of spatial and temporal scales. In spite of the notable effort applied to matsutake research in recent years, several important topics remain to be addressed. Managers wishing to predict matsutake production and management effects at the individual shiro, stand, landscape, and regional scales will need reliable and long-term information for a wide variety of habitat types. Understanding local, regional, national, and international production and market factors will aid decision-making and policy-making. Ectomycorrhizal fungi, such as the matsutake, have co-evolved over millennia as a component of diverse and complex natural forest ecosystems operating across a variety of spatial and temporal scales.

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