# Seasonality and Abundance of Truffles from Oak Woodlands to Red Fir Forests[1]

**Malcolm P. North**[2]

## Abstract

Truffles are an important food source for many small mammals in forest ecosystems; however, we know little about the seasonality, abundance, or diversity of the truffle community in the Sierra Nevada. This study examined how truffle abundance and diversity varied between oak woodland, ponderosa pine (*Pinus ponderosa*), mixed-conifer, and red fir (*Abies magnifica*) forests. Species richness (number of species) and abundance of truffles were highest in ponderosa pine stands, but species evenness was greatest in mixed-conifer stands. Truffle biomass peaked in late spring and fall, tracking precipitation patterns with a 1-2 month lag. At least 65 species of truffles were identified in a 1-ha sample of the forest. This number is still only a fraction of the fungal species present, as many mycorrhizae rarely produce fruiting bodies. Truffle production depends on the condition of the truffle's mycorrhizal host trees. Natural or human disturbances, which affect the age and composition of the forest, will affect truffle abundance and the animals that depend on them for a substantial portion of their diet.

Scientists and managers are becoming increasingly aware of the importance of the fungal community in forest ecosystems. Mycorrhizal fungi are essential for plant growth and survival; they provide food for many soil biota (Warnock and others 1982); they reduce soil pathogens and bacteria (Marx 1972); and they improve soil structure (Tisdall and Oades 1979). Fungi also produce fleshy fruiting bodies that are an important part of a forest's food chain. Mycorrhizal fungi form above- and below-ground fruiting bodies known, respectively, as epigeous and hypogeous sporocarps, commonly called "mushrooms" and "truffles." Although many forest animals are opportunistic consumers of sporocarps (mycophagy) (Fogel and Trappe 1978), several species of small mammals rely on truffles for a substantial portion of their diet (Maser and others 1978). Animal mycophagists include many species of Geomyidae (pocket gophers), most Microtidae (voles), and almost all Sciuridae (squirrels and chipmunks) in North America (Fogel and Trappe 1978, Maser and others 1978), as well as many forest-dwelling marsupials in Australia (Johnson 1994, Seebeck and others 1989). Many truffle consumers comprise the base of the forest food chain for higher predators (Grenfell and Fasenfest 1979). A well-know example is the connection between truffles, the dominant food source of the northern flying squirrel (*Glaucomys sabrinus*) (Hall 1991; Maser and others 1985, 1986; McKeever 1960), and the squirrel's importance as the principal prey of the spotted owl (*Strix occidentalis*) in mesic forests (Forsman and others 1984, 1991; Verner and others 1992). It is essential that we understand how truffle abundance changes with forest conditions because of their substantial influence on small mammal populations and, consequently, the higher predators in the forest's food web.

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[2] Research Ecologist, Pacific Southwest Research Station, USDA Forest Service, 2081 E. Sierra Ave., Fresno, CA 93710.

Changes in forest composition resulting from succession, disturbance, or timber harvesting will affect truffle abundance and diversity because truffles are produced by mycorrhizal fungi, which rely on carbohydrates from their tree hosts (Harley and Smith 1983). Other site characteristics, such as local edaphic conditions (North and others 1997) and the size and the decay state of coarse woody debris, may also influence truffle production (Amaranthus and others 1994). North and Greenburg (1998) found a highly significant association between the most abundant truffle species in western hemlock (*Tsuga heterophylla*) forest and thick organic layers with a high density of fine roots. In stands that lacked these soil conditions because they had been clearcut and burned 60 years earlier, truffle biomass was only 20 percent of that found in adjacent old-growth stands. In the Sierra Nevada, forest managers need information on truffle biomass in different forest types and what forest conditions are associated with truffle production to assess the impact of their management decisions on truffle biomass and to evaluate the potential abundance of this food source for small mammals.

This study was designed to answer two questions regarding truffles in forests of the Sierra Nevada: how do truffle abundance and species diversity vary among forest types and with seasons; and what are the biomass and species diversity of truffles in 1 ha of typical mixed-conifer forest?

## Methods

We selected two stands in each of four forest types in the Sierra National Forest: oak woodlands, ponderosa pine, mixed-conifer, and red fir. The two oak woodland stands were at 320 m in elevation and dominated by blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and a mixture of exotic grasses. The two ponderosa pine (*Pinus ponderosa*) stands were at 1,400 m in elevation, dominated by ponderosa pine but with a substantial density of smaller white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*) stems. The two mixed-conifer stands, within the Teakettle Experimental Forest at 2,200 m in elevation, had white fir, red fir (*Abies magnifica*), incense cedar, Jeffrey pine (*Pinus jeffreyi*), and sugar pine (*Pinus lambertiana*). The red fir stands were at 2,800 m in elevation and dominated by red fir and occasional lodgepole pine (*Pinus contorta*).

Beginning in February of 1996, all eight stands were sampled each snow-free month. In each stand, two parallel transects 10 m apart were randomly located, and 4-$m^2$ circular plots were raked for truffles every 10 m along each transect. New transects and plots were sampled with each stand visit because raking disturbed soil structure and mycorrhizae. A total of 100 $m^2$ was sampled in each stand during each sample period. All truffles were labeled, bagged, cut in half, and dried for 48 hr at 60$^o$ C. Truffles were identified to species using a combination of visual cues and microscopic spore patterns against published keys. Difficult identifications were sent to Dr. Jim Trappe at Oregon State University.

To investigate biomass, diversity, and stand conditions associated with truffles, we selected a 1-ha plot in mixed-conifer forest near Ross Crossing, at 1,500 m in elevation. All locations of truffles, trees, snags, logs, and shrubs were recorded using a surveyor's total station. For weather data, we relied on records from two long-established weather stations. One, at the USDA Forest Service's Trimmer Guard Station near Pine Flat Reservoir, was at the same elevation (300 m) as the oak woodland stands. The other was at Wishon Reservoir, about equidistant between the mixed-conifer and red fir sites, at an elevation of 2,400 m.

## Results

The highest truffle abundance was in the ponderosa pine stands, where the biomass in June 1996 was 4.4 kg/ha (*fig. 1*). Truffle biomass, at 2.2 kg/ha, also peaked in the mixed-conifer at this time. All stands in oak woodlands and red fir

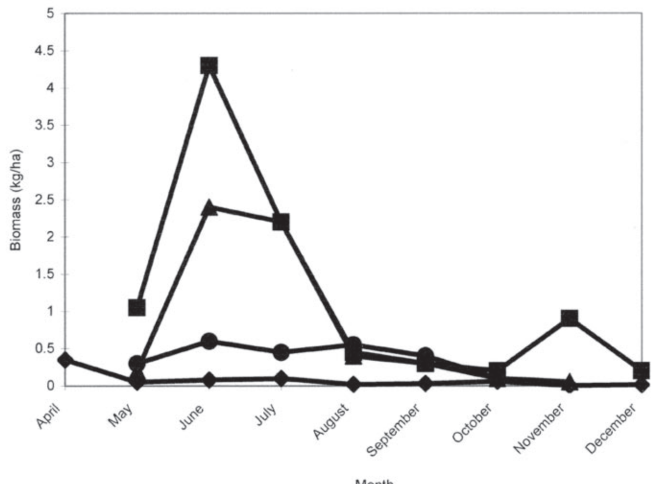


**Figure 1**—Truffle biomass by forest type and month (diamonds = oak woodlands, squares = ponderosa pine, triangles = mixed conifer, and circles = red fir).

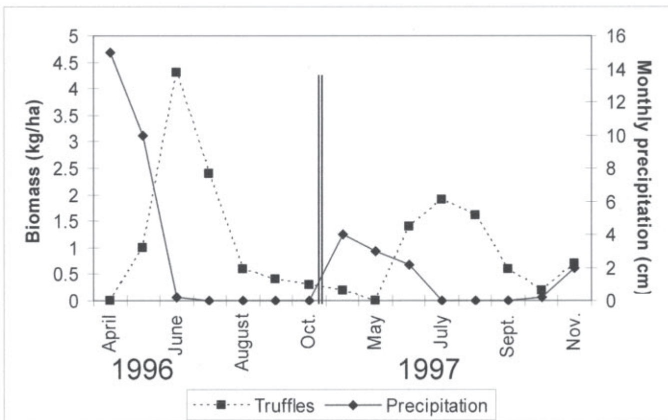


**Figure 2**—Truffle biomass and precipitation by month from April through October in 1996 and April through November in 1997.

**Table 1**—*Truffle species richness (number of species) and evenness in four forest types. Evenness values, using the Berger-Parker diversity index (Magurran 1988), indicate whether the truffle community is dominated by a single species (lower values) or if species are equitably distributed (higher values)*

| Forest type | Richness | Evenness |
|---|---|---|
| Oak woodlands | 14 | 1.63 |
| Ponderosa pine | 22 | 3.12 |
| Mixed-conifer | 9 | 4.35 |
| Red fir | 6 | 1.80 |

forest had consistently low truffle biomass. The highest values for all sites occurred in the spring and late fall. Fluctuations in truffle biomass correlated with the abundance of precipitation. With a lag of 1-2 months, the peaks in truffle biomass during the spring and fall were closely and positively correlated with total rainfall at the Trimmer weather station (*fig. 2*). Species richness was highest in ponderosa stands (*table 1*), but species evenness was greatest in mixed-conifer stands, indicating a community in which no single species dominated truffle abundance.

In the 1-ha plot, we located 869 truffles of 65-71 species, with a total dry biomass of 573 gm (*table 2*). Several individuals were immature, precluding a determination of whether they were new species or one already tallied. Nine new, undescribed species collected from the 1-ha plot now await final taxonomic classification at Oregon State University.

**Table 2**—*Number of individuals and biomass (gm) of truffles by species found in a 1-ha plot in mixed-conifer forest. The 65-71 species (some truffles were too immature to identify) include nine new, undescribed species*

| Sum of biomass | Number of individuals | Species |
|---|---|---|
| 0.01 | 1 | *Mycolevis siccigleb* |
| 0.04 | 1 | *Hymenogaster* sp (immature) |
| 0.06 | 1 | *Endogone flammicorona* |
| 0.07 | 1 | *Martellia brunnescens* |
| 0.16 | 9 | *Hymenogaster alnicola* |
| 0.16 | 3 | *Hymenogaster* sp. nov. #19914 |
| 0.21 | 8 | *Hymenogaster gilkeyae* |
| 0.25 | 3 | *Martellia* sp. (immature) |
| 0.25 | 1 | *Rhizopogon roseolus* |
| 0.26 | 8 | *Genea intermedia* |
| 0.27 | 2 | *Gymnomyces cinnamomeus* |
| 0.32 | 3 | *Gymnomyces* sp. (immature) |
| 0.36 | 1 | *Rhizopogon ellipsosporus* |
| 0.45 | 5 | *Endogone lactiflua* |
| 0.53 | 1 | *Hysterangium setchellii* |
| 0.57 | 1 | *Alpova trappei* |
| 0.57 | 4 | *Endogone* sp. nov. #19927 |
| 0.60 | 11 | *Rhizopogon evadens* A.H. Smith var. *evadens* |
| 0.66 | 1 | *Tuber gibbosum* |
| 0.76 | 3 | *Hysterangium* sp. nov. #19912 |
| 0.81 | 3 | *Martellia californica* |
| 0.83 | 1 | *Tuber shearii* Harkness |
| 0.91 | 2 | *Gymnomyces* sp. nov. #22596 |
| 0.91 | 1 | *Leucogaster microsporus* |
| 0.93 | 2 | *Trappea darkeri* |
| 1.00 | 1 | *Arcangiella crassa* |
| 1.03 | 5 | *Hysterangium coriaceum* |
| 1.05 | 6 | *Macowanites luteolus* Smith and Trappe |
| 1.19 | 7 | *Martellia fallax* |
| 1.27 | 7 | *Hysterangium separabile* |

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| **Sum of biomass** | **Number of individuals** | **Species**<br>*y g p* |
|---|---|---|
| 1.29 | 2 | *Martellia gilkeyae* |
| 1.41 | 1 | *Gautieria parksiana* |
| 1.47 | 30 | *Genabea cerebriformis* |
| 1.54 | 4 | Unknown (too immature) |
| 1.90 | 14 | *Tuber* sp. immature |
| 1.99 | 2 | *Gautieria crispa* |
| 2.39 | 4 | *Hymenogaster sublilacinus* |
| 2.39 | 7 | *Martellia foetens* |
| 2.63 | 3 | *Radiigera* sp. (immature) |
| 2.85 | 7 | *Tuber rufum var. nitidum* |
| 3.66 | 11 | *Gymnomyces* sp. nov. #19913 |
| 3.79 | 7 | *Rhizopogon vulgaris* |
| 3.98 | 2 | *Tuber californicum* |
| 4.19 | 2 | *Rhizopogon subcaerulescens* |
| 4.76 | 11 | *Melanogaster tuberiformis* |
| 5.02 | 13 | *Tuber murinum* |
| 5.20 | 20 | *Rhizopogon* sp. immature |
| 5.41 | 10 | *Balsamia magnata* Harkness |
| 5.60 | 7 | *Rhizopogon pedicellus* |
| 5.70 | 11 | *Martellia subochracea* |
| 6.64 | 28 | *Tuber monticola* |
| 6.85 | 59 | *Zelleromyces* sp. nov. #19929 |
| 9.56 | 6 | *Rhizopogon* sp. nov. w/pink stain |
| 9.57 | 4 | *Rhizopogon subgelatinosus* |
| 12.40 | 8 | *Rhizopogon variabilisporus* |
| 12.46 | 13 | *Hydnotryopsis setchellii* |
| 12.75 | 5 | *Balsamia nigrens* |
| 13.00 | 1 | *Rhizopogon* sp. nov. #19920 |
| 14.42 | 9 | *Gautieria gautierioides* |
| 17.64 | 27 | *Hydnotryopsis* sp. nov. #19890 |
| 18.16 | 51 | *Tuber rufum* var. *rufum* |
| 18.77 | 7 | *Gautieria graveolens* |
| 19.98 | 7 | *Geopora cooperi f. gilkeyae* |
| 20.13 | 19 | *Hydnotrya cerebriformis* |

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| Sum of biomass | Number of individuals | Species |
|---|---|---|
| 20.13 | 19 | *Hydnotrya cerebriformis* |
| 21.60 | 23 | *Rhizopogon brunnescens* |
| 22.63 | 10 | *Gautieria caudate* |
| 22.68 | 50 | *Leucophleps spinispora* |
| 24.57 | 100 | *Hydnoplicata* sp. nov. #19923 |
| 35.28 | 12 | *Gautieria monticola* |
| 35.28 | 57 | *Leucogaster rubescens* |
| 96.45 | 74 | *Radiigera taylori* |
| 573.58 | 869 | Total |

## Discussion

Forest types with the highest densities of truffle consumers also contain the greatest truffle abundance. Ponderosa pine and mixed-conifer forests are home to most Sierra forest mycophagists, including the northern flying squirrel. Low truffle abundance in oak woodlands may correspond to long dry seasons or a low density of tree hosts. In red fir forests, long, cold winters probably reduce the duration of available soil moisture and may depress truffle production.

The observed relation between truffle productivity, with peaks in late spring and fall, and precipitation patterns in the Sierra Nevada, is consistent with other studies of both epigeous (Richardson 1970) and hypogeous fruiting bodies (Hunt and Trappe 1987). It is reasonable to infer from these results that fungal fruiting is strongly conditioned on soil moisture, which is certainly influenced by a variety of stand factors, including canopy cover, litter depth, and root density. Truffle production should follow peak periods of nutrient and moisture uptake because mycorrhizal fungi require carbohydrates from their host plant to produce fruiting bodies.

The observed patterns of species diversity are consistent with theories of fungal community competition. In ponderosa pine stands, which may have the longest period of available soil moisture, a high number of species may occur in the soil, but truffle production is dominated by a few superior competitors. In mixed-conifer forests, fewer species occur but dominance is less pronounced.

The 1-ha plot was searched in June of 1997, after an exceptionally dry spring. Even under these conditions, 65-71 species were collected from the plot. Much of the Sierra Nevada has not yet been sampled for truffles, so probably many new species of truffles are as yet undescribed. Furthermore, because truffles are produced by only a fraction of the fungal species in the soil, even the 65 identified species in this sample comprise only a portion of the species present. As such, the data suggest that the soil fungal community may have even more species than the invertebrate community. We have yet to identify many of these species and to understand their role in "healthy" ecosystem functions.

The observation that truffles are most abundant in the ponderosa pine and mixed-conifer forests is reason for extra care in planning for forest management, as most stand altering projects occur in these forest types. Further research is needed to understand the effects of thinning, burning, soil scarification, and compaction on this important below-ground food source.

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