

TRUFFLE ABUNDANCE IN RECENTLY PRESCRIBED BURNED AND UNBURNED FORESTS IN YOSEMITE NATIONAL PARK: IMPLICATIONS FOR MYCOPHAGOUS MAMMALS

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ABSTRACT

Truffles are an important food resource for wildlife in North American forests, but decades of fire exclusion have altered the availability of this resource. In Yosemite National Park, resource management policies seek to restore essential forest processes such as fire while minimizing adverse ecological impacts that may result from burning decades of accumulated fuels. Burning can impact truffles through heat stress, elimination of soil organic layers, and damage to tree hosts, but these effects may be dependent on time lags between fires and fire frequency. We examined truffle abundance, and species diversity and composition in four paired burned and unburned sites (8 sites total) in Yosemite to determine the short-term effect of fire on truffles and its implications for truffle-consuming mammals. Burned and unburned sites had similar truffle biomass and species richness, but truffle frequency was greater in unburned than burned sites. Truffle species composition was distinctively different between burned and unburned sites, although seven species were found exclusively in both burned and unburned sites. Truffles were positively associated with litter depth in burned and unburned sites, although this association was stronger in burned sites. Prescribed burning may enhance the regional diversity of truffles for mycophagous mammals across the forest landscape without impacting total abundance in Yosemite National Park.

Keywords: ectomycorrhizal fungi, litter depth, prescribed fire, Sierra Nevada, truffles

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INTRODUCTION

A diverse and important functional component of forest ecosystems are ectomycorrhizal fungi (EMF), which are required by most temperate forest conifer species for increased water and nutrient uptake (Molina *et al.* 1992). The EMF fruiting bodies, especially below-ground truffles, form the base of a complex food web in forests (Johnson 1996, North *et al.* 1997) and are a major part of the diet of many mammals (Fogel and Trappe 1978, Maser *et al.* 1978). In Sierra Nevada forests, truffles are the primary food of northern flying squirrels (*Glaucomys sabrinus*; Pyare and Longland 2001, Meyer *et al.* 2005b), which in turn constitute the main prey of California spotted owls (*Strix occidentalis occidentalis*) (Williams *et al.* 1992). Truffles also comprise a frequent 92 % of the diet of fisher (*Martes pennanti*) and 44 % of the diet of American marten (*Martes Americana*), key management species in Sierra Nevada forests (Zielinski and Duncan 2004). Viable fungal spores pass through the digestive system of mycophagous (i.e., fungus consuming) mammals and are dispersed to new soil patches where they facilitate conifer succession (Terwilliger and Pastor 1999) and promote EMF diversity (Johnson 1996, Izzo *et al.* 2005).

Prescribed burning can reduce both EMF (Stendell *et al.* 1999, Smith *et al.* 2005) and truffle abundance, diversity, and consumption by small mammals (Meyer *et al.* 2005a) in the short-term (<2 years). Truffle abundance returns to pre-burn levels nine years after burning, although changes in species composition often persist for more than a decade (Waters *et al.* 1994). The abundance of EMF and richness of truffle species peaks in areas with well-developed surface litter and organic material (Amaranthus *et al.* 1994, Stendell *et al.* 1999, Claridge *et al.* 2000, Lehmkuhl *et al.* 2004, Smith *et al.* 2005) and a

higher density of large-diameter trees with greater canopy closure (States and Gaud 1997, Lehmkuhl *et al.* 2004). Consequently, forest stands unharvested and unburned for long periods (>100 years) often have greater truffle abundance than recently harvested and burned stands (Meyer *et al.* 2005). Burning can directly impact truffle-producing EMF through heat stress (Dahlberg *et al.* 2001, Smith *et al.* 2005) and indirectly by damaging tree hosts and impacting tree root biomass (Stendell *et al.* 1999, Smith *et al.* 2005).

Yosemite National Park in the central Sierra Nevada of California contains a highly diverse flora and fauna (Davis and Stoms 1996, Burns *et al.* 2003) that are historically adapted to fire (Shaffer and Laudenslayer 2006, van Wagtenonk and Fites-Kaufman 2006). For the past three decades, Yosemite has maintained an active fire management program using prescribed and managed wildfires, particularly in mixed-conifer forests of the western slope (National Park Service 2004). This management policy has created a heterogeneous landscape of burned and unburned stands throughout Yosemite's mixed-conifer zone, and may increase biotic diversity across the forest landscape (Martin and Sapsis 1992, Huntzinger 2003). However, the effects of this management program on truffles and the implications for forest food webs have not been previously examined.

Our research objective was to determine the effects of recent prescribed burning on patterns of truffle abundance (frequency, biomass), diversity (species richness), and species composition in Yosemite National Park. We define recent as equal to or less than eight years, which is the minimum median fire return interval in mixed-conifer forests of the Sierra Nevada (Skinner and Chang 1996). Specifically, we examined three hypotheses concerning the effect of fire on truffles: 1) truffle abundance and diversity are lower in recently burned sites compared to sites

unburned for >75 years; 2) truffle abundance and diversity are positively associated with organic litter depth and tree (>30 cm dbh) proximity in recently burned sites, but are not associated with these variables in unburned sites; and 3) recently burned sites have a distinct species composition compared to unburned sites.

METHODS

Study Area and Design

We selected four paired research sites at four separate prescribed burn locations in the southwest corner of Yosemite National Park: Yosemite West (burned in 1998), Turner Ridge (burned in 1999), Big Creek (burned in 2005), and Mariposa Grove (burned in 1999 and 2002). Each burn site was in a separate watershed. Within each site, we selected a burned and unburned sample location using a random set of locations defined by the Yosemite National Park fire management vegetation map (National Park Service 2004). Burned sites were selected based on the following criteria: 1) prescribed burned in the past eight years, 2) burned site ≥ 5 ha in size, 3) located between 1300 and 1800 m elevation (primary elevation range of mixed-conifer forest in Yosemite), and 4) located >200 m from a road and >100 m inside a burned stand (to minimize edge effects). We selected paired unburned sites that were located within 500 m from burned areas at the same elevation, aspect, slope, and forest type, and where fire has been absent for >75 years (75 years is the extent of the Yosemite National Park fire history record at the onset of this study; National Park Service 2004). All sample sites burned at low severity with the exception of 7 % of sample sites that burned at moderate severity, especially in the Mariposa Grove site. The frequency of tree species at all sites included 41 % white fir (*Abies concolor*), 20

% incense cedar (*Calocedrus decurrens*), 17 % sugar pine (*Pinus lambertiana*), 13 % ponderosa pine (*Pinus ponderosus*), 4 % Jeffrey pine (*P. jeffreyi*), 4 % black oak (*Quercus kelloggii*), and 1 % Pacific dogwood (*Cornus nuttallii*). Common shrubs included *Arctostaphylos patula*, *Ceanothus cordulatus*, *Ceanothus integerrimus*, *Chamaebatia foliolosa*, *Chrysolepis sempervirens*, *Corylus cornuta californica*, *Cornus nuttallii*, *Quercus berberidifolia*, and *Ribes roezlii*. Average canopy closure was 78 % in both burned and unburned sites (based on digital hemispherical photos [Jennings et al. 1999]).

Truffle and Stand Measurements

Beginning at a random point in our study area, we placed 25 4 m² circular quadrats every 10 m in a five by five grid at each study site. From June 14 through July 6, 2006, (Turner Ridge, Yosemite West, Mariposa Grove) and June 10 through June 30, 2007 (Big Creek), we sampled quadrats for truffles by searching through the organic litter, humus, and upper 5 cm of mineral soil (5 cm to 20 cm total depth) using a 4-tined rake, yielding a total sample area of 800 m² (4 paired sites \times 100 m²). All truffles were collected and counted, placed in wax bags, dried for 24 h at 60 °C, weighed to the nearest 0.01 g, and identified to species. We used truffle collections to estimate frequency, biomass, and species richness of truffles in burned and unburned sites. All truffle voucher specimens were stored and catalogued in the USDA Forest Service Sierra Nevada Research Center in Davis, California, USA, or in the Yosemite Museum, Yosemite National Park, California, USA.

Based on our review of the truffle literature for dry interior forests (States and Gaud 1997, Waters et al. 1997, North 2002, Lehmkuhl et al. 2004, Meyer and North 2005, Meyer et al. 2005a), we selected and measured the following microsite variables in each 4 m²

quadrat: distance to nearest tree (>30 cm dbh), litter depth (includes litter and humus layers), distance to nearest shrub (>30 cm height), and char height. We measured distance to the nearest tree from the center of each quadrat. To measure litter depth, we dug three shallow pits at the edge of each quadrat (at 0°, 120°, and 240° from the center point) and took two depth measurements at each pit of the combined organic litter and humus layers. We measured char height on all sampled nearest trees to estimate fire intensity or potential heat stress (Borchert *et al.* 2002). We also estimated canopy closure at the center of ten randomly chosen quadrats at each site using hemispherical photographs that were analyzed using Gap Light Analyzer 2.0 software.

Statistical Analysis

We used dependent t-tests to examine the effect of burning on truffle frequency, biomass, and species richness, as well as litter depth, tree distance, shrub distance, and canopy closure. We also conducted these dependent t-tests to examine the effect of burning on truffle and forest variables using only data from sites sampled in 2006 (i.e., Turner Ridge, Mariposa Grove, and Yosemite West). The results that included all sites were similar to the analyses that excluded Big Creek (2007); therefore, we only present the former results. We evaluated data for normality with the Kolmogorov-Smirnov test and for homoscedasticity with Levene's test. We used logistic regression to relate microsite variables (i.e., litter depth, tree distance, shrub distance) to truffle occurrence. To reduce model over-fitting, we only included significant ($P < 0.10$) predictors in our logistic regression analyses, and tested for multicollinearity by examining potential correlation between independent factors in each model. For each significant parameter in the logistic regression model, we calculated odds-ratios and their confidence intervals

based on a Quasi-Newton estimation method (Statistica 2003). We interpreted the odds-ratio estimates as the odds of truffle occurrence given a one unit change in a microsite parameter after being adjusted for the effects of other parameters in the model. We used a sensitivity analysis of each treatment type to evaluate the performance of the reduced logistic regression model and to assess model accuracy in successfully predicting occurrence of truffles among sample points (Hosmer and Lemeshow 2000). All statistics were conducted with Statistica 6.1 (Statistica 2003) and an α level of 0.10.

RESULTS

A total of 47 (40.83 g) and 63 (71.59 g) truffles were collected from burned and unburned sites, respectively. The greatest truffle biomass was collected from Yosemite West (4.45 kg ha⁻¹), followed by Turner Ridge (3.76 kg ha⁻¹), Mariposa Grove (1.73 kg ha⁻¹), and Big Creek (1.33 kg ha⁻¹). Truffle species richness was greatest at Turner Ridge (15 species), followed by Mariposa Grove (8 species), Yosemite West (7 species), and Big Creek (4 species). The total cumulative richness was 15 species at both burned and unburned sites; total richness among all sites was 22 species. Truffle species richness ($t = -1.124$, $df = 3$, $P = 0.343$) and biomass ($t = -1.216$, $df = 3$, $P = 0.311$) were similar between burned and unburned areas, but truffle frequency was greater in unburned (29 ± 6 % [SE]) than burned areas (17 ± 8 %; $t = -5.196$, $df = 3$, $P = 0.014$; Table 1). Truffle species composition was distinctively different between burned and unburned sites, although seven species were found exclusively in both burned and unburned sites (Table 2). Ten and twelve truffle species were more abundant in burned and unburned areas, respectively.

Litter depth ($t = -3.416$, $df = 3$, $P = 0.076$) was greater in unburned than burned sites, but

Table 1. Truffle abundance and diversity, and mean values of microsite variables at four burned and four unburned paired sites in Yosemite National Park, California. Yosemite West was burned in 1998, Turner Ridge in 1999, Big Creek in 2005, and Mariposa Grove in 1999 and 2002.

Site and Treatment	Frequency (%)	Species Richness	Biomass (kg ha ⁻¹)	Litter depth (cm)	Distance to tree (m) ^a	Canopy cover (%)	Char height (m)
Yosemite West							
Burn	24	5	1.69	2.0	2.7	78	1.2
No Burn	32	4	2.76	6.3	2.9	75	
Turner Ridge							
Burn	36	10	2.37	4.4	3.3	82	1.8
No Burn	44	9	1.39	6.4	2.6	79	
Mariposa Grove							
Burn	8	2	0.05	1.3	3.8	76	2.9
No Burn	24	8	1.68	7.5	7.5	81	
Big Creek							
Burn	0	0	0.00	1.1	2.4	77	1.1
No Burn	33	4	1.33	7.6	2.3	75	

^a Distance to nearest tree (>30 cm dbh).

Table 2. Biomass of truffle species at 4 burned and 4 unburned sites in Yosemite National Park, California (June and July 2006, 2007).

Species	Biomass (kg ha ⁻¹)	
	Burned	Unburned
<i>Alpova trappei</i>	0.462	–
<i>Balsamia magnata</i>	0.028	0.031
<i>Cortinarius verrucisporus</i>	0.055	–
<i>Elaphomyces granulatus</i>	–	0.326
<i>Endogone lactiflua</i>	–	0.221
<i>Gastroboletus ruber</i>	0.209	–
<i>Gautieria monticola</i>	0.321	0.476
<i>Genabea cerebriiformis</i>	–	0.006
<i>Gilkeya compacta</i>	0.002	0.012
<i>Geopora cooperi</i>	–	0.595
<i>Gymnomyces brunnescens</i>	–	0.343
<i>Hydnotrya cerebriiformis</i>	–	0.129
<i>Hydnotrya variiformis</i>	0.282	0.141
<i>Hysterangium coriaceum</i>	0.088	0.364
<i>Leucogaster citrinus</i>	0.103	–
<i>Leucophleps spinispora</i>	0.304	0.046
<i>Macowanites luteolus</i>	0.365	0.343
<i>Pyrenogaster atroleba</i>	0.025	–
<i>Radiigera taylorii</i>	–	0.432
<i>Rhizopogon ponderosus</i>	1.152	–
<i>Rhizopogon subcaerulescens</i>	0.635	3.692
<i>Truncocolumella citrine</i>	0.077	–
Unidentified (immature)	–	0.013

tree distance ($t = 0.065$, $df = 3$, $P = 0.811$), shrub distance ($t = -0.800$, $df = 3$, $P = 0.507$), and canopy closure ($t = 0.179$, $df = 3$, $P = 0.869$) were similar between treatments (Table 1). Char height was different among burned sites ($F_{1,4} = 3.260$, $P = 0.046$), being greater at Mariposa Grove than at Yosemite West (Bonferroni: $P = 0.043$). The occurrence of truffles was positively associated with litter depth in burned and unburned sites (although this association was stronger in burned sites) and negatively associated with tree distance in burned sites (Table 3). The selected logistic regression models correctly classified 77 % and 89 % (burned sites) and 45% and 66 % (unburned) of truffle-present and truffle-absent stations, respectively.

DISCUSSION

Our study was conducted with limited sampling over one season (summer) and four sites in a single region and forest type of Yosemite National Park, and we do not know how applicable our results are to a broader range of forests in the Sierra Nevada. In our study, sites that burned eight years before our sampling (i.e., Turner Ridge, Yosemite West)

Table 3. Results of logistic regression models relating microsite variables with the occurrence of truffles in Yosemite National Park, California (2006).

Treatment	Independent variable	Estimate (SE)	χ^2	Odds ratio ^a (95 % CI)	P
Burned	Litter depth	0.96 (0.37)	6.901	2.6 (1.2 to 5.5)	0.009
	Tree distance	0.96 (0.44)	4.705	0.4 (0.2 to 0.9)	0.030
Unburned	Litter depth	0.21 (0.12)	2.885	1.2 (1.0 to 1.7)	0.089

^a Effect of a 1 cm increase in litter depth or 1 m distance to the nearest tree on the probability of truffle occurrence.

had similar truffle biomass, frequency, and richness as nearby unburned stands. However, sites burned more recently (i.e., Mariposa Grove, 4 yr; Big Creek, 2 yr) had lower truffle abundance and richness compared to nearby unburned sites (Table 2). These results suggest that the time since burning is important in determining fire effects on truffles. The two sites burned eight years before sampling had more time for ectomycorrhizal fungi communities to reestablish following burning than the two sites burned 2 yr to 4 yr ago. Additionally, unlike the sites burned more recently, sites burned eight years before sampling had thicker litter layers, and these thicker layers were positively associated with truffles across all burned sites. In mixed-fir forests of northeastern California, the biomass and frequency of truffles did not differ between prescribed burned and unburned sites, nine years after burning (Waters *et al.* 1994). In contrast, the frequency, biomass, and species richness of truffles were greater in unburned mixed-conifer stands than stands burned one year to two years before sampling in the southern Sierra Nevada (Meyer *et al.* 2005a).

Burning can influence several microsite variables associated with truffle production, including litter depth (Waters *et al.* 1994, North and Greenberg 1998) and tree densities (Kobziar *et al.* 2007). Decaying woody debris in the form of organic litter is an important reservoir of moisture and nutrients that may provide conditions favorable for fruiting fungi (Amaranthus *et al.* 1994), especially in forests where the soils are relatively dry (Clarkson

and Mills 1994, Meyer and North 2005). Reduced decayed woody debris following burning may have decreased the abundance of truffles in our burned sites compared to unburned sites. In mixed-conifer forests of the southern Sierra Nevada, truffles were generally greater in unburned stands with thicker litter layers than burned or unburned stands with thinner litter layers (Meyer *et al.* 2005a). Interestingly, the truffle-consuming northern flying squirrel (*Glaucomys sabrinus*) was more frequently captured at sites with thicker litter in burned mixed-conifer stands of the southern Sierra Nevada (Meyer *et al.* 2007).

The negative association of truffles with tree distance in burned sites may be a result of greater fire severity patterns near large trees. In unburned Douglas-fir (*Pseudotsuga menziesii*) stands of western Oregon, truffle abundance peaks at 2 m from the base of a tree (Fogel 1976), a pattern we did not observe in our burned or unburned sites, perhaps because tree distance consistently averaged greater than 2 m (Table 1). However, fire severity is positively associated with tree proximity in many western forests because litter and sloughed bark accumulate near the base of large-diameter (>50 cm dbh) trees (Ryan and Frandsen 1991). Consequently, burning may have had a greater negative impact on truffles near the base of large-diameter trees than farther away from these trees through direct (heat) or indirect (tree root mortality, litter consumption) fire-related impacts.

Several of the most abundant truffles at our study sites included *Rhizopogon*

subcaerulescens, *Gautieria monticola*, and *Geopora cooperi*. These species had greater overall biomass in the unburned sites than burned sites, and were notably reduced in sites burned two years to four years before sampling. These three species also had greater overall biomass in unburned stands than prescribed burned stands in the southern Sierra Nevada (Meyer et al. 2005a). These genera were among the most frequently occurring truffle genera in northern flying squirrel diets in the southern Sierra Nevada (Meyer et al. 2005b) and in Yosemite National Park (*Rhizopogon* and *Gautieria* only; M. Meyer, unpublished data). The reduction of frequently consumed truffle genera within burned sites could potentially diminish foraging habitat quality for mycophagous small mammals (Meyer et al. 2005a), decrease relative abundance of northern flying squirrels in burned compared to unburned stands (Roberts 2008), or cause flying squirrels to forage more selectively in patches with greater probability of truffle occurrence (i.e., patches with thicker litter; Meyer et al. 2007).

A primary goal of Yosemite National Park's fire management program is to reduce fuel levels and restore fire-dependent ecosystem processes and biodiversity (National Park Service 2004). To meet the goal of enhancing the biodiversity of truffle-producing EMF and the wildlife species dependent on these taxa, we recommend: 1) the continuation of active prescribed burning programs in Yosemite National Park to enhance habitat quality for wildlife and promote key ecosystem processes, 2) prescribed fire return intervals of ≥ 8 yr, when feasible, to allow adequate time for truffle abundance to rebound from burning in mixed-conifer stands, and 3) managing fire for heterogeneous fuel consumption so that patches of litter (>3 cm depth) and overstory host trees are retained. Such recommendations may substantially benefit truffle-producing fungi and the mycophagous mammals dependent on these key forest ecosystem components in Yosemite National Park.

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