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Effects of mushroom harvest technique on subsequent American matsutake production

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Abstract

The commercial harvest of American matsutake (*Tricholoma magnivelare*) is a multi-million dollar industry in the Pacific Northwest region of North America. How to best manage for sustainable mushroom production is uncertain and concerns remain about the cumulative effects of picking in the same areas year-after-year and whether raking of surface litter and mineral soil layers to find mushrooms will reduce subsequent fruiting. Here, we evaluate the effects of several mushroom harvest techniques on American matsutake production.

This study was established in the Oregon Cascades in 1994 with the selection of 18 shiros of similar mushroom production. Six mushroom harvest treatments were implemented in 1995: (1) control, (2) best management practice (BMP), (3) shallow rake, litter replaced, (4) shallow rake, no replacement, (5) deep rake, litter replaced, (6) deep rake, no replacement. These treatments were pooled into three litter disturbance groups for analysis: (a) no raking of the litter, (b) litter raked with replacement, and (c) litter raked without replacement.

Matsutake production on additional shiros was monitored to further compare the control and BMP treatments. Our results demonstrate that careful picking (BMP) was not detrimental to mushroom production during the initial 10 years of mushroom harvest activity. One-time treatments in which the forest floor litter layers were removed and not replaced were strongly detrimental to matsutake production and the effects have persisted for 9 years. Matsutake production was reduced to an intermediate degree by the raking with litter replacement treatments. Damage to shiros caused by repeated raking was not tested, however we expect that the effects of repeated raking would be more severe than those reported here. Negative treatment effects were particularly noticeable in years with abundant fruiting. When environmental conditions are poor for fruiting all shiros experience low production, thereby obscuring treatment effects.

Within-year and year-to-year variation in fruiting is a major challenge to studies of matsutake ecology, particularly with regard to documenting treatment effects. Further studies spanning years or even decades will likely be needed to quantify production, effects of management activities, and investigate the biology of *Tricholoma magnivelare*.

Because this study was limited to one habitat type, extension of the results to substantially different habitats types must be made with caution. However, we speculate that since the underlying biology of matsutake fruiting is similar across a wide range of habitats, careful picking should generally not hinder subsequent fruiting when other substantial disturbance to the shiro is absent.

Keywords: Fungi; Sporocarp biomass; Shiro; Wild harvest

1. Introduction

Public land management is increasingly aimed at providing sustainable levels of the entire range of forest ecosystem attributes. Given the important ecosystematic functions of fungi in forests, they have received increased attention. Ectomycorrhizal fungi, for example, are essential for nourishing trees (Trappe and Strand, 1969; Smith and Read, 1997) and many produce edible sporocarps – truffles and mushrooms – that are commercially harvested.

The commercial harvest of edible, forest fungi is a multi-million dollar industry with several thousand tons harvested annually (Watling, 1997; Koo and Bilek, 1998; Table 1). In the last decade in the Pacific Northwest, supplemental income from

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Table 1
Estimated total weight and dollar value of the wild mushroom harvest in Washington State, 1989–1990[a]

Species	1989		1990	
	Total kilograms	Total dollars	Total kilograms	Total dollars
Tricholoma magnivelare	1179	35,075	48,229	602,530
Boletus edulus	1842	24,315	7166	122,655
Cantharellus spp.	112,876	586,355	125,885	437,922
Dentinum repandum	0	0	2547	9376
Hiericium sp.	17	108	55	212
Lactarius "deliciosus"	0	0	45	151
Polyozellus multiplex	0	0	425	1406
Laetiporus conifericola	2	15	34,399	88,087
Sparassis radicata	973	6,366	4,989	16,549
Pleurotus porrigens	1	3	0	0
Other	0	0	36	20
Totals	116,890	652,247	223,777	1,278,910

[a] Washington State Department of Agriculture (1990). The reported numbers are estimated to represent about 10–20% of the actual harvest (Molina et al., 1993).

mushroom harvesting has grown substantially for unemployed timber industry and other rural workers (Pilz and Molina, 2002). The growth of the industry in the Pacific Northwest coincides with the decline of mushroom harvests in Europe (Arnolds, 1991, 1995). Reduction of *Cantharellus cibarius* Fr. production has been documented in The Netherlands and correlated to levels of air pollution (Cairney and Meharg, 1999) but not to levels of mushroom harvesting (Egli et al., 2006).

In the Pacific Northwest, concerns about the wild mushroom harvest center around logging practices, gradual loss of the mushroom resource by potential over harvest, conflict between recreational users and commercial harvesters, regulation of mushroom pickers, and monitoring of future harvests (Molina et al., 1993). A key to wisely managing the edible mushroom resource is common understanding among resource managers, the mushroom industry, and the concerned public about the biology of these unique forest organisms, their ecological importance in forest ecosystems, and effects of disturbance on their survival (Pilz et al., 1999; Pilz and Molina, 2002).

The pine mushroom or American matsutake (*Tricholoma magnivelare* (Peck) Redhead) is widespread in North America but fruits most abundantly in British Columbia, Washington, Oregon, and northern California. American matsutake (hereafter referred to simply as matsutake) occurs with a wide range of hosts (Lefevre, 2002) including lodgepole pine (*Pinus contorta* Dougl.), ponderosa pine (*Pinus ponderosa* Dougl.), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), true firs (*Abies* spp.), tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.), and Pacific madrone (*Arbutus menziesii* Pursh.). It occupies a variety of habitats in the northern Rockies, Oregon coastal sand dunes, Cascade Mountains, and sclerophyll forests of the Klamath Mountains. Commercial harvest is most frequent in lodgepole pine forests. Fruiting typically begins with the advent of fall rains starting in southeast Alaska and British Columbia and progressing southward to northern California (Hosford et al., 1997).

Like many mushroom species, the American matsutake forms sporocarps that vary greatly in abundance and distribution from year to year. Numerous factors influence fruiting of matsutake such as rainfall and temperature (Hosford and Ohara, 1995), and other biotic and abiotic factors (Ohara, 1994). Matsutake typically cluster and associate with specific trees and substrates (Amaranthus et al., 2000). The association between matsutake and its mycorrhizal host frequently varies by geographic location. Fruiting is non-uniform spatially and frequently occurs in arcs or partial arcs (shiros) of a few to numerous sporocarps. The distribution of shiros can also vary widely from a few scattered groups to concentrated clusters (Hosford et al., 1997). The spatial and temporal variability in fruiting and insufficient ecological knowledge of the mycorrhizal mycelium has challenged research and monitoring efforts.

The commercial harvest of American matsutake is growing in local and regional importance. Millions of dollars in economic activity are generated annually by mushroom pickers who receive prices ranging from \$7 to 220 per kilogram (\$15–34/kg, modal range) depending upon supply and quality (Schlosser and Blattner, 1995). The harvest from private, state, and federal lands in the fall season employs thousands of people each year and considerable controversy remains regarding how the resource should be managed (Alexander et al., 2002). Management issues include concerns over logging practices, a lack of information on the ecology and habitat requirements of American matsutake, and the potential effects of the type and intensity of matsutake harvest on future mushroom productivity (Weigand, 1998). This uncertainty hinders efforts to manage the valuable matsutake resource on a sustained basis.

We undertook this study to address issues raised by the community of matsutake harvesters and Forest Service managers. The sheer number of people engaged in matsutake harvest raises sustainability issues. A primary concern has been the practice of raking the soil to uncover the young and most valuable matsutake. Experienced pickers realize that the mushroom is the fruit of an underground fungal colony, and that disturbing tree roots that nourish the colony may interfere with its growth in later years. Therefore, we evaluated the effect of various mushroom harvesting techniques on subsequent matsutake production.

2. Methods

2.1. Study area

The Diamond Lake Matsutake Study site was located near the crest of the Oregon Cascades near Crater Lake National Park on the Umpqua National Forest, Diamond Lake Ranger District (T27S, R5E). The 5.3 ha study site was occupied by the coldest of the mountain hemlock plant associations in the Cascades: the mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.)/grouse huckleberry (*Vaccinium scoparium* Leiberg)/ prince's-pine (*Chimaphila umbellata* (L.) Bart.) plant association (Atzet et al., 1996). The site was also characterized by a deep winter snow pack and substantial summer drought stress.

The forest was old-growth habitat, as defined by the Northwest Forest Plan: forest stands that are typically 180–220 years old [to >400] with moderate to high canopy closure; a multi-layered, multi-species canopy dominated by large overstory trees; high incidence of large trees, some with broken tops and other indications of old and decaying wood (decadence); numerous large snags; and heavy accumulations of wood, including large fallen trees (USDA and USDI, 1994).

The overstory was comprised of >200 year-old noble fir (*Abies procera* Rehder) and remnant old-growth Douglas-fir, mountain hemlock, western white pine (*Pinus monticola* Dougl.), and lodgepole pine. Noble fir and Douglas-fir were the dominant matsutake host species (Amaranthus et al., 2000). Overstory canopy closures ranged from 50 to 90%. Conifer understories occurred in gaps throughout the study area and were comprised of the same species, with the addition of Pacific silver fir (*Abies amabilis* (Dougl.) Forbes). The understory ranged in height from 0.3 to 7.6 m. Quantitative structural parameters are provided in Table 2 and qualitative visualizations of forest structure are provided in Fig. 1.

Herbaceous cover was light and consisted of grouse huckleberry, prince's pine, pinemat manzanita (*Arctostaphylos nevadensis* Gray), and whitevein pyrola (*Pyrola picta* Sm.). Candystick (*Allotropa virgata* Torr. & Gray ex Gray), an indicator of matsutake presence (Lefevre, 2002), was scattered throughout the study site (Fig. 2). The partially decomposed organic litter (O_2) layer was 2–3 cm deep over a Mazama air-laid pumice A horizon, much of it in the lapilli size class (2–64 mm diameter). Elevation ranged from 1585 to 1705 m, aspects were generally north to northeast, and slopes ranged from 0 to 14°.

At a landscape scale, the site was identified as belonging to Fire Regime Group V (having a stand replacement fire return interval of >200 years) and fire condition class 1—characterized as being within its historical range and with low risk of losing key ecosystem components as a result of wildfire. Vegetation attributes (species composition and structure) were intact and functioning within an historical range. Fire effects would be similar to those expected during historical times (USDI, 2005).

2.2. Location of shiros

Matsutake occur in shiros. "Shiro" is a Japanese term that traditionally referred to the location of a group of matsutake that tended to bear fruit year-after-year. As knowledge of the mycorrhizal symbiosis increased, shiro also came to refer to the distinctive mycelial colony in the soil that is formed by the Japanese matsutake (*Tricholoma matsutake* (S. Ito & S. Imai) Singer) and related species (Ogawa and Hamada, 1965; Ohara and Hamada, 1967). Shiro analysis has been used for monitoring *T. matsutake* in Japan (Ogawa, 1975; Ohara, 1994) and *T. magnivelare* in North America (Hosford et al., 1997).

During the first year of this study (1994) individual matsutake sporocarps were located and mapped in order to identify the shiros to which the treatments would be applied. Objective criteria were used to assign individual sporocarps to shiros. A shiro was defined as a group of sporocarps that were each others nearest neighbors and no sporocarp was >50 cm from another sporocarp that belonged to that group. The sporocarps often formed in an arc-shaped pattern (Fig. 3) that indicated their growth from the same mycelial colony (Ohara and Hamada, 1967; Ogawa, 1975; Hosford et al., 1997). Only shiros that produced a minimum of four matsutake in 1994 were considered for inclusion in the raking treatment study.

Three "blocks" or forest stands that were relatively homogenous internally with respect to aspect, slope, elevation, stand structure, vegetation, and soil conditions were established within the matsutake fruiting area. Each block contained six shiros that produced similar numbers of matsutake mushrooms in the baseline year (1994).

2.3. Treatments

In 1995, the raking study was initiated and the following treatments were randomly assigned among the six shiros in each of the three blocks:

(1) C (control): no matsutake harvest.
(2) BMP (best management practice): harvest with minimal disturbance to the O_2 litter layer and mushrooms removed by gentle rocking and pulling.

Table 2
Forest structural characteristics, presented as ranges from three 405 m^2 sample plots in the study area

Trees per hectare by DBH[a] size class (cm)				SDI[b]	QMD[c] (cm)	Standing volume (m^3/ha)	Basal area (m^2/ha)
<15	15–30	31–61	>61				
1482–3952	25–124	139–247	27–74	400–665	13–20	75–160	33–76

[a] DBH = tree diameter at 1.4 m above the ground.
[b] SDI = stand density index.
[c] QMD = quadratic mean diameter.

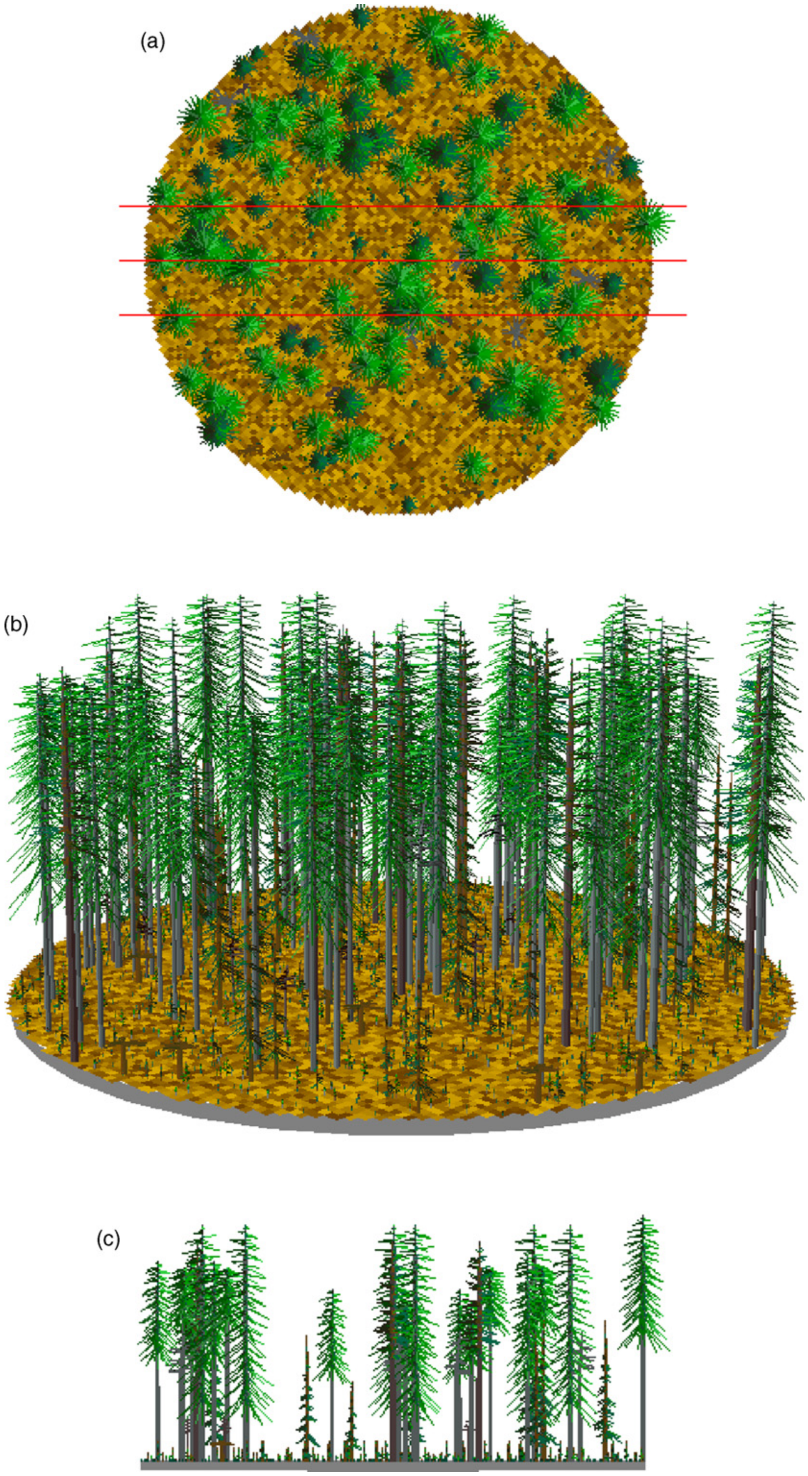

Fig. 1. Qualitative visualizations of study site forest structure generated from plot data by the Forest Vegetation Simulator, Western Cascades Variant software (Dixon, 2003): plane (a), oblique (b), and cross sectional (c) views. Location of cross section indicated in plane view by overlaid lines. Plot diameter equals 22.7 m.

(3) SRR (shallow rake, replacement): shallow raking of litter layers to the interface with the mineral soil surface, sporocarp removal, and replacement of the litter onto the shiro.
(4) SRNR (shallow rake, no replacement): shallow raking of litter layers, sporocarp removal without replacement of the litter.
(5) DRR (deep rake, replacement): raking of the litter layers and raking into the top of the mineral soil (7–10 cm total depth), sporocarp removal and replacement of litter and mineral soil onto the shiro.
(6) DRNR (deep rake, no replacement): raking of the litter layers and raking into the top of the mineral soil (7–10 cm

Fig. 2. Candystick (*Allotropa virgata*) is an above-ground indicator of the presence of *Tricholoma magnivelare* (D. Luoma photo).

total depth), sporocarp removal without replacement of litter and mineral soil.

Treatments were implemented at the first indication of matsutake production of commercial size (≥5 cm in length) at each shiro. One shiro that had been assigned to the DRNR treatment failed to fruit in 1995 and was dropped from the study since it could not be treated according to the established protocol. Also, one control treatment shiro was removed from the study because it stopped fruiting after producing only one more fruitbody. The purpose of the control shiros was to provide reference as healthy fungal colonies that were capable of producing fruitbodies.

2.4. Data collection

Shiros were examined at least once a week during the fruiting season. For the un-harvested control shiros, mushroom cap diameter was measured and the caps were painted with a non-toxic, black ink to discourage commercial harvest. The black ink marking was eventually discontinued as the security

Fig. 3. Flags mark past fruiting locations of matsutake and indicate the arc-shaped (almost ring shaped) nature of the shiro (A. Moore photo).

of the site became apparent. On treated shiros, individual mushrooms were located, harvested if commercial sized, placed in a wax or brown paper bag, and subsequently weighed. Indications of mushroom consumption by wildlife were also recorded. A small "engineering flag" was used to mark the location of each harvested mushroom (Fig. 4). The date, collectors initials, site, block, shiro, and mushroom number were recorded for each mushroom.

In post-treatment years, matsutake in all but the control treatments were harvested using the BMP rocking and pulling technique with litter replacement to the resultant hole. At a field station, mushrooms were carefully examined for grade, commercial value, and damage. This information, along with fresh weight (to 0.1 g) was recorded on the field collection bag.

2.5. Additional BMP and C treatment shiros

Since the 18 original shiros were assigned treatments in 1995, best management practice (BMP) and control (C)

Fig. 4. Sub-emergent matsutake and engineering flags used to mark their locations (D. Luoma photo).

treatments have been randomly assigned to additional shiros throughout the study area that met these criteria: (1) the shiro contained ≥ 5 flagged matsutake that had previously fruited during the course of a single season, (2) matsutake were within 0.5 m of each other, and (3) the shiro produced at least one commercial sized mushroom the year the treatment was assigned. Since 1996, 50 additional C and 37 BMP treatments have been assigned and were monitored in an effort to address long-term effects of careful removal of sporocarps and to document animal use. Data collection protocols on the additional shiros followed those listed above for the original treatments.

2.6. Data analysis

The loss of two treatment shiros, one in each of two blocks, decreased statistical power. To compensate, data from the raking treatment study were pooled into new analytical groups and a blocked analysis was not used. Three groups based on the litter treatment were made: (a) no raking of the litter (C, BMP) $N = 5$, (b) litter raked with replacement (SRR, DRR) $N = 6$, and (c) litter raked without replacement (SRNR, DRNR) $N = 5$, where N equals the number of shiros in each litter treatment group.

One-way analysis of variance (ANOVA) was used to test the null hypothesis of no treatment effects on numbers of matsutake produced or weight of matsutake produced over the 10 years of the study. Response variables were post-treatment mean annual total number of matsutake per shiro and post-treatment mean annual total wet weight of matsutake per shiro. Numbers and weights of each shiro's matsutake were summed for the post-treatment period (9 years) and the sums divided by 9 to obtain the post-treatment annual mean in the response variable for each shiro.

Since wet weights could not be determined in the no harvest control, cap diameters were measured and wet weights were calculated using a regression model ($Y = 0.478 + 1.483 \times X$, $R = 0.70$, $P \leq 0.0001$) that was developed using data gathered from harvested sporocarps. Cap diameter and wet weight data were log transformed in the regression model. Estimated log wet weight values were back-transformed for use in the ANOVA model.

To more closely meet the ANOVA assumptions of normal distribution and constant variance, the count and weight values were transformed (Sabin and Stafford, 1990). A hyperbolic arcsine transformation $[\ln(x + (x^2 + 1)^{1/2})]$ (SAS Institute, 1998) was applied to the count data and a square-root transformation to the wet weight data.

Main ANOVA effects were required to be significant at $P \leq 0.05$ before post hoc tests were carried out. Fisher's protected least significant difference test was used to test for differences among the litter disturbance groups.

In the second analysis, repeated measures ANOVA was used to test the null hypothesis of no difference in mean number of matsutake produced per shiro between the C and BMP treatments during the 1997–2004 time period. Forty-three C treatment shiros and 23 BMP shiros were included in the analysis. Two each of the C and BMP shiros used were from the raking treatment study (above). New shiros were identified in 1997 using the same establishment criteria (above) and BMP harvest commenced in 1999 (no matsutake fruited on the newly identified shiros in 1998). A hyperbolic arcsine transformation $[\ln(x + (x^2 + 1)^{1/2})]$ (SAS Institute, 1998) was applied to the matsutake count data. All statistical procedures were performed with StatView 5.0.1 (SAS Institute, 1998).

3. Results

Statistically significant differences were found between the undisturbed litter treatment group (C, BMP) and the litter raked without replacement group (SRNR, DRNR) for numbers of matsutake produced ($P = 0.016$). Weight of matsutake produced by the undisturbed litter treatment group (C, BMP) was different from the litter raked with replacement group (SRR, DRR) ($P = 0.022$) and the litter raked without replacement group (SRNR, DRNR) ($P = 0.005$). Table 3 summarizes these results.

Repeated measures ANOVA failed to reject the null hypothesis of no difference in numbers of matsutake produced by the C and BMP treatment shiros ($P = 0.502$). Year-to-year differences in matsutake production were detected and those annual differences could vary by treatment ($P = 0.0003$).

4. Discussion

While the no litter replacement treatments (SRNR, DRNR) as a group showed decreased matsutake production, shallow rake versus deep rake differences may also exist within that group. The one-time deep rake, no litter replacement treatment (DRNR) strongly suppressed subsequent fruiting of matsutake over the ensuing 9 years of monitoring. The total number of sporocarps produced by that treatment during those 9 years was less than half the production recorded for the pre-treatment baseline year (1994) alone (Fig. 5). The shallow rake, no litter replacement treatment (SRNR) treatment seemed to be less affected during the first 2 years after treatment than the DRNR treatment, but since 1998 the SRNR treatment has exhibited strongly suppressed sporocarp production (Fig. 5).

Table 3
Mean response of matsutake to forest floor litter raking treatments applied in old-growth *Abies procera* dominated stands on the Diamond Lake Ranger District, Umpqua National Forest, Oregon (standard errors in parentheses)

Mean response/shiro/year	Forest floor litter treatment		
	Intact	Raked, replaced	Raked, not replaced
Number of matsutake	2.9^{a} (2.4)	1.2^{ab} (0.7)	0.5^{b} (0.2)
Weight of matsutake (g)	184^{a} (126)	55^{b} (27)	30^{b} (17)

Across-row values that do not share the same superscript letters are different at $P \leq 0.05$, see Section 3 for exact P-vales of significantly different comparisons. Statistical tests were performed using transformed data. Means were derived from 9 years of data gathered after the one-time raking treatment.

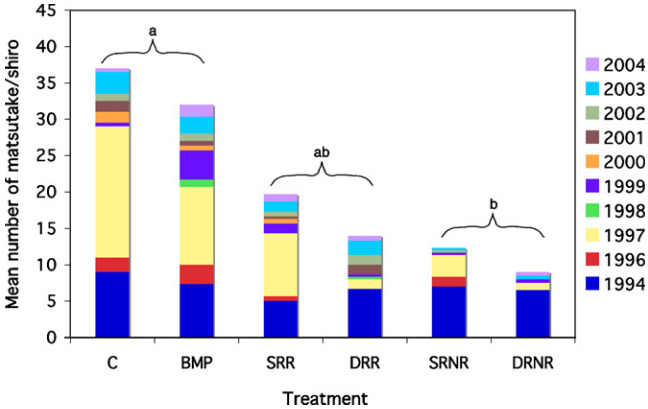

Fig. 5. Mean total number of matsutake per shiro. The 1994 mean number of matsutake per shiro is included to provide baseline reference. Data from the treatment year (1995) were excluded. The analysis was performed on transformed values of the 1996–2004 mean total number/shiro for the three litter disturbance groups (C, BMP), (SRR, DRR) and (SRNR, DRNR). Groups not sharing the same letter overscript were different (Table 3, $P \leq 0.05$, see Section 3 for exact P-values). Values for individual years are shown to illustrate year-to-year variation but were not analyzed separately.

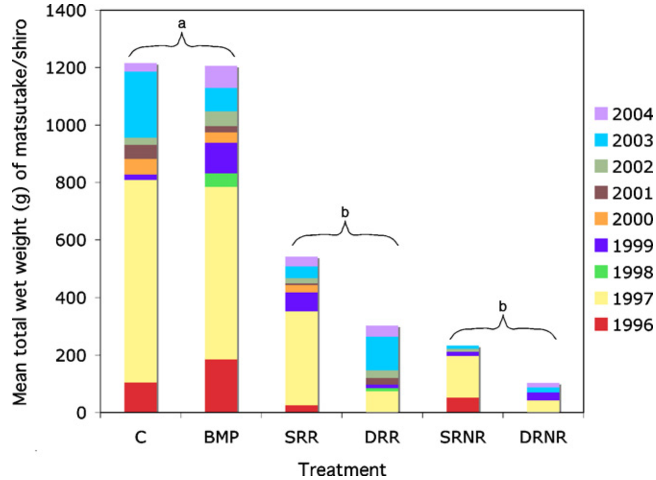

Fig. 6. Mean total weight (g) of matsutake per shiro. The analysis was performed on transformed values of the 1996–2004 mean total weight (g/shiro) for the three litter disturbance groups (C, BMP), (SRR, DRR) and (SRNR, DRNR). Groups not sharing the same letter overscript were different (Table 3, $P \leq 0.05$, see Section 3 for exact P-values). Values for individual years are shown to illustrate year-to-year variation but were not analyzed separately.

In terms of numbers of matsutake produced, the raking with litter replacement treatments (SRR, DRR) could not be statistically separated from the no litter raking treatments (C, BMP) even though the number of matsutake produced over the monitoring period was substantially less (Fig. 5). Failure to reject the null hypothesis in this comparison ($P = 0.15$) may be related to the amount of variation in matsutake production relative to the low number of replications, a situation that increases the risk of a Type I error (Campbell, 1989).

Mushroom pickers are paid according to the quality and weight of the mushrooms (Hosford et al., 1997). Therefore, the effect of treatments on mushroom weight is of particular interest. The general pattern of the matsutake mean fresh weight response to the treatments mirrored that of mushroom numbers (Figs. 5 and 6). Not surprisingly, the significantly lower numbers of matsutake in the no litter replacement treatments (SRNR, DRNR) was accompanied by a significant decrease in mean total matsutake wet weight (Fig. 6). However, the mean total weight of matsutake was also significantly lower in the litter raked with replacement treatment group (SRR, DRR) as compared to the non-raked litter treatments (C, BMP) (Fig. 6). This result of significantly lower weight per shiro lends further credence to the hypothesis that the difference in numbers of matsutake between these treatments (Fig. 5) reflected a biological, if not statistical, difference.

The treatments with litter replacement appeared to exhibit improved matsutake production in recent years, in terms of both numbers and fresh weight. The SRR treatment has fruited regularly since 1999 and the DRR treatment since 2001 (Figs. 5 and 6). That trend should be regarded as hypotheses to be tested when more data are available, however. Ogawa (1982) notes that warming of the soil to stimulate production of Japanese matsutake (*Tricholoma matsutake*) has been accomplished by removal of ‘‘excess’’ forest floor litter in some situations while in other cases addition of litter for a mulching effect has been beneficial.

The best management practices (BMP) harvest technique did not affect levels of matsutake production over the course of this study (Fig. 7). In some years, BMP shiros produced more matsutake than the controls. Detection of significant annual variation in matsutake production was not surprising since other research from our region has noted such variation in truffle and mushroom production (Fogel, 1976, 1981; Luoma, 1991; Smith et al., 2002).

A parallel study to the one reported here was also established in 1994 at the Oregon Dunes National Recreation Area. The intent was to broaden the scope of inference for the treatment effects, in that case by including lodgepole pine stands

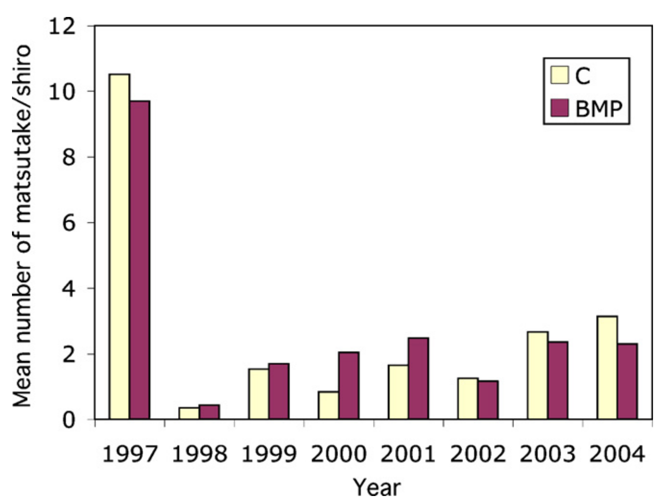

Fig. 7. Mean number of matsutake per shiro comparing the control (C) to the best management practices (BMP) shiros. Repeated measures ANOVA showed no difference between the treatments ($P = 0.502$). Picking on 21 of the 23 BMP shiros started in 1999, 2 were initiated in 1995 as part of the raking treatment study.

established on stabilized sand dunes. Although the experimental design was the same as for the study reported here, differences in experimental unit establishment precluded analysis of the data within the scope of this paper. Additionally, the study at the Oregon Dunes site was terminated after 3 years of post-treatment data collection. It was possible, however, to compare the C and BMP treatments using repeated measures ANOVA for those 3 years. As with the Diamond Lake study, the best management practices (BMP) harvest treatment did not differ from the control in numbers of matsutake produced ($P = 0.859$). Other short-term trends (D. Pilz, unpublished data) also suggested that negative impacts from raking were somewhat ameliorated by replacing raked layers of organic matter and sand. Interestingly, one DRNR treated shiro fruited abundantly in subsequent years. Observations that the fruiting bodies formed well below the exposed sand surface suggested the mycelium of this shiro grew deeper than the raking treatment had reached.

In a study of mushroom harvest effects on chanterelle production, Egli et al. (2006) found no direct negative impact of mushroom picking on sporocarp production over a period of 29 years. They did, however, find that ‘‘normal walking associated with mushroom harvesting’’ reduced chanterelle production by about 30%. Since this level of ‘‘trampling’’ is integral to the harvest of wild mushrooms it must be regarded as a constantly associated effect.

The current study did not test for potential trampling effects. Egli et al. (2006) hypothesized that walking on their plots damaged some mushroom primordia but did not damage the mycelium. The volcanic pumice soils of the Diamond Lake study site are likely much different than the soils of the Egli et al. (2006) study site which was conducted in a *Picea abies* (L.) Karst forest in Switzerland. The lapilli of the Diamond Lake site would seem to offer physical protection to the primordial from the walking about associated with mushroom picking. Additionally, sporocarp formation is generally initiated more deeply in the soil for *Tricholoma magnivelare* than for *Cantharellus* (compare Figs. 4 and 8). Therefore, it is a reasonable hypothesis that matsutake primordia at the Diamond Lake study site were better protected from potential trampling effects than the chanterelles of the Egli et al. (2006) study. Sites with erodible sandy soils or other easily disturbed or compacted soil types may also be at risk from trampling effects.

Another chanterelle picking study has been ongoing in Oregon's Cascade Mountains since 1986. Results through 1999 showed no detrimental effect of mushroom picking on levels of chanterelle production (Oregon Mycological Society, unpublished data, cited in Pilz et al., 2003).

4.1. Management Implications

This study has shown that soil disturbance, specifically organic litter and mineral soil displacement, can be detrimental to the sustainability of matsutake fruiting in the short term (less than 10 years). Other forest management practices that could have similar effects on matsutake production include timber harvest and associated slash treatment. Those practices typically displace and potentially compact soils within timber harvest sale areas through skidding and yarding logs, piling and burning slash, and road construction. Additional detrimental soil effects can include soil layer mixing and severe soil burning. Most National Forest Plans address detrimental soil effects by limiting such disturbance to 20% of the timber sale activity area (USDA, 1990).

Fig. 8. *Cantharellus formosus* sporocarp (D. Pilz photo).

Based on the findings of this study, when management goals include maintaining matsutake production, soil disturbance could be minimized within highly productive matsutake fruiting areas. This could be accomplished by designating skid trails, yarding corridors, and haul roads away from known areas of productive matsutake fruiting. Communication with local pickers and mapping of high quality matsutake habitat through stand exams could aid in this effort. Precise mapping of shiros, within areas of proposed activities, can be accomplished by locating fruit bodies or noting the presence of *Allotropa virgata*.

Commercial matsutake picking can also disturb and displace organic litter layers and mineral soil due to the quest to uncover matsutake with the highest value. On federal lands in the Pacific Northwest, raking to harvest matsutake is illegal and the best management practice (which allows the aid of a small prying tool) is required under the commercial permit system (USDA, 2005). Since this study found that simulated commercial mushroom harvest activity that displaces forest floor organic material can adversely affect matsutake fruiting in the short term, continued protection of the soil litter layer by use of BMP techniques is supported.

Efforts to remediate disturbed sites may also benefit from the results of this study. The disturbed litter with replacement treatments (SRR, DRR) showed signs of recovery in matsutake production as the replaced litter layers experienced recruitment of small branch, twig, and needle fall. Restoration techniques that replace litter layers in areas of soil displacement might aid in the recovery of matsutake fruiting in both the short and long term. These could include uneven aged silvicultural treatments that continually leave canopy cover to recruit branch, twig, and needle fall. Such silvicultural prescriptions could be combined with mechanical or manual treatments that restore organic material to nominal levels.

Unlike Japanese matsutake (*Tricholoma 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 (Hosford et al., 1997) as is the case at the Diamond Lake study site. Uneven-aged silvicultural prescriptions within stands similar to the study site may maintain and possibly promote high quality matsutake habitat. Uneven-aged management would maintain old-growth host trees, canopy closure, litter layers, and microsites around advanced natural regeneration and down trees—all to the potential benefit of matsutake production. This silvicultural approach would also develop old-growth host trees to replace dead and dying matsutake host trees and would promote maintenance of large down woody material through time. An objective of uneven-aged stand conditions is consistent with the range of natural variability for Fire Regime V (USDI, 2005).

A variety of animals consume matsutake (Hosford et al., 1997). The control treatments were monitored for animal use on a weekly basis. Matsutake within the study were regularly eaten by deer (*Odocoileus*), elk (*Cervus*), bear (*Ursus*), squirrels (*Spermophilus, Tamiasciurus*, *Glaucomys*), chipmunks (*Tamias*), and voles (*Clethrionomys*). Between 1999 and 2004, evidence of animal use of matsutake (tooth marks, pawing of the forest litter, fragmented mushrooms) was found associated with 50–90% of the sporocarps (e.g. Fig. 9). Tooth marks ascribed to small mammals were associated with a majority of this activity. Pilz et al. (1999) reported 25% of matsutake examined were browsed. Given this level of apparent animal use of matsutake as a food source, studies that target quantification of this behavior are warranted. There is a potential concern that human competition for matsutake may affect certain wildlife populations. Limits on commercial picking of low value matsutake (grades 5 and 6, Hosford et al., 1997) or prohibition of collecting matsutake that show signs of active animal browsing (which are also of low commercial value) are potential measures to address this concern.

Fig. 9. Excavated *Tricholoma magnivelare* stipes bitten by a deer. Noticeable tooth marks are evident across one remnant base (D. Luoma photo).

The Diamond Lake study site has been monitored for 12 years. Observations from the C and BMP treatments demonstrate high yearly (Fig. 7) and weekly (data not presented) variability in mean values of matsutake production. There was also among-shiro variability in constancy of fruiting from year-to-year. Some shiros seemed to be more ‘‘vigorous’’ in that they fruited reliably each year, whereas most shiros did not fruit every year. Year-to-year variation in mean sporocarp biomass production has been attributed to natural variation in weather patterns or other natural, non-treatment related variation (Fogel, 1976, 1981; Luoma, 1991; Luoma et al., 1991; O'Dell et al., 1996, 1999). Investigations into conditions associated with high vigor of specific shiros, those that seem to be resilient in the face of sub-optimal environmental conditions, may benefit managers by increasing their ability to provide, maintain, or enhance habitat conducive to matsutake production.

5. Conclusions

Our results demonstrate that careful picking (the BMP treatment) was not detrimental to mushroom production during the initial 10 years of mushroom harvest activity. One-time treatments in which the forest floor litter layers were removed and not replaced (DRNR and SRNR) were strongly detrimental to matsutake production and the effects have persisted for 9 years. We expect that the effects of repeated raking would be more severe than those reported here. Negative treatment effects were particularly noticeable in years with abundant fruiting such as 1997. When environmental conditions are poor for matsutake production (i.e. 1998) all shiros experience low production thereby obscuring treatment effects.

Our monitoring efforts demonstrate the importance of treatment replication. Within-year and year-to-year variation in mushroom production is a major challenge to studies of matsutake ecology, particularly with regard to documenting treatment effects with precision. Many years or even decades of monitoring will likely be needed to quantify variations in production, determine the effects of management activities, and investigate the biological and ecological roles of the American matsutake in ecosystems (Hosford et al., 1997). Future studies that encompass more shiros will enable us to document trends in shiro longevity and reliability of matsutake production.

In order to obtain multiyear data sets, long-term access to secure sites is critical (Hosford et al., 1997). Due to its remoteness and a locked gate which deters access to the area, the Diamond Lake study site is potentially a key link in any region-wide effort to assess matsutake production and management.

Because this study was limited to one habitat type, inferences concerning the applicability of the litter raking treatment results to substantially different habitats types must be made with caution. However, we speculate that since the underlying biology of matsutake fruiting is similar across a wide range of habitats (Ogawa, 1975; Ohara, 1994; Hosford et al., 1997), careful picking should generally not hinder subsequent fruiting, if other substantial disturbance to the shiro is absent.

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