



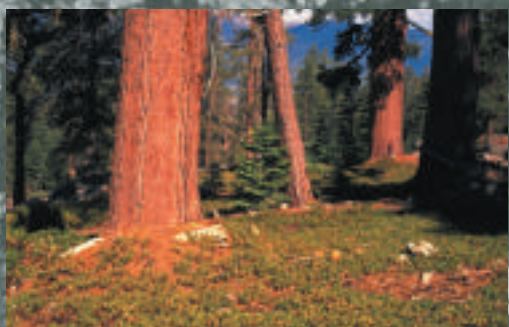
United States
Department
of Agriculture
Forest Service

**Pacific Southwest
Research Station**

General Technical Report
PSW-GTR-186



Vegetation and Ecological Characteristics of Mixed-Conifer and Red Fir Forests at The Teakettle Experimental Forest



Publisher

Albany, California
Mailing address:
PO Box 245, Berkeley CA
94701-0245

(510) 559-6300

Pacific Southwest Research Station

Forest Service
U.S. Department of Agriculture

Abstract

North, Malcolm; Oakley, Brian; Chen, Jiquan; Erickson, Heather; Gray, Andrew; Izzo, Antonio; Johnson, Dale; Ma, Siyan; Marra, Jim; Meyer, Marc; Purcell, Kathryn; Rambo, Tom; Rizzo, Dave; Roath, Brent; Schowalter, Tim. 2002. **Vegetation and Ecological Characteristics of Mixed-Conifer and Red Fir Forests at the Teakettle Experimental Forest**. Gen. Tech. Rep. PSW-GTR-186. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 52 p.

Detailed analysis of mixed-conifer and red fir forests were made from extensive, large vegetation sampling, systematically conducted throughout the Teakettle Experimental Forest. Mixed conifer is characterized by distinct patch conditions of closed-canopy tree clusters, persistent gaps and shrub thickets. This heterogeneous spatial structure provides contrasting microclimate, habitat and resource conditions probably associated with the high diversity of understory plants, fungi, and invertebrates found in ongoing studies in the Teakettle Experiment. In contrast, red fir forests are more homogeneous with continuous high canopy cover, cooler, more consistent microclimate conditions and fewer plant species. In both forests, annual fluctuations in available soil moisture resulting from El Niño influences on snow pack depth may have a significant influence on tree establishment and understory diversity. In depth descriptions of Teakettle's mixed conifer may provide a target of historic old-growth conditions for forest management.

The Authors

Malcolm North is a research plant ecologist with the Sierra Nevada Research Center, Pacific Southwest Research Station, USDA Forest Service, 2121 2nd St. Suite A-101, Davis, CA, 95616. He is the principal investigator for the Teakettle Experiment.

Brian Oakley is a post-doctoral researcher in the Department of Environmental Biology, University of Washington, Seattle, Washington 98195. He was the site manager at the Teakettle Experimental Forest from 1997-1999.

Jiquan Chen is an associate professor in Landscape Ecology and Ecosystem Science, Bowman-Oddy Laboratory, MS 604 at the University of Toledo, Toledo, OH 43606.

Heather Erickson is an assistant professor in the Departamento de Ciencias Y Tecnologia, PO Box 21150, Universidad Metropolitana, San Juan, Puerto Rico 00928.

Andrew Gray is a research ecologist with the Forest Inventory and Analysis Program, Pacific Northwest Research Station, USDA Forest Service, PO Box 3890, Portland, OR 97208.

Antonio Izzo is a doctoral candidate in the Department of Plant and Microbial Biology at the University of California, Berkeley, California, 94720.

Dale Johnson is a professor in Environmental and Resource Science, MS 370, 1664 North Virginia Street, University of Nevada, Reno, Nevada 89557.

Siyan Ma is a doctoral candidate in Landscape Ecology and Ecosystem Science, Bowman-Oddy Lab, MS 604 at the University of Toledo, Toledo, OH 43606.

Jim Marra is a postdoctoral researcher in the College of Forest Resources, Box 352100, University of Washington, Seattle, Washington, 98195.

Marc Meyer is a doctoral candidate in the Department of Wildlife, Fish, and Conservation Biology, One Shields Ave., University of California, Davis, California 95616.

Kathryn Purcell is a research wildlife biologist with the Forestry Sciences Laboratory, Pacific Southwest Research Station, USDA Forest Service, 2081 E. Sierra Ave, Fresno, California 93710.

Tom Rambo is a doctoral candidate in the Department of Environmental Horticulture, One Shields Ave., University of California, Davis, California, 95616.

Dave Rizzo is an associate professor in the Department of Plant Pathology, One Shields Ave., University of California, Davis, California, 95616.

Brent Roath is a forest soil scientist at the Sierra National Forest, 1600 Tollhouse Road, Clovis, California, 93611.

Tim Schowalter is a professor in the Department of Entomology, 404 Life Sciences Bldg., Louisiana State University, Baton Rouge, LA 70803.

In Brief

North, Malcolm; Oakley, Brian; Chen, Jiquan; Erickson, Heather; Gray, Andrew; Izzo, Antonio; Johnson, Dale; Ma, Siyan; Marra, Jim; Meyer, Marc; Purcell, Kathryn; Rambo, Tom; Rizzo, Dave; Roath, Brent; Schowalter, Tim. 2002. **Vegetation and Ecological Characteristics of Mixed-Conifer and Red Fir Forests at the Teakettle Experimental Forest.** Gen. Tech. Rep. PSW-GTR-186. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 52 p.

Retrieval Terms: ectomycorrhizae, fire history, flying squirrels (*Glaucomys sabrinus*), hydrology, hypogeous fungi, incense cedar (*Calocedrus decurrens*), invertebrates, Jeffrey pine (*Pinus jeffreyi*), old growth, pathogens, plant association, red fir (*Abies magnifica*), Sierra Nevada, soil nutrients, songbirds, sugar pine (*Pinus lambertiana*), truffles, vegetation classification, white fir (*Abies concolor*).

Mixed conifer and red fir are the dominant forest types in the Sierra Nevada and have been substantially impacted by logging and fire suppression. There are, however, only a few studies of the composition and structure of these important communities, and even fewer studies of the functional dynamics and species associated with these forests. We used a nested sampling design to quantify and describe vegetation conditions in mixed-conifer and red fir forests in the Teakettle Experimental Forest, a 1,300 ha reserve of old-growth, 80 km east of Fresno, California. We first established mapped plots on a regular grid throughout the entire forest to classify the forest types and plant associations. We then used this grid to characterize in greater detail the vegetation conditions and patch types of mixed conifer and red fir. This report also presents background environmental data and summarizes ongoing studies in Teakettle's mixed-conifer forest that describe soil nutrients, canopy and soil arthropods, breeding birds, snag dynamics, flying squirrels and truffles, lichens, pathogens and insects, ectomycorrhizae, tree regeneration, and soil moisture as a baseline for future research.

Teakettle has four main forest types. Mixed conifer comprises about 65 percent of the forest, predominantly between 1,900 and 2,300 m elevation. Jeffrey pine (5.5 percent) is prevalent on shallow soil conditions within the mixed-conifer type. Red fir (28 percent) dominates elevations above 2,300 m except for very moist locations where lodgepole pine (0.5 percent) is dominant. Within the mixed-conifer forest, we found a fine-scale mosaic of four patch types: closed canopy, shrub patches dominated by mountain whitethorn, open gaps, and areas of rock and extremely shallow soils. Each of these patches has a distinct set of growing conditions. In contrast, red fir forests are more homogenous with greater, more continuous canopy cover and higher tree basal area and density than mixed conifer.

The high spatial and temporal variability of environmental conditions in mixed conifer at Teakettle is an important influence on ecological pattern and process. Ongoing studies highlight a species-rich and diverse ecosystem structured by patch types that have high contrast microclimate and nutrient conditions. Canopy invertebrates and pathogenic insects are diverse and generally host-tree specific. Different soil substrates contain distinct species-rich communities of soil microarthropods. Organic horizons are discontinuous and, particularly in mountain whitethorn patches, are significantly enriched in available forms of soil nitrogen relative to surrounding areas. Truffles in riparian corridors are associated with high densities of flying squirrels in these areas, although overall flying squirrel densities are lower than those reported in the Pacific Northwest. Flying squirrels are also associated with high densities of large diameter snags that may also influence the large number of primary cavity-nesting birds. Epiphytic lichens are abundant and one species, *Bryoria fremontii*, provides an important winter food source for flying squirrels. Tree seedling success varies greatly by patch type and is strongly linked to soil moisture that rapidly declines after snowmelt, falling

below 10 percent on exposed sites by early July. The ectomycorrhizal community is also species-rich, with a high number of equally abundant taxa (>70), even during dry conditions.

In their old-growth seral stage, mixed-conifer forests have persistent gaps that are not colonized by regenerating conifers. Although tree clusters have high canopy cover and basal area, these groups are separated by large, persistent gaps and areas dominated by shrubs. Our research on the functional roles of mixed conifer suggests these distinct patches are dynamically linked. Management prescriptions that focus on tree aggregates or groups as the scale for thinning or fire application, scale their activity to a homogeneous unit that is but a subset of mixed-conifer conditions. It is this array of forest structure and composition that provides different microclimates, nutrient and moisture conditions, and host plant diversity that may be associated with mixed conifer's high invertebrate, fungal, and habitat diversity.

As an old-growth, mixed-conifer ecosystem, Teakettle may serve as a useful metric to gauge the effects of management practices in this forest type. Management activities that alter the scale and pattern of forest vegetation are likely to significantly influence ecosystem dynamics, particularly in these structurally diverse forests where microclimate and resource variability may be strongly associated with ecosystem productivity and diversity.

Acknowledgments

We are grateful to Neil Berg, Pacific Southwest Research Station, USDA Forest Service, Albany, California, and Joanna Clines, Sierra National Forest, Clovis, California, who reviewed the historical and botanical sections, respectively, of the manuscript. We are particularly indebted to Michael Barbour, Department of Environmental Horticulture, University of California, Davis, and John Battles, Department of Environmental Science, Policy and Management, University California, Berkeley, for providing insightful reviews of the whole manuscript. Many Sierra National Forest personnel assisted with the Teakettle project including John Exline, Rick Larson, Dave McCandliss, Toby Oesterich, Steve Parr, and Mark Smith. Special thanks are also due to the members of many hard-working field crews.

Vegetation and Ecological Characteristics of Mixed-Conifer and Red Fir Forests at The Teakettle Experimental Forest

Malcolm North Brian Oakley Jiquan Chen Heather Erickson Andrew Gray

Antonio Izzo Dale Johnson Siyan Ma Jim Marra Marc Meyer Kathryn Purcell

Tom Rambo Dave Rizzo Brent Roath Tim Schowalter

Contents

In Brief.....	iii
Acknowledgments	iv
Introduction.....	1
Location, Access and Accommodations.....	2
History.....	3
Historical Data	3
Hydrology	3
Fire.....	4
Logging.....	5
Environment and Climate.....	5
Soils	7
Vegetation Analysis	10
Methods	10
Results and Discussion	12
Initial Survey Results	12
Vegetation Classification	18
Comparisons and Distributions of Forest Types.....	21
Comparisons with Existing Classifications of Mixed-Conifer and Red Fir Forests.....	23
Intensive Measurements of Mixed-Conifer and Red Fir Forests	24
Mixed-Conifer Patch Conditions.....	26
Ecological Components of Mixed Conifer.....	26
Canopy Arthropods	26
Soil and Coarse Woody Debris Microarthropods	28
Breeding Bird Richness and Density.....	31
Snag Survey.....	33
Northern Flying Squirrels and Truffles	33
Lichens	34

**Pacific Southwest
Research Station**

USDA Forest Service
General Technical Report
PSW-GTR-186

September 2002

Pathogens and Insects at Teakettle.....35

Mycorrhizae37

Tree Seedlings and Soil Moisture38

Summary38

References.....41

Appendix A: The Teakettle Experiment45

Design45

Treatments46

Appendix B: Plant List.....47

Introduction

About 42 percent or 170,000 km² of California is forest and woodland, 56,000 km² of which occurs in the Sierra Nevada (Davis and Stoms 1996). Along the Sierra's western slope, four main forest types occur along an elevation gradient: ponderosa pine (1,100-1,600 m), white fir-mixed conifer (1,500-2,300 m), red fir (2,100-2,900 m) and lodgepole pine (2,600-3,800 m) (Barbour 1988, Kuchler 1964, Raven and Axelrod 1978, Rundel and others 1977). Since European arrival, productive and accessible forests such as mixed conifer and ponderosa pine have been the focal areas for timber harvesting and fire suppression efforts. The alteration in the mean fire return interval from historical to current conditions has been estimated as a change from 15 to 644 years (McKelvey and Busse 1996). The ecosystem dynamics of most Sierra forest communities, with the possible exception of giant sequoia (*Sequoiadendron giganteum*) forests, is still poorly understood. Given the importance of Sierra forests for water production, biodiversity and recreation, a better understanding of the impacts of management activities on ecosystem structure and function is sorely needed.

In 1996 the Sierra Nevada Ecosystem Project (SNEP) published an assessment of current conditions and a suggestion of research priorities to address several critical concerns for the future of the Sierra Nevada ecosystem. One of these findings focused on the role of fire and mechanical thinning in forest restoration. Thinning has been proposed as a means of reducing fuel loads before an area is prescribe-burned, or as a surrogate for restoring a forest's structure and composition to historic conditions when prescribed fire cannot be used because of the presence of houses, air quality restrictions, etc. Although thinning may produce a stand structure and composition that copies the results of burning, it may have significantly different effects on many ecosystem processes. According to SNEP (1996, p. 4-5):

Although silvicultural treatments can mimic the effects of fire on structural patterns of woody vegetation, virtually no data exist on the ability to mimic ecological functions of natural fire. Silvicultural treatments can create patterns of woody vegetation that appear similar to those that fire would create, but the consequence for nutrient cycling, hydrology, seed scarification, nonwoody vegetation response, plant diversity, disease and insect infestation, and genetic diversity are mostly unknown.

To compare the effects of different levels of thinning and burning on mixed-conifer ecosystems, an experiment was initiated in 1998 at the Teakettle Experimental Forest (Appendix A). As a precursor to this experiment, extensive analysis of vegetation conditions at Teakettle was made to map and identify different forest communities and intensively analyze mixed-conifer conditions to appropriately size and locate permanent plots for thinning and burning treatments.

Although Teakettle has been briefly described in previous reports (Berg 1990, Keeler-Wolf 1990), we provide additional historical information, a comprehensive vegetation map based on systematic sampling, quantitative analysis of the mixed-conifer and red fir portions of the forest, and data from ongoing research in Teakettle's mixed-conifer areas. This intensive analysis of forest vegetation at Teakettle was needed to establish plots with replicated structure and composition, and to understand the appropriate scale and pattern for designing field sampling (North and Oakley 2003). We also studied the structure, composition and patch pattern of the trees, shrubs and herbs of these two forest types from intensive mapping and field sampling. The mixed-conifer forest type in particular demands spatially-explicit, intensive measurements to understand its inherent heterogeneity. Confusion about the pattern of structural organization in mixed conifer has generated uncertainty about how to scale management activities, inventory the amount and distribution of remaining old growth, and evaluate restoration efforts (USDA 2001). Mixed-conifer forests are complex, with a high tree and shrub diversity for a western coniferous forest, and a structure that is both horizontally (ranging

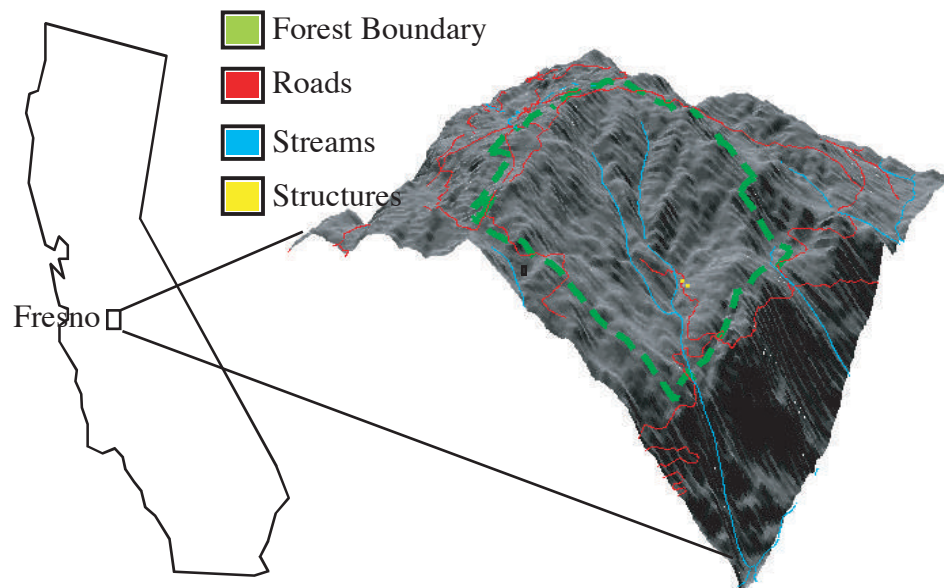
from large open gaps to dense tree clusters) and vertically (multiple vegetation layers) intricate. Mixed conifer is also primary habitat for more vertebrate species than any other Sierra forest type (California Department of Fish and Game 1994). New information has been gathered by researchers in the Teakettle Experiment detailing soils, pathogens and various species associated with the mixed-conifer forest type. Many of these ecological attributes are directly influenced by patterns in forest composition and structure that we quantitatively describe.

The purpose of this paper is to provide quantitative information on vegetation characteristics of mixed-conifer and red fir forests in the southern Sierra Nevada; present a detailed summary of the vegetation and environment of the Teakettle Experimental Forest that will provide baseline information to researchers involved in long-term experiments; and provide information on species and ecological characteristics common to mixed-conifer forests.

Location, Access and Accommodations

The Teakettle Experimental Forest is located on the Kings River Ranger District of the Sierra National Forest, approximately 80 km east of Fresno above the north fork of the Kings river in T 11 S, R 27 E. The center of the forest is at 36° 58' N latitude and 119° 2' W longitude on the Patterson Mountain U.S. Geological Survey 7.5' topographic map. Teakettle encompasses ca. 1,300 ha and ranges in elevation from 1,880 m at the southeast corner to 2,485 m at the top of Patterson Mountain along the western boundary (fig. 1). It consists primarily of old-growth, mixed-conifer and red fir forests typical of mid-elevations on the western slopes of the southern Sierra Nevada range. These two forest types cover 17 percent of the state. The major tree species in mixed-conifer forests include white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), and black oak (*Quercus kelloggii*), and in the northern Sierra include Douglas-fir (*Pseudotsuga menziesii*) (Barbour 1988, Rundel and others 1977). Giant sequoia can intermix with mixed conifer, but it is limited to 68 groves in the southern Sierra and is not present at Teakettle. Red fir (*A. magnifica*) normally dominates forests above mixed conifer, but white fir, Jeffrey pine, western white pine (*Pinus monticola*), and lodgepole pine (*Pinus contorta*) may also be present (Barbour and Woodward 1985).

Figure 1—Location and topography of the Teakettle Experimental Forest east of Fresno as displayed from a U.S. Geological Survey 30m resolution digital elevation model. Teakettle creek drains the main elevational gradient from the NW corner at 2,485m to the SE corner at 1,880m. The two structures in the figure are the main cabin for housing researchers and an equipment storage shed.



Roads to Teakettle are generally snow-free, accessible from May to November and do not require four-wheel drive. Research facilities include a cabin with full amenities that sleeps four, seasonal lodging to accommodate additional researchers, and one emergency shelter. A garage is used for equipment storage and as a workshop. The main entrance to Teakettle is gated and locked, and a second road provides access to the top of Patterson Mountain.

History

In the 1930s State and Federal agencies began exploring how the Central Valley's water supply might be increased through management of Sierra Nevada watersheds. Beginning in 1936, three potential experimental watersheds were the subjects of intensive geology and soil studies: Onion Creek (Tahoe National Forest), and Big Creek and Teakettle Creek (Sierra National Forest). In 1938 a 1,300 ha area surrounding Teakettle creek was designated the Teakettle Experimental Area and five drainages were chosen for study. Stream-gauging stations and sediment basins were built and research begun. The Civilian Conservation Corps built the original cabin and storage shed in 1938. Research continued at Teakettle until 1942 when work was halted during World War II. Starting in 1957, studies were reactivated and regular records of snowfall and water yields were collected again. The area was officially designated "The Teakettle Creek Experimental Forest" on December 16, 1958 and Teakettle's mineral rights were withdrawn on December 13, 1963.

The objective of the experimental forest was to develop timber harvest patterns that would increase water yield. However, studies completed in the 1950s and 1960s at Yuba Pass and Sagehen Creek suggested moderate forest cover removal had little effect on water yield in the Sierra Nevada. In the 1960s the focus of Teakettle research switched to waterflow measurements in relation to weather patterns. This study was continued into the 1980s until budget constraints and the logistics of maintaining a remote site stopped the study.

In the 1980s and early 1990s studies of songbirds and snag dynamics were begun. In 1998 the Teakettle Experiment (appendix A) was started and is planned to continue for several years into the new century.

Historical Data

Hydrology

Five stream gauging stations at Teakettle provided stream flow data from 1957 to 1983. For the main catchment on Teakettle Creek, we summarized data by month, and peak flows for each month were identified by year. Two patterns are evident from the data: a strong seasonal phenomenon of peak spring flows from snowmelt, and large interannual variability with peak flows associated with El Niño years (*fig. 2*).

Intense winter storms can dramatically increase stream flows in the Sierra. At Teakettle's elevation, rain can occur even in winter, and snow can quickly melt after a storm's colder temperatures. Rapid increases in stream flow may occur after large storms. These pulses, however, are not as large as the peak flow rates caused by snowmelt in May, June, and July. A 1963 letter requesting repair funds indicates the main catchment pond on Teakettle overflowed with debris after a January 29, 1963 storm, which dropped 58 cm of rain in less than 24 hours. This intense storm, however, produced a peak February flow of 4 cfs, less than one-fourth the June flow rate in the El Niño year of 1983.

Figure 2—Mean, minimum, and maximum monthly streamflows from a gauging station on Teakettle Creek for data collected from 1957 to 1983. Numbers next to maxima indicate the year in which maximum flow for that month occurred. Bold numbers represent El Niño years.

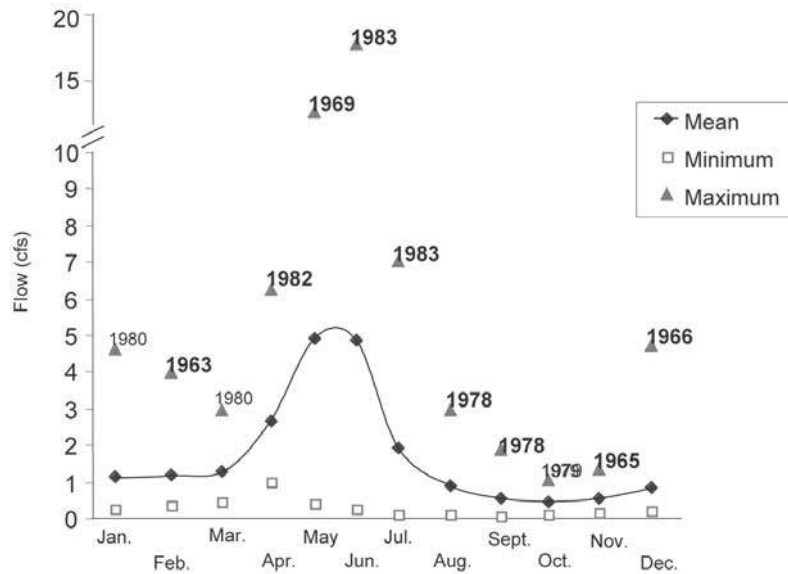


Table 1—Location of lightning strike fires at the Teakettle Experimental Forest between 1972 and 1999. Data are from the Sierra National Forest fire incident database.

Fire Number	Date	Area (ha)	Slope (percent)	Elevation (m)
02	August 27, 1972	0.16	35	2,170
04	October 4, 1972	0.04	35	2,360
10	August 10, 1978	0.81	75	2,060
11	August 10, 1978	0.04	25	2,060
16	September 9, 1980	0.04	15	2,255
27	July 17, 1984	0.04	25	2,060
30	May 15, 1987	0.04	35	1,950
31	June 19, 1987	0.08	25	2,235
33	July 17, 1987	0.20	35	2,380
36	August 8, 1989	0.08	25	2,235
37	August 15, 1990	0.04	15	2,100
41	May 31, 1994	0.04	25	1,865
48	August 31, 1998	0.08	30	2,090
49	August 31, 1998	0.08	25	2,410
52	September 23, 1999	0.00	00	2,255

Fire

Historical documentation of fires in Teakettle is limited. A survey of fire scars on stumps in an adjacent watershed indicated the average fire return interval for mixed-conifer forest in this area was 12 to 15 years (Drumm 1996). Sierra National Forest records from 1972 to 1999 list 13 lightning strikes within Teakettle's 1,300 ha for an annual average of 0.36 strikes/1,000 ha (table 1). All Teakettle fires recorded in this period originated from lightning, with a median ignition date of August 10. Before 1972 there are only two archive reports of large fires, each of which burned partly within Teakettle (fig. 3). A fire history study using scars on mapped logs, snags, and cut stumps has been completed for a 150 ha area of mixed conifer (Fiegenger 2002). Mean fire return interval for recording trees (i.e., those that have been scarred before) is 17 years. Although aggressive fire suppression in the Teakettle area did not occur till the 1930s when an access road was completed, the fire



Figure 3—Topographic map showing the location of lightning strikes within and adjacent to the Teakettle Experimental Forest. Each lightning strike is indicated by a number and described in more detail in *table 1*. The shaded areas are the approximate boundaries of a 1911 (blue) and 1943 (grey) wildfire.

scar record indicates an abrupt change in the fire regime in the 1880s. We do not know the exact reason for this pattern. Other studies have suggested a change in climate, a reduction in ground fuels from a widespread increase in grazing, or a reduction of Native-American initiated ignitions.

Logging

As a designated experimental area, logging within Teakettle has been very limited. Before 2000, commercial logging had only occurred along the periphery in connection with timber sales in adjacent areas. A few hazard trees associated with the construction of the weirs were removed in the 1930s, and several stumps are found in the mixed-conifer area, which may have been an effort to remove blister-rust infected sugar pine. In the summer of 2000 and 2001, six 4 ha plots were thinned each year for the Teakettle Experiment treatments (*appendix A*).

Environment and Climate

Teakettle's climatic conditions are typical of the west side of the Sierra Nevada range: hot, dry summers and mild, moist winters. Most of the annual precipitation falls as snow between November and May, and accumulations of snow generally persist until late May or early June. Mean annual precipitation from 1958 to 1969 and 1977 to 1983 was 125 cm/yr (Kattelmann 1989). The Wishon Dam meteorological station (<http://cdec.water.ca.gov/cgi-progs/queryF?WSD>), located 5 km NE of Teakettle at 2,000 m elevation, has recorded temperature and precipitation data since 1996. The record shows a strong seasonal difference in temperature and moisture that follows a Mediterranean pattern (*fig. 4*).

The nearest snow survey station with a long-term record is Cliff Camp (4 km NE of Teakettle and at a similar elevation of 1,920 m), with monthly snow depth



Figure 3—Topographic map showing the location of lightning strikes within and adjacent to the Teakettle Experimental Forest. Each lightning strike is indicated by a number and described in more detail in *table 1*. The shaded areas are the approximate boundaries of a 1911 (blue) and 1943 (grey) wildfire.

scar record indicates an abrupt change in the fire regime in the 1880s. We do not know the exact reason for this pattern. Other studies have suggested a change in climate, a reduction in ground fuels from a widespread increase in grazing, or a reduction of Native-American initiated ignitions.

Logging

As a designated experimental area, logging within Teakettle has been very limited. Before 2000, commercial logging had only occurred along the periphery in connection with timber sales in adjacent areas. A few hazard trees associated with the construction of the weirs were removed in the 1930s, and several stumps are found in the mixed-conifer area, which may have been an effort to remove blister-rust infected sugar pine. In the summer of 2000 and 2001, six 4 ha plots were thinned each year for the Teakettle Experiment treatments (*appendix A*).

Environment and Climate

Teakettle's climatic conditions are typical of the west side of the Sierra Nevada range: hot, dry summers and mild, moist winters. Most of the annual precipitation falls as snow between November and May, and accumulations of snow generally persist until late May or early June. Mean annual precipitation from 1958 to 1969 and 1977 to 1983 was 125 cm/yr (Kattelmann 1989). The Wishon Dam meteorological station (<http://cdec.water.ca.gov/cgi-progs/queryF?WSD>), located 5 km NE of Teakettle at 2,000 m elevation, has recorded temperature and precipitation data since 1996. The record shows a strong seasonal difference in temperature and moisture that follows a Mediterranean pattern (*fig. 4*).

The nearest snow survey station with a long-term record is Cliff Camp (4 km NE of Teakettle and at a similar elevation of 1,920 m), with monthly snow depth

Figure 4—Average monthly temperature and precipitation patterns from June 1996 through June 2000 at the Pacific Gas & Electric Wishon Dam site located at 2,000 m elevation 1.2 km NE of Teakettle.

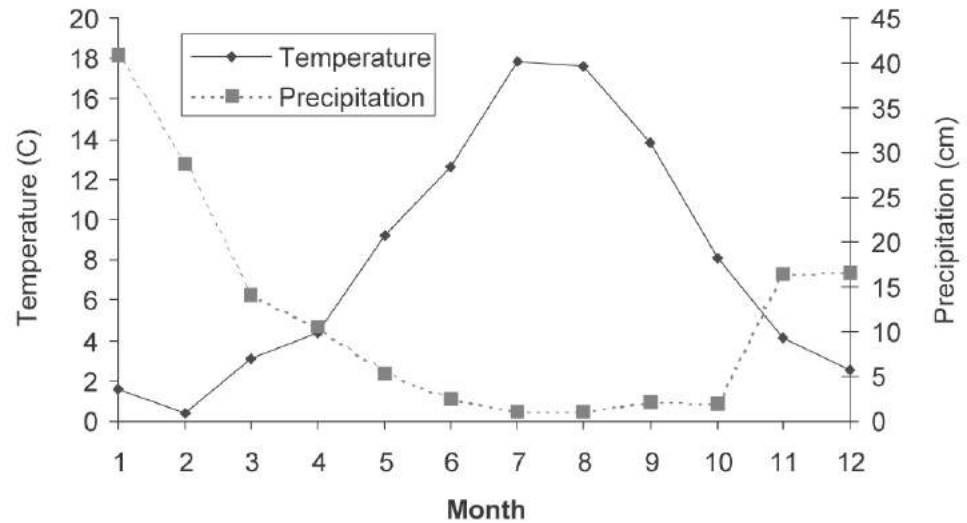
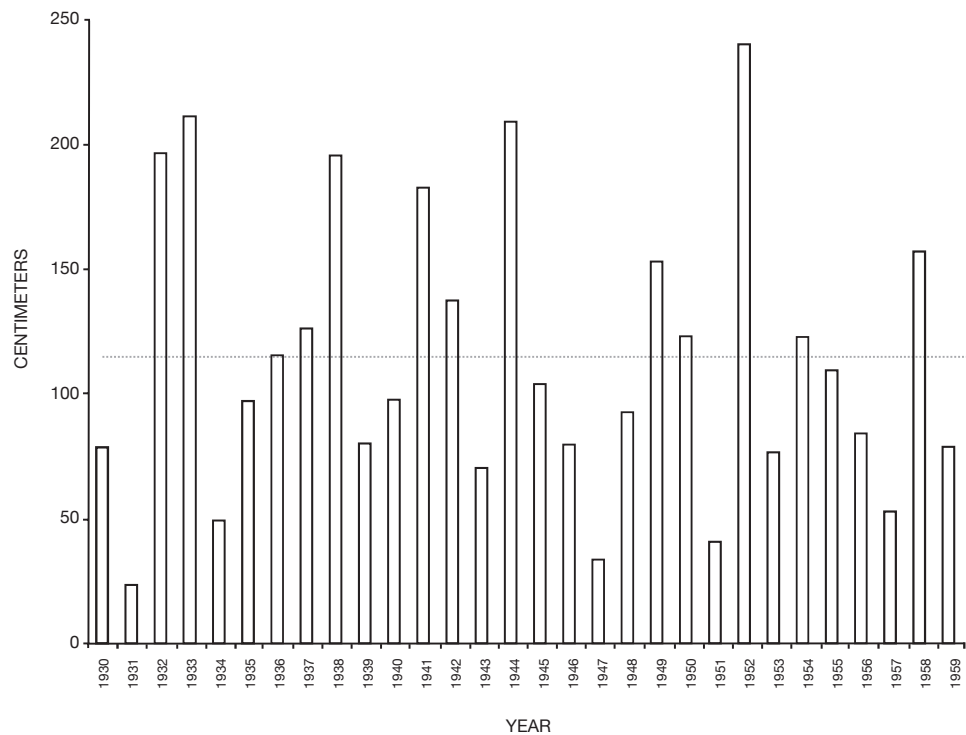


Figure 5—Thirty-year record of the maximum recorded snow depth at Cliff Camp station, 3 km NE of Teakettle. Dotted line indicates the mean maximum depth of 114 cm.



measurements from 1930 to 1960. The mean maximum depth for the 30-year record was 114 cm, but the snow pack was highly variable with a range of 24 to 241 cm (fig. 5). Greatest snow depth by month was equally split between February, March, and April.

Beginning in 1998, 18 micro-meteorological stations were established within a mixed-conifer portion of Teakettle. Each of these stations records precipitation, air temperature, soil moisture, and temperature at the surface and 15 cm below the surface; wind speed and direction; and solar radiation throughout the year. Using these data, Ma and others (2002a) found higher spatial variability in surface temperatures than has been reported in other studied forests. Differences in soil surface temperatures are strongly influenced by vegetation patch and high summer temperature even at 2,000 m in elevation. In open-canopy areas, July surface temperatures can reach almost 60°C, while 10 m away in closed-canopy forest, the temperature is 28°C.

In an analysis of air (T_a), soil surface (T_{sf}), and soil (at 15 cm deep) (T_{s15}) temperatures, the most variable were T_a during the spring (table 2). Spring and fall

Table 2—Mean and range (difference between the mean maximum and minimum) air (T_a), surface (T_{sf}), and soil (T_{s15}) temperatures by season. Values ($^{\circ}\text{C}$) are calculated from 23,000-54,000 records collected with continuous datalogger measurements.

Temperature	Spring		Summer		Fall		Winter	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
T_a	6.8	20.5	15.5	7.9	8.8	18.1	0.7	11.4
T_{sf}	7.5	15.1	17.1	4.5	9.4	14.7	1.2	2.9
T_{s15}	6.8	13.2	15.9	3.1	9.7	12.6	1.8	3.0

seasons have the greatest diurnal range in temperatures, as summer and winter have smaller fluctuations. In general air temperatures are the most variable followed by soil surface and soil temperatures. T_a , T_{sf} , and T_{s15} reached their maximum at different times of day in the different seasons. During the spring and winter period, T_a reached its maximum around 1300 hours, but the lowest T_a during a diurnal cycle appeared around 700 hours in the winter and 500 hours in the spring. A similar pattern occurred in the summer and the fall with the minimum T_a occurring at 500 hours, and the maximum T_a at 1400 hours. The highest T_{sf} appeared at the same time in the summer and fall as T_a did, but it was about 2 hours later than maximum T_a in the spring and 3 hours in the winter. The lowest T_{sf} was observed at 600 hours in the spring and summer, 700 hours in the fall and at 800 hours in the winter. Overall, maximum and minimum T_{s15} lagged 0-3 hours behind that of T_{sf} in all seasons. Mean soil surface and soil temperatures do not drop below freezing in the winter (table 2).

Soils

Most soils in the southern Sierra Nevada developed from granitic parent materials. Within Teakettle, some areas of metasedimentary and volcanic substrates occur, but the majority of the experimental forest consists of granite-based soils (fig. 6). The most common granitic soils, the Cannell and Cagwin series (Inceptisols and Entisols, respectively), have a coarse sandy loam texture throughout the profile, are highly permeable, and have a relatively low water holding capacity (table 3). These poorly developed soils also have very low clay content, usually less than 5 percent. Soil development is usually limited to the formation of a dark A horizon or a weak B horizon, based upon color change.

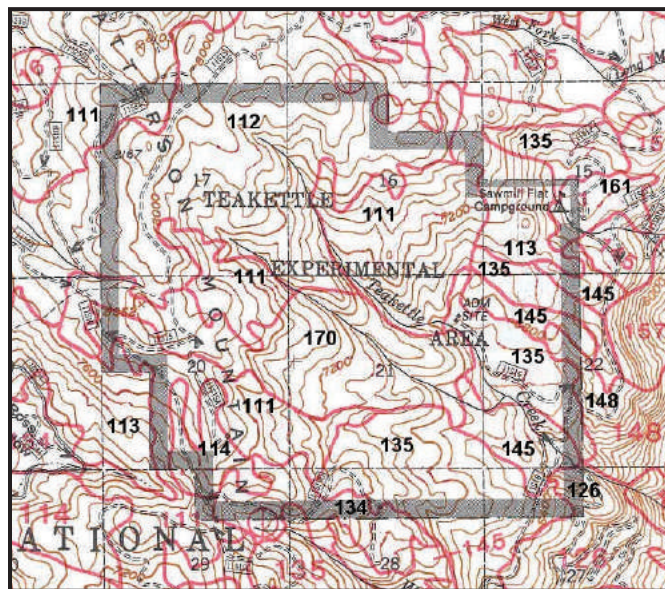


Figure 6—Map of soil types within Teakettle. Numbers represent different soil types that are described in table 3.

Table 3—Classification and characteristics of soil types within the Teakettle Experimental Forest in descending order of area covered (USDA Forest Service and Soil Conservation Service 1993). Each map zone is likely to contain smaller areas dominated by other soil types.

Soil Map Units	Major Soil Series	Classification	Characteristics	Comments
111 113 114	Cagwin	Mixed, frigid, Dystric Xero-psamments	A horizon: 0-18 cm; brown gravelly loamy coarse sand; weak granular structure; pH 5.4 C horizon: 18-80 cm	Occurs near areas of shallow soil and on steeper slopes. Types 113 and 114 have rock outcrops and tend to be on 15-45 percent and 45-65 percent slopes, respectively.
112	Cannell	Coarse-loamy, mixed, frigid, Dystric Xerochrepts	A horizon: 0-18 cm; grayish brown gravelly coarse sandy loam; weak granular structure; pH 6.0 B horizon: 18-80 cm; very pale brown gravelly coarse sandy loam; weak granular structure; pH 6.0 C horizon: 80-130 cm; very pale brown gravelly loamy coarse sand; weak granular structure; pH 6.0	In Teakettle Cannell is more common than Cagwin in soil map unit 112. Similar to Cagwin but total depth is ≥ 90 cm. Also found in soil type 111 on slopes < 30 percent.
134 135	Gerle	Coarse-loamy, mixed, frigid Typic Xerumbrepts	A horizon: 0-36 cm; brown gravelly coarse sandy loam, weak granular structure; pH 5.8 B horizon: 36-66 cm; light yellowish brown cobbly coarse sandy loam; weak subangular blocky structure; pH 5.5 C horizon: 66-97 cm; pale brown cobbly loamy coarse sand; massive; loose; pH 5.2	Has a moist, thick A horizon, often found near streams. Type 134 occurs on 5-35 percent slopes and type 135 on 35-55 percent slopes.
145 148	Lithic Xero-	Lithic Xero-psamments	0-28 cm; brown gravelly loamy coarse sand, single grain; loose; pH 5.6	Soil type 145 has a thin layer over unweathered granodiorite. Soil type 148 is exposed granitic outcrops.

Soil depth is important for water storage and potential vegetation. Soils with higher water holding capacity or longer retention times may have a significant influence on microsite differences in plant species composition and biomass. Where Jeffrey pine, black oak, live oak or manzanita occurs, soil depth is usually less than 50 cm (*fig. 7a*). On sites where soils are more than 1 meter deep, closed canopy forest and ceanothus often dominate the vegetation.

Bulk density, organic matter content, and soil cover were measured along randomly located transects in the Cagwin and Cagwin-Cannell soil series. Bulk density, determined from samples taken at a 20-25 cm depth, was 1.09 g/cm³. Based on loss on ignition (LOI) methods, organic matter content of the 0-10 cm soil depth was 6.35 percent by weight. The amount of fine organic matter is patchily distributed and is an important influence on water and nutrient holding capacity in these coarse soils. Many canopy gaps have little or no accumulation of litter on the soil surface.

Three different patch conditions in the Cagwin series—closed canopy (>75 percent canopy cover), mountain whitethorn (*Ceanothus cordulatus*) patches, and open canopy (<25 percent canopy cover)—were compared by measuring pH, bulk density and moisture in the O horizon and mineral soil. Soil moisture in the organic horizon was highest in closed-canopy patches. Mineral soil bulk density was highest in open-canopy patches (*table 4*). Soil pH of the organic horizon in mountain whitethorn and open-canopy patches was also significantly lower than in closed-canopy patches (*table 4*).

**7a**

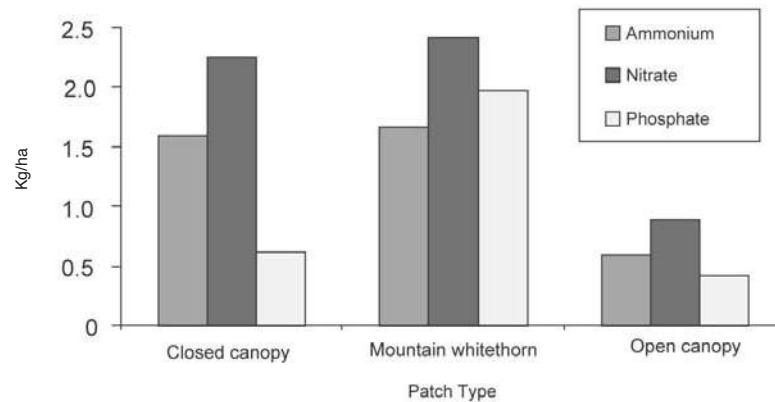
Figure 7a and b—Patchy nature of forest understory at Teakettle: a) Note areas of shallow soils and rock outcrops in background, and b) closed canopy forest and ceanothus on relatively deep soils. The two locations are within 30 m of each other.

**7b**

Table 4—Soil characteristics of organic (O) and mineral soil horizons in three patch types: closed canopy, mountain whitethorn patches, and open canopy. Values represent means and 1 standard error in parentheses. Bulk density (Db) was measured at 0-7 cm and 8-14 cm depths in the mineral soil. Soil moisture was measured with the gravimetric method on soils collected in June 1999. Within a horizon, different superscripts in a column indicate significant differences by patch type (ANOVA, $P < 0.05$).

Patch Type	Depth (cm)	Mass (g/m ²)	Db (g/cm ³)	pH	Moisture (percent)	Db 0-7 cm (g/cm ³)	Db 8-15 cm (g/cm ³)
O Horizon							
Closed canopy	5.60 ^a	6830 ^a	0.124 ^a	5.36 ^a (0.09)	43.00 ^a (4.60)	—	—
Mountain whitethorn	3.20 ^b	3140 ^b	0.122 ^a	5.21 ^{ab} (0.08)	15.00 ^b (2.60)	—	—
Open canopy	0.90 ^c	1130 ^c	0.098 ^b	4.98 ^b (0.15)	7.00 ^c (0.80)	—	—
Mineral Horizon (0-15 cm)							
Closed canopy	—	—	—	5.79 (0.05)	7.70 ^{ab} (0.40)	0.90 ^a	0.99 ^a
Mountain whitethorn	—	—	—	5.75 (0.06)	8.20 ^b (0.45)	0.85 ^a	0.97 ^a
Open canopy	—	—	—	5.62 (0.06)	6.00 ^a (0.61)	1.10 ^b	1.13 ^b

Figure 8—Inorganic nitrogen and phosphorus fluxes measured by resin lysimeters in mineral soil. For the two types of nitrogen, open canopy values are significantly less ($P < 0.05$) than closed canopy or mountain whitethorn values. For phosphorus only the mountain whitethorn and open canopy values are significantly different.



Nitrogen (N) and phosphorus (P) fluxes (from atmospheric input, canopy throughfall, and in the soil) have been measured for 1 year at Teakettle using resin lysimeters. Lysimeter locations were stratified by the same three patch conditions used for soil sampling—closed canopy, mountain whitethorn patches, and open canopy. Open-canopy areas have lower N and P inputs than mountain whitethorn or closed-canopy areas (fig. 8). It is not clear to what extent these fluxes are affected by anthropogenic input from Central Valley air pollution; however, the values are low, as is typical of relatively unpolluted ecosystems.

In temperate forests nitrogen is generally a limiting resource for plant growth. At Teakettle a large amount of nitrogen exists in the litter layers,¹ but slow litter decomposition probably keeps nitrogen supply rates low. Mountain whitethorn may play an important role in the N economy of Sierra Nevada forests. It has high N concentrations in its foliage and soil beneath the plant due to its symbiosis with the N-fixing bacteria *Frankia* (Oakley and others [In press]). Rates of net N mineralization are high in mountain whitethorn patches compared to gap or closed canopy patches, suggesting that mountain whitethorn may enhance nitrogen availability at Teakettle.

A previous study of soil CO₂ efflux was partially conducted at Teakettle by Wang and others (1999). CO₂ efflux had a strong negative correlation with soil temperature and a positive correlation with soil moisture. Current soil respiration studies (Ma and others 2002b) indicate CO₂ efflux rates vary by vegetation patch type and may be influenced by temperature only when water is not limited.

Vegetation Analysis

Methods

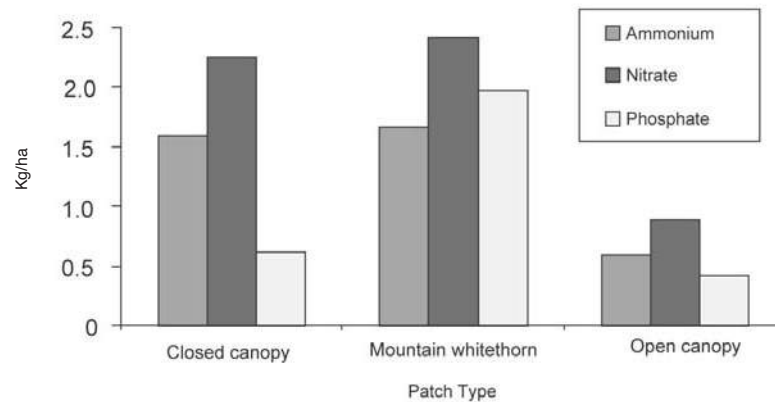
Initial Vegetation Sampling

Our first goal was to census the entire Experimental Forest to identify and locate different plant associations. We devised a systematic sampling scheme using a Cartesian grid across Teakettle and established a total of 1,264 vegetation sample plots located at 100 m intervals (fig. 9). Plot center points were located using a Criterion 400 survey laser and at each point a 1/20 ha circular plot (12.6 m radius) was established.

From the center of each plot, metric factor 4 prisms were used to estimate the tree basal area by species. Factor 4 prisms were used to ensure that plots were independent (i.e., a large diameter tree [dbh = 200 cm] equidistant between plot centers would not be double counted). Canopy cover estimates were derived from the average readings of a moosehorn device (Garrison 1949) used at five locations within each plot (four measurements at the edge of the plot along each

¹Unpublished data, H. Erickson, Universidad Metropolitana, San Juan, Puerto Rico.

Figure 8—Inorganic nitrogen and phosphorus fluxes measured by resin lysimeters in mineral soil. For the two types of nitrogen, open canopy values are significantly less ($P < 0.05$) than closed canopy or mountain whitethorn values. For phosphorus only the mountain whitethorn and open canopy values are significantly different.



Nitrogen (N) and phosphorus (P) fluxes (from atmospheric input, canopy throughfall, and in the soil) have been measured for 1 year at Teakettle using resin lysimeters. Lysimeter locations were stratified by the same three patch conditions used for soil sampling—closed canopy, mountain whitethorn patches, and open canopy. Open-canopy areas have lower N and P inputs than mountain whitethorn or closed-canopy areas (fig. 8). It is not clear to what extent these fluxes are affected by anthropogenic input from Central Valley air pollution; however, the values are low, as is typical of relatively unpolluted ecosystems.

In temperate forests nitrogen is generally a limiting resource for plant growth. At Teakettle a large amount of nitrogen exists in the litter layers,¹ but slow litter decomposition probably keeps nitrogen supply rates low. Mountain whitethorn may play an important role in the N economy of Sierra Nevada forests. It has high N concentrations in its foliage and soil beneath the plant due to its symbiosis with the N-fixing bacteria *Frankia* (Oakley and others [In press]). Rates of net N mineralization are high in mountain whitethorn patches compared to gap or closed canopy patches, suggesting that mountain whitethorn may enhance nitrogen availability at Teakettle.

A previous study of soil CO₂ efflux was partially conducted at Teakettle by Wang and others (1999). CO₂ efflux had a strong negative correlation with soil temperature and a positive correlation with soil moisture. Current soil respiration studies (Ma and others 2002b) indicate CO₂ efflux rates vary by vegetation patch type and may be influenced by temperature only when water is not limited.

Vegetation Analysis

Methods

Initial Vegetation Sampling

Our first goal was to census the entire Experimental Forest to identify and locate different plant associations. We devised a systematic sampling scheme using a Cartesian grid across Teakettle and established a total of 1,264 vegetation sample plots located at 100 m intervals (fig. 9). Plot center points were located using a Criterion 400 survey laser and at each point a 1/20 ha circular plot (12.6 m radius) was established.

From the center of each plot, metric factor 4 prisms were used to estimate the tree basal area by species. Factor 4 prisms were used to ensure that plots were independent (i.e., a large diameter tree [dbh = 200 cm] equidistant between plot centers would not be double counted). Canopy cover estimates were derived from the average readings of a moosehorn device (Garrison 1949) used at five locations within each plot (four measurements at the edge of the plot along each

¹Unpublished data, H. Erickson, Universidad Metropolitana, San Juan, Puerto Rico.

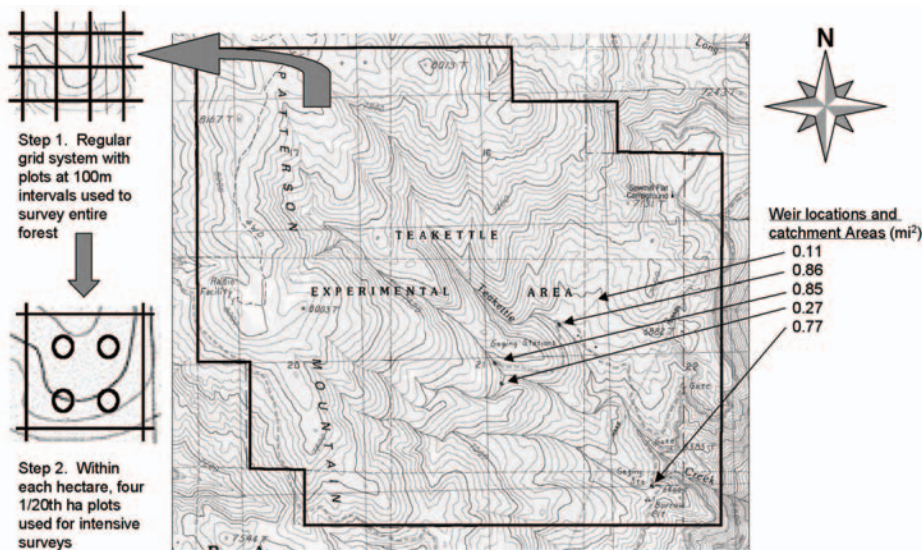


Figure 9—Nested sampling scheme used to sample vegetation in this study. In the first summer of fieldwork, a regular 100 m grid was established and used to survey all 1,300 ha of the forest. Subsequently, this grid system was used to intensively survey 167 ha within the two most dominant forest types: mixed-conifer and red fir. At all plots, measurements were taken of the tree, shrub, and herb layers. Locations of stream gauging stations and catchment basin areas are also shown.

of the cardinal directions, and one measurement at the plot center). We used a moosehorn because a comparison of methods found the moosehorn was a more accurate measure of light conditions, and repeated measurements with different observers were significantly more consistent than with a spherical densitometer.² Digital hemispherical photos gave the best results but were not practical for our study because of the time required for fieldwork and analysis. The large study area and number of plots also necessitated visual estimates of percent cover of the three most dominant shrubs and herbs within each plot, which were done after dividing the plot into quarters. Independent estimates by at least two field personnel were averaged for each plot. Samples of any unknown herbs were transported to the University of Washington herbarium for positive identification.

Vegetation Classification

Plots were classified into forest types and plant associations by using a series of iterative cluster analyses. First, the divisive hierarchical cluster analysis routine in S-Plus 2000 (Insightful Corporation, Seattle, Washington)³ was used to determine the appropriate number of clusters. Once this was determined, a k-means clustering routine was used, to classify each plot and calculate its distance from the cluster center. This process was implemented in two hierarchical steps. First, plots were classified by using a data set of tree species composition and basal area, and then each of the resulting groups were further subdivided by using the same statistical procedures with shrub and herb cover data. We used only tree composition to determine the first division in the plant communities because Teakettle's shrub and herb cover is sparse.

Traditional approaches to plant classification often use ordination (e.g., DECORANA) and cluster (e.g., TWINSpan) analysis to investigate plant communities and infer the environmental gradients influencing species composition. We did not follow this approach for several reasons. Because we did not take direct measures of temperature, moisture, light or soil nutrients, an ordination of plots would likely indicate elevation and aspect influenced plant composition. Changes in elevation and aspect, however, indicate a simultaneous change in many growing conditions and provide little information about which factors are driving community composition (Pausas and Austin 2001). To classify plant associations, we used cluster analysis because TWINSpan does not perform well when there is more than one underlying gradient (McCune and Mefford 1999). Unlike TWINSpan, cluster analysis has no inherent reduction in dimensionality (Belbin and McDonald 1993, Van Groenewoud 1992).

² Unpublished data on file at the Sierra Nevada Research Center, Davis, Calif.

³ Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

Intensive Measurements of Mixed-Conifer and Red Fir Forests

After our initial survey, we sampled the mixed-conifer and red fir forests more intensively to establish a detailed description of these forest types. We surveyed a total of 167 ha based on the 100 m grid system described above. Within each hectare, four 1/20th ha circular plots were located systematically 33.3 m from the nearest edges of the hectare (fig. 9). Data collected at each plot included the diameter at breast height (DBH) of each tree and snag greater than 2 m tall and 5 cm DBH, canopy cover determined with a moosehorn and averaged from five locations (plot center and at the edge of each plot in the four cardinal directions), and diameter and length measurements of logs greater than 30 cm in diameter.

Use of Data to Establish Plots for Long-term Experimentation

Our analyses of mixed conifer led us to investigate the patterns of vegetation conditions that characterize its variable composition and structure. The initial vegetation surveys were used to establish 18 four ha plots that received different burning and/or thinning treatments in the Teakettle Experiment (appendix A). Within these 18 plots, 402 systematic grid points were mapped for coordinated sampling. At each of these grid points, vegetation, coarse woody debris, and litter depth were measured in 1/500th ha circular plots (2.52 m radius) to assess fine scale vegetation patterns. Based on these data, we characterized the patch types within mixed conifer using the same hierarchical cluster analysis routines as in the vegetation classification described above.

For each of the 18 four ha plots, a complete stem map of all trees and snags \geq cm dbh has been made. We have used this extensive data set to establish tree and snag basal area for each plot. We compared these detailed basal area estimates to those calculated from the prism point and fixed-radius plots to evaluate sampling strategies for mixed-conifer's patchy distribution.

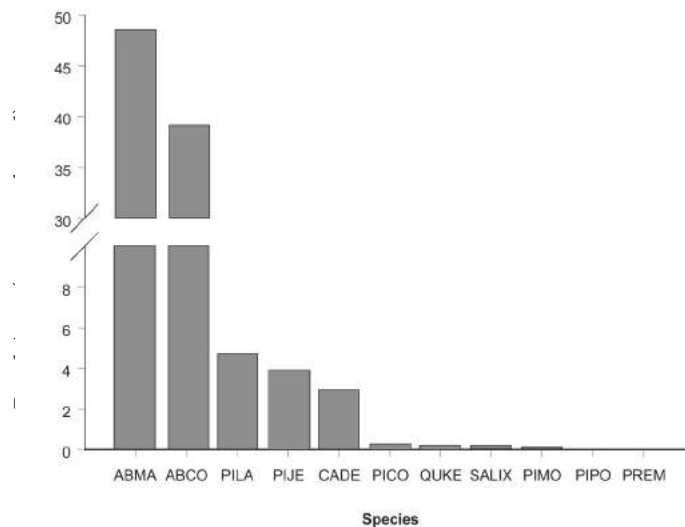
Results and Discussion

Initial Survey Results

Trees

Together, red fir and white fir comprise about 86 percent of the basal area at Teakettle, while sugar pine, Jeffrey pine, and incense cedar nearly account for the remaining 13 percent (fig. 10). Other tree species characteristic of mixed-conifer or red fir forest types include lodgepole pine (*Pinus contorta*), black oak, willow (*Salix* spp.), western white pine (*P. monticola*), ponderosa pine, and bitter cherry (*Prunus emarginata*); however, these species together account for only a small proportion (<1 percent) of the total basal area (fig. 10).

Figure 10—Proportion of basal area accounted for by each tree species within Teakettle (note break in y axis). Species acronyms are listed in appendix B.



Intensive Measurements of Mixed-Conifer and Red Fir Forests

After our initial survey, we sampled the mixed-conifer and red fir forests more intensively to establish a detailed description of these forest types. We surveyed a total of 167 ha based on the 100 m grid system described above. Within each hectare, four 1/20th ha circular plots were located systematically 33.3 m from the nearest edges of the hectare (fig. 9). Data collected at each plot included the diameter at breast height (DBH) of each tree and snag greater than 2 m tall and 5 cm DBH, canopy cover determined with a moosehorn and averaged from five locations (plot center and at the edge of each plot in the four cardinal directions), and diameter and length measurements of logs greater than 30 cm in diameter.

Use of Data to Establish Plots for Long-term Experimentation

Our analyses of mixed conifer led us to investigate the patterns of vegetation conditions that characterize its variable composition and structure. The initial vegetation surveys were used to establish 18 four ha plots that received different burning and/or thinning treatments in the Teakettle Experiment (appendix A). Within these 18 plots, 402 systematic grid points were mapped for coordinated sampling. At each of these grid points, vegetation, coarse woody debris, and litter depth were measured in 1/500th ha circular plots (2.52 m radius) to assess fine scale vegetation patterns. Based on these data, we characterized the patch types within mixed conifer using the same hierarchical cluster analysis routines as in the vegetation classification described above.

For each of the 18 four ha plots, a complete stem map of all trees and snags \geq cm dbh has been made. We have used this extensive data set to establish tree and snag basal area for each plot. We compared these detailed basal area estimates to those calculated from the prism point and fixed-radius plots to evaluate sampling strategies for mixed-conifer's patchy distribution.

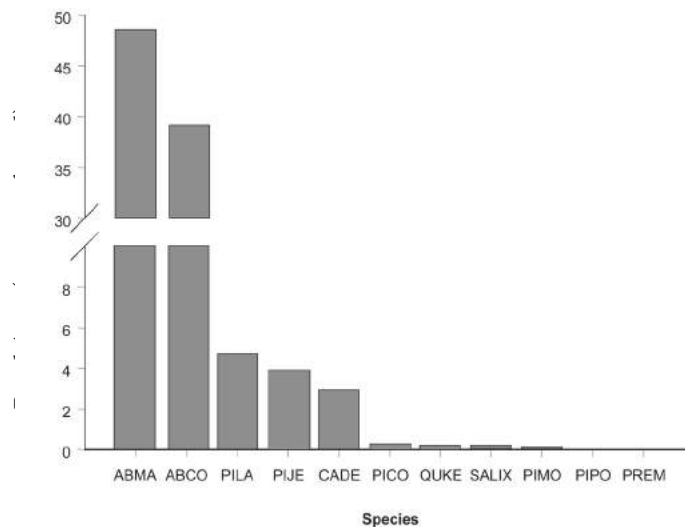
Results and Discussion

Initial Survey Results

Trees

Together, red fir and white fir comprise about 86 percent of the basal area at Teakettle, while sugar pine, Jeffrey pine, and incense cedar nearly account for the remaining 13 percent (fig. 10). Other tree species characteristic of mixed-conifer or red fir forest types include lodgepole pine (*Pinus contorta*), black oak, willow (*Salix* spp.), western white pine (*P. monticola*), ponderosa pine, and bitter cherry (*Prunus emarginata*); however, these species together account for only a small proportion (<1 percent) of the total basal area (fig. 10).

Figure 10—Proportion of basal area accounted for by each tree species within Teakettle (note break in y axis). Species acronyms are listed in appendix B.



The elevational gradient of Teakettle creates distinct species distributional patterns and a strong division between the two main forest types. Red fir dominates at the higher elevations in the west and northwest of Teakettle, while below about 2,150 m, white fir, sugar pine, Jeffrey pine, and incense cedar are dominant (fig. 11). Red fir is also sometimes locally common in riparian areas at lower elevations. Several tree species have more limited distributions, which are indicative of particular environmental conditions. For example, Jeffrey pine and black oak are largely restricted to the most xeric sites in the eastern portion of the forest along ridgetops and areas with shallow soils. Lodgepole pine is found only on mesic sites at the highest elevations in the NW corner of Teakettle (fig. 11). Similarly, several species of willow are restricted to a small number of moist riparian sites (fig. 11).

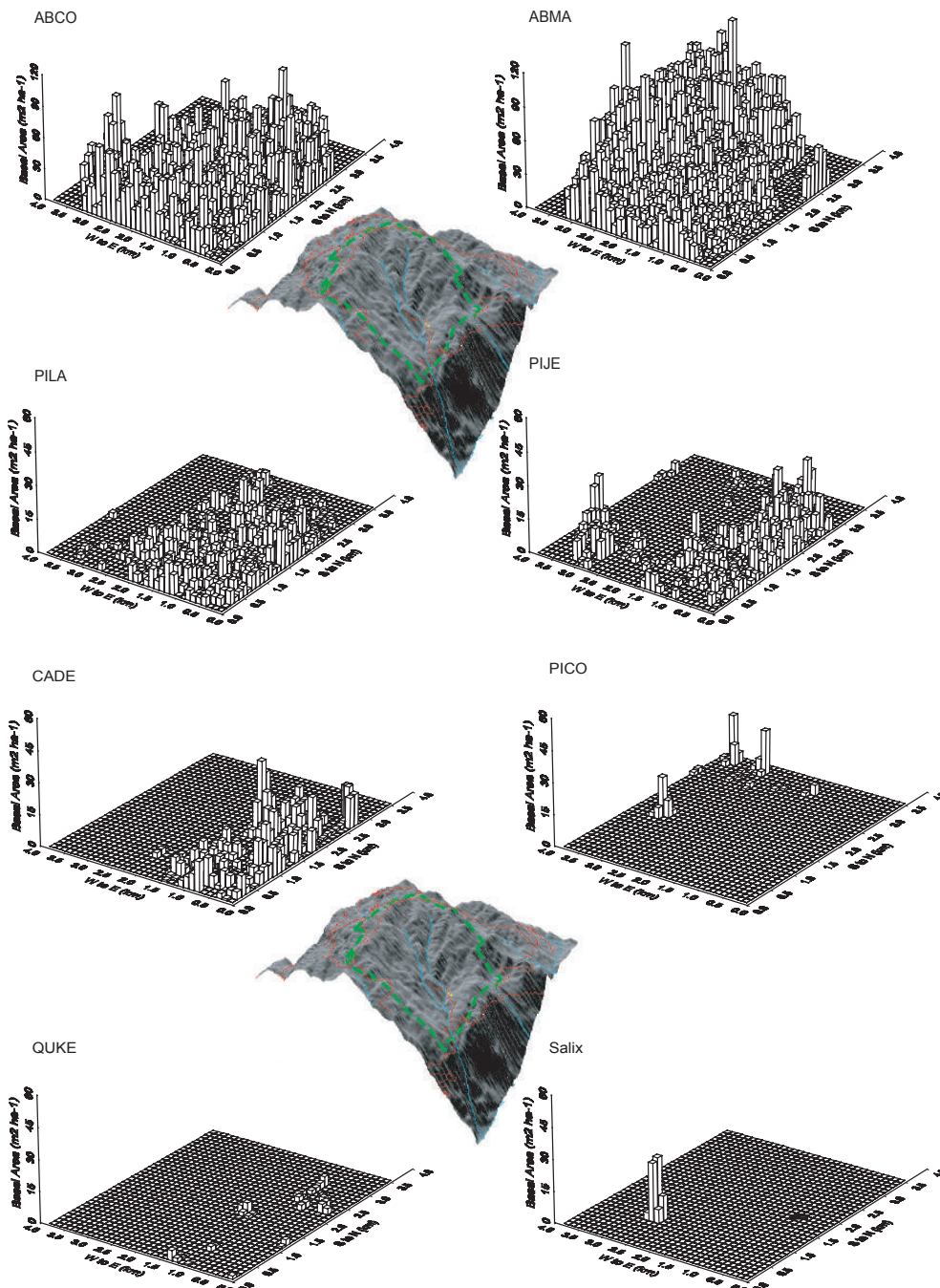


Figure 11—Spatial distribution of basal area of major tree species within Teakettle. Data are from 1,264 plots regularly spaced at 100 m intervals throughout the entire Experimental Forest. Note different Z-axis scaling for ABCO and ABMA plots. The major elevational gradient runs from the SE corner in the foreground to the NW corner in the background. Species acronyms are listed in appendix B.

Shrubs

The shrub component of Teakettle's understory is dominated by mountain whitethorn (*Ceanothus cordulatus*), both in terms of cover and frequency among sample plots (fig. 12). Mountain whitethorn accounted for almost 1/3 (30 percent) of the total shrub cover, averaged 6.4 percent and was found on 36 percent of all plots. Other common shrubs include bush chinquapin (*Chrysolepis sempervirens*), pinemat manzanita (*Arctostaphylos nevadensis*), snowberry (*Symphoricarpos mollis*), green leaf manzanita (*Arctostaphylos patula*), shrub forms of bitter cherry (*Prunus emarginata*), red flowering currant (*Ribes sanguineum*), Sierra gooseberry (*R. roezlii*), and hazelnut (*Corylus cornuta* var. *californica*) (fig. 12).

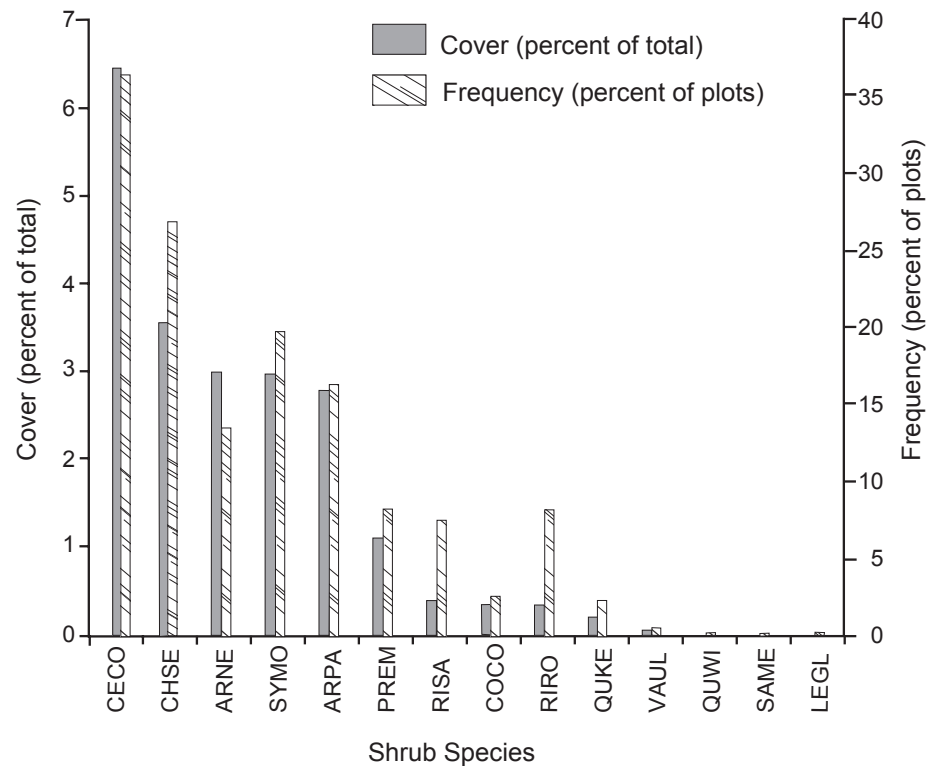
The two most abundant shrubs at Teakettle, mountain whitethorn and chinquapin, are generally found throughout the entire forest, while other shrub species have more restricted distributions (fig. 13). Greenleaf manzanita is generally limited to lower elevation hot and dry sites, while pinemat manzanita is most abundant at higher elevation xeric sites (fig. 13). Similarly, snowberry, Sierra gooseberry, bitter cherry, and hazelnut are most abundant at mesic mid-elevation sites (fig. 13). The most uncommon shrub species were each found on only one plot: deer brush (*Ceanothus integerrimus*) and manzanita (*Arctostaphylos manzanita*) were only found on exposed sites at the lowest elevations of Teakettle, and western Labrador tea (*Ledum glandulosum*) and western blueberry (*Vaccinium uliginosum* ssp. *occidentale*) were only found in high elevation wet meadows.

Herbs, Snags and Logs

A total of 123 herbaceous species were identified within Teakettle (appendix B). The most frequent herbaceous species was *Monardella odoratissima*, while *Lupinus adsurgens* was most dominant in terms of percent cover (fig. 14a, b). Total herb cover generally increased with elevation (fig. 15), most likely associated with cooler and moister microclimates.

Snags and downed logs were fairly evenly distributed throughout Teakettle (fig. 16), although there is a trend toward higher values in the red fir forest plots. The mean snag basal area per plot was 9.03 m²/ha, and mean log volume was 153.6 m³/ha.

Figure 12—Percent cover and frequency for all shrub species within Teakettle. Frequency is expressed as the percentage of plots on which a shrub was found. Data are from 1/20th ha circular plots (N=1,264). Species acronyms are listed in appendix B.



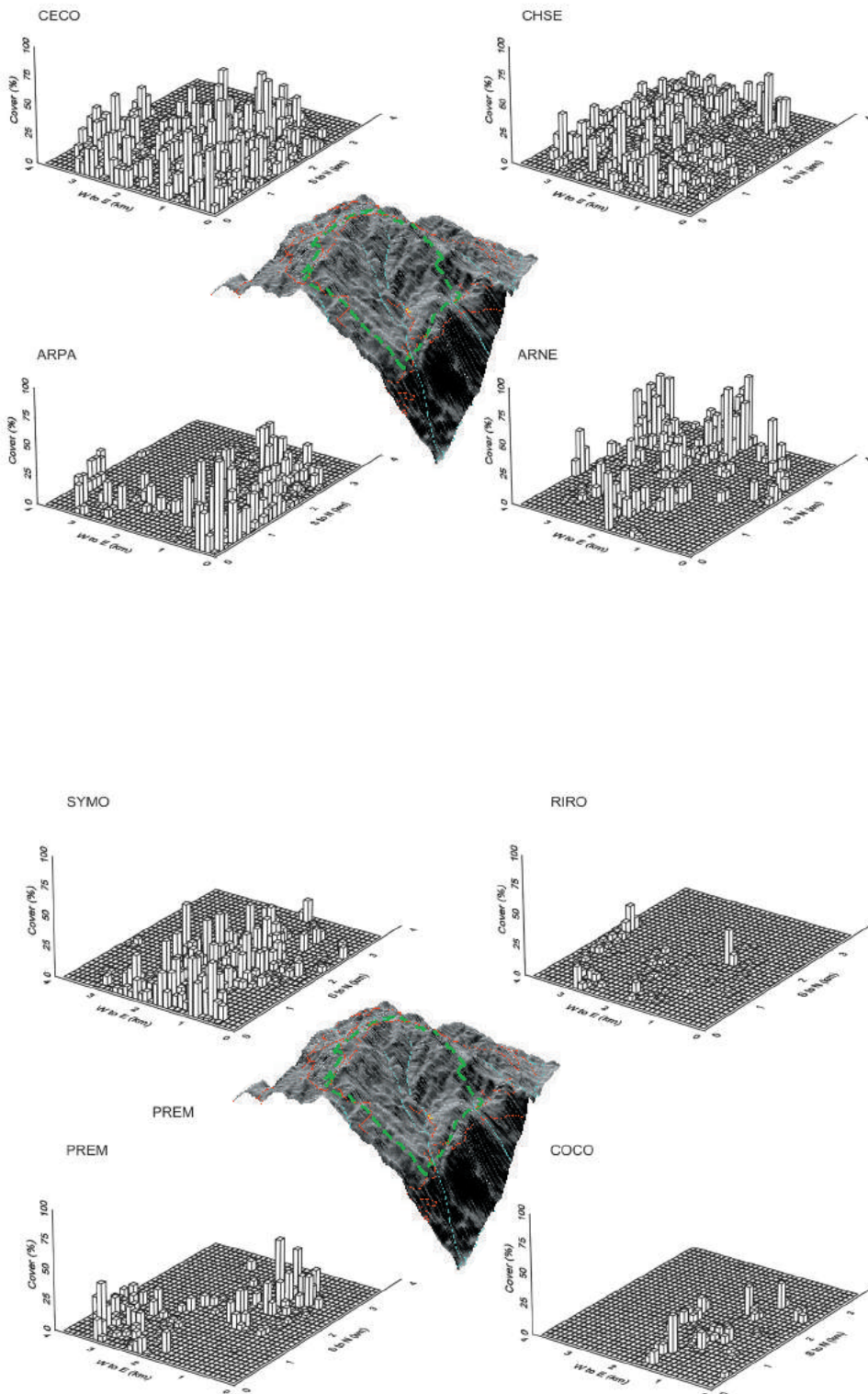


Figure 13—Spatial distribution of percent cover of major shrub species within Teakettle. Data are from 1,264 plots regularly spaced at 100 m intervals throughout the entire Experimental Forest. The major elevational gradient runs from the SE to the NW corner. Species acronyms are listed in *appendix B*.

Figure 14a—Dominance and frequency for herb species encountered on at least 1 percent of plots within Teakettle. Dominance is expressed as a percentage of total cover, and frequency is expressed as the percentage of plots on which a species was found. Data are from 1/20th ha circular plots (N=1,264). Species acronyms are listed in *appendix B*.

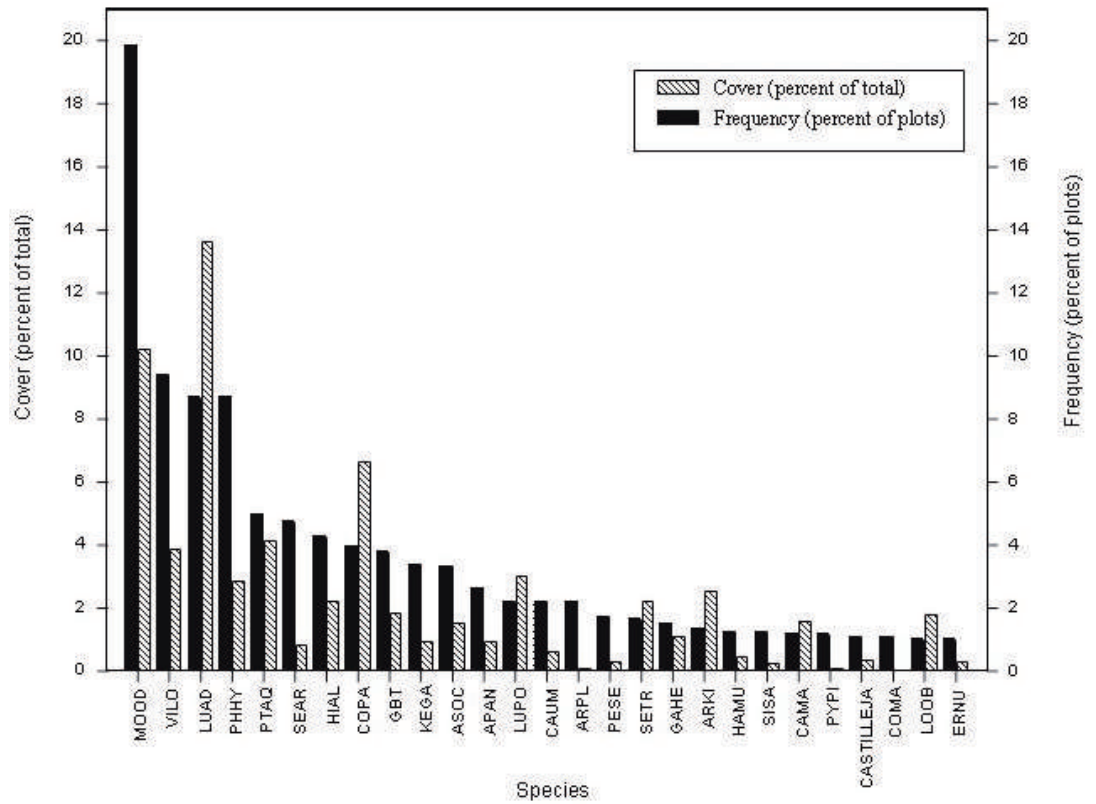
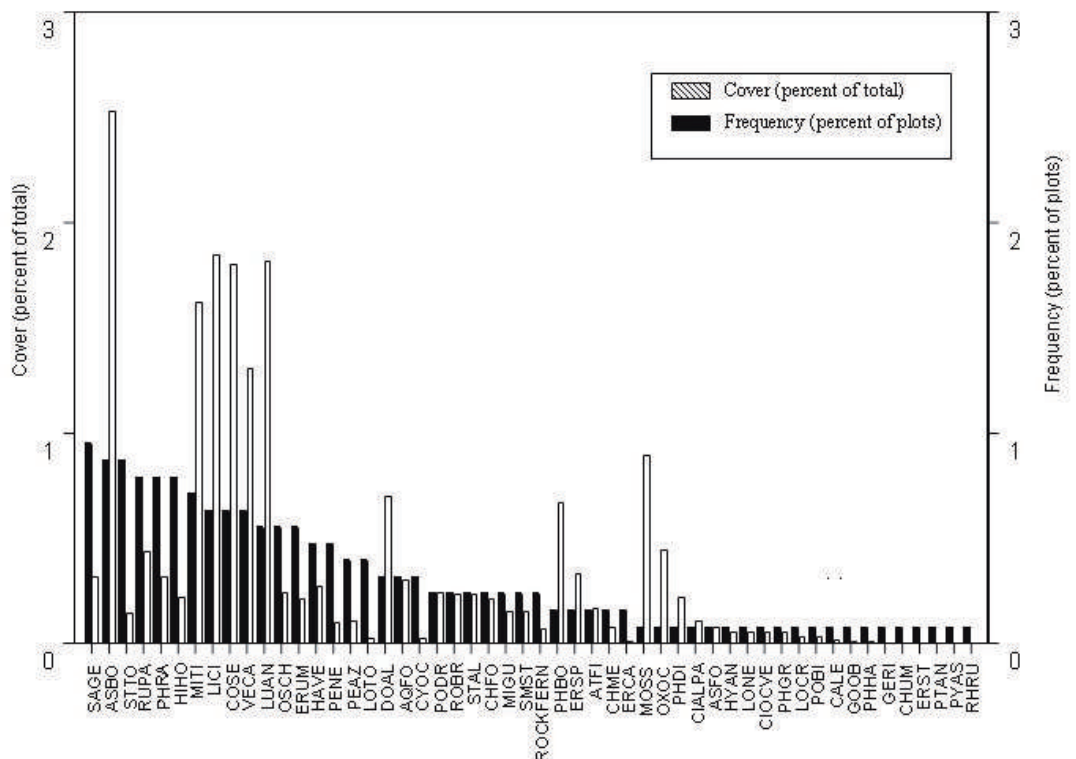


Figure 14b—Dominance and frequency for herb species encountered on less than 1 percent of plots within Teakettle. Species acronyms are listed in *appendix B*. Note different scale of y-axis.



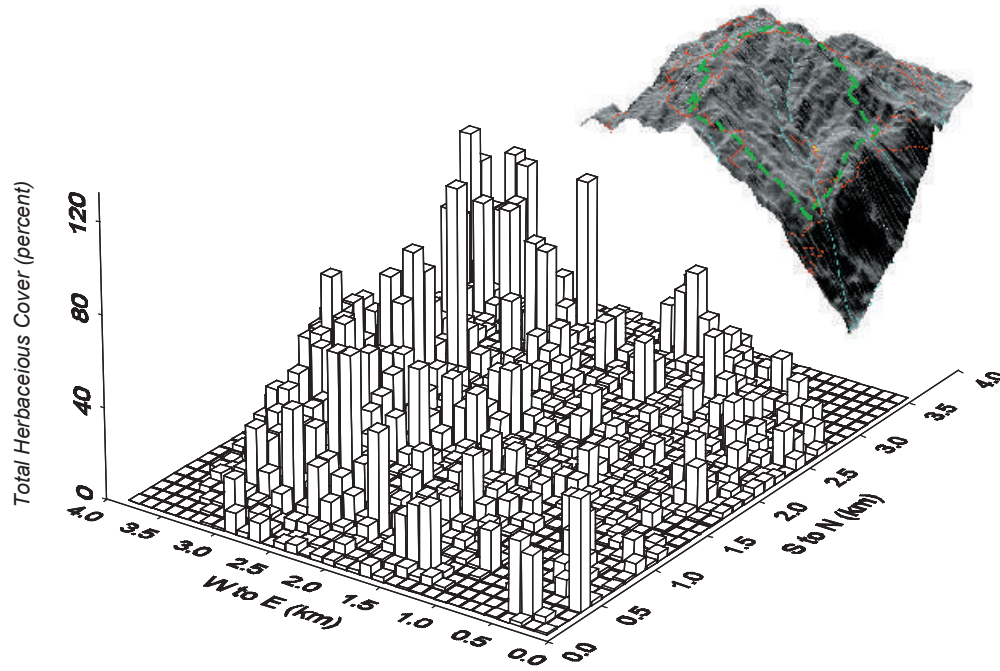


Figure 15—Spatial distribution of total herb cover for the 1,264 plots surveyed within Teakettle. Because herb cover on each plot was calculated for each species individually, total cover values may exceed 100 percent.

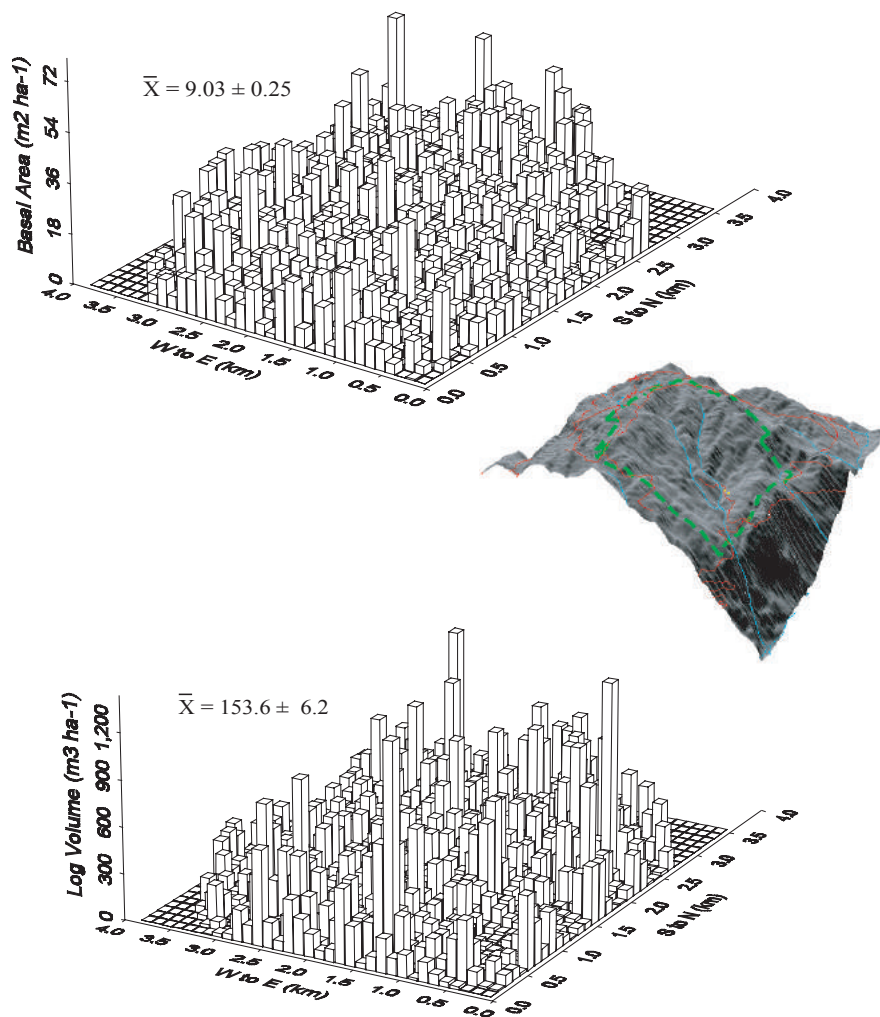


Figure 16—Spatial distribution of snag basal area and log volume for the 1,264 plots surveyed within Teakettle. Values above graphs indicate means and standard errors. Log volume was calculated using the formula: $V = L(A_1 + A_2)/2$ where V is the volume, L is the length, and A_1 and A_2 represent the area of each end of the log (Harmon and Sexton 1996).

Vegetation Classification

On the basis of the iterative cluster analysis process, we grouped all of the 1,264 plots in the initial sample into six main vegetation types based on tree composition. These six vegetation types delineate the main forest types within Teakettle (*table 5, fig. 17*).

Mixed-Conifer Forest Type

Mixed conifer is the most common forest type within Teakettle, covering nearly two-thirds of the forest (818/1,264 plots). It is dominated by white fir and red fir and contains a mix of all other tree species, particularly incense cedar, Jeffrey pine, and sugar pine (*fig. 18*).

We further divided the mixed-conifer forest type into one of six subtypes (associations) based on the composition of understory plants (*figs. 17, 19*). Most of the plots (531/818 or 65 percent) contained an even mix of shrub and herb species and thus were simply classified in the mixed-conifer association (*fig. 19*). The other five associations within the mixed-conifer forest type were based on the dominance of one or two shrub species (*fig. 19*). Attempts at further subdivisions of each association based on herb composition and abundance using the cluster analysis process did not produce any further significant ($p < 0.05$) splits of the data.

Red Fir Forest Type

The red fir forest type accounts for almost one-third of the plots at Teakettle (352/1264 or 28 percent), and while dominated by red fir, it also contains a large proportion of white fir (*fig. 20*).

The red fir forest type was divided into five associations based on understory plant composition (*figs. 17, 20*). Most of the plots (295/352) contained an even mix of shrub species and therefore were classified in the red fir association (*fig. 20*). The other four associations within the red fir forest type were based on dominance by one or two shrub species (*fig. 20*). Understory herb composition and abundance data did not affect the classification.

Jeffrey Pine Forest Type

On the 69 plots classified in the Jeffrey pine forest type, Jeffrey pine accounts for >50 percent of the basal area (*fig. 21*). This forest type also contains large proportions of sugar pine, white fir, and a mix of the other coniferous tree species (*fig. 21*).

We identified three associations within the Jeffrey pine type, again based on shrub dominance (*figs. 17, 21*).

Table 5—Summaries of mean vegetation characteristics and cover values for each forest type at Teakettle.

Forest Type	Tree BA (m ² /ha)	Snag BA (m ² /ha)	Shrub cover (percent)	Herb cover (percent)	Rock cover (percent)	Log vol. (m ³ /ha)
Mixed-conifer (N=818)	42.7	8.4	27.2	6.1	4.0	164.0
Red fir (N=352)	57.0	12.4	17.9	8.4	1.0	160.0
Jeffrey pine (N=69)	18.4	2.4	26.8	3.1	31.3	60.0
Treeless (N=18)	0.0	0.7	36.2	19.2	32.1	10.0
Lodgepole pine (N=6)	26.0	3.3	22.7	63.5	8.3	14.0
Black oak (N=1)	28.0	0.0	70.0	10.0	1.0	38.0

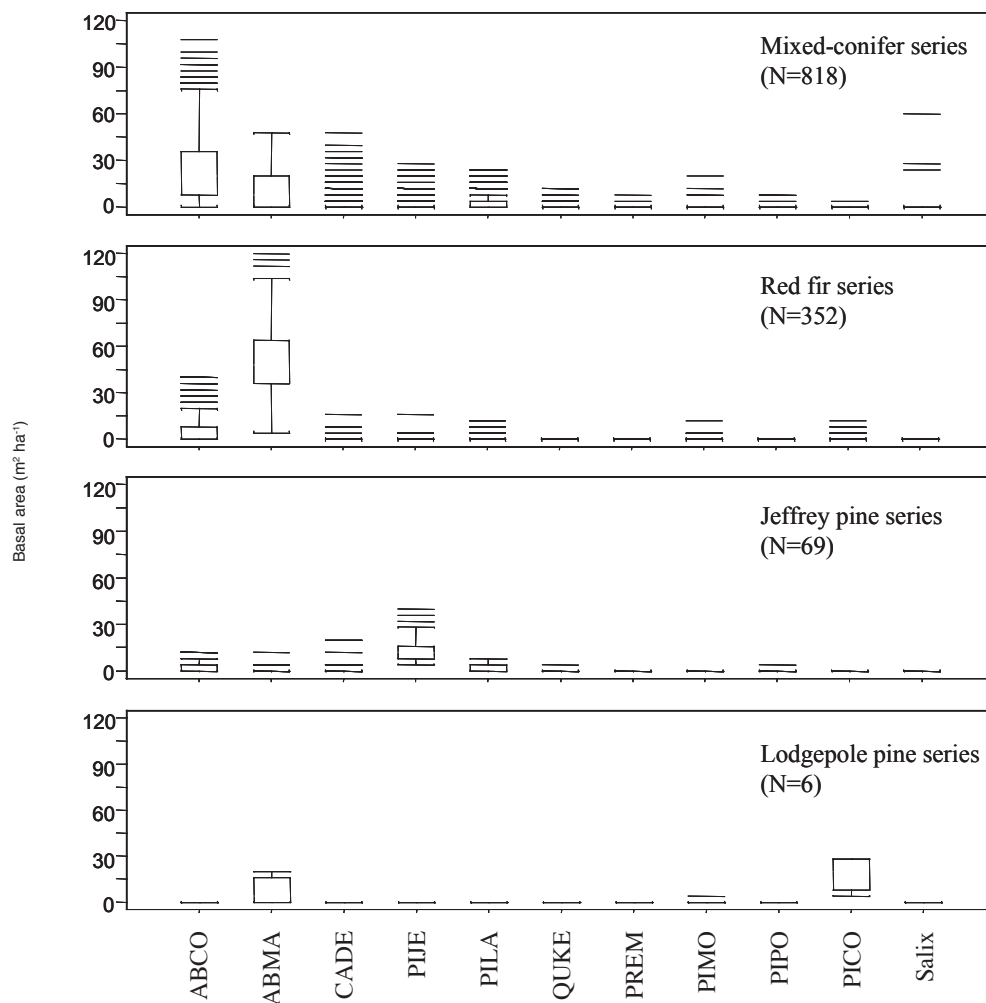
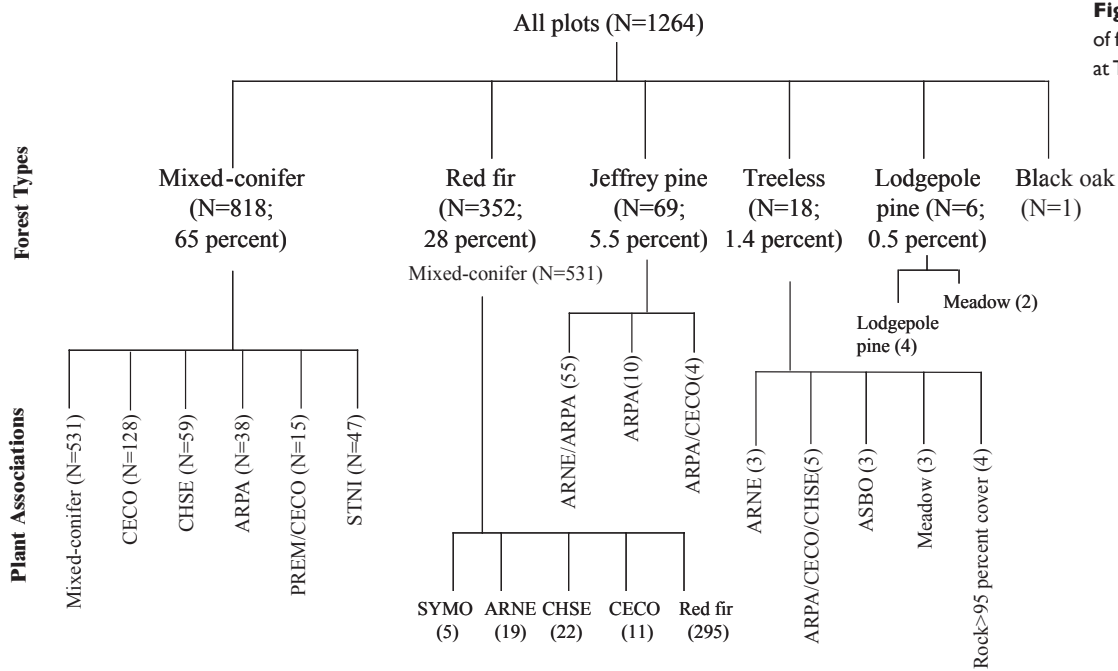
Figure 17—Classification scheme of forest types and plant associations at Teakettle.**Figure 18**—Basal area distributions of tree species within each of four major forest types at Teakettle. The black oak series (N=1) and a sixth series (N=18), which contain no trees, shown in figure 17, are not included here. Box plots show minimum, 1st quartile, median, 3rd quartile, maximum, and outliers greater than 1.5x the interquartile range. Tree species acronyms listed on the x-axis are listed in *appendix B*.

Figure 19—Distribution of percent cover of each shrub species within the six plant associations of the mixed-conifer forest type. Box plots show minimum, 1st quartile, median, 3rd quartile, maximum, and outliers. Shrub species acronyms listed on the x-axis are listed in *appendix B*.

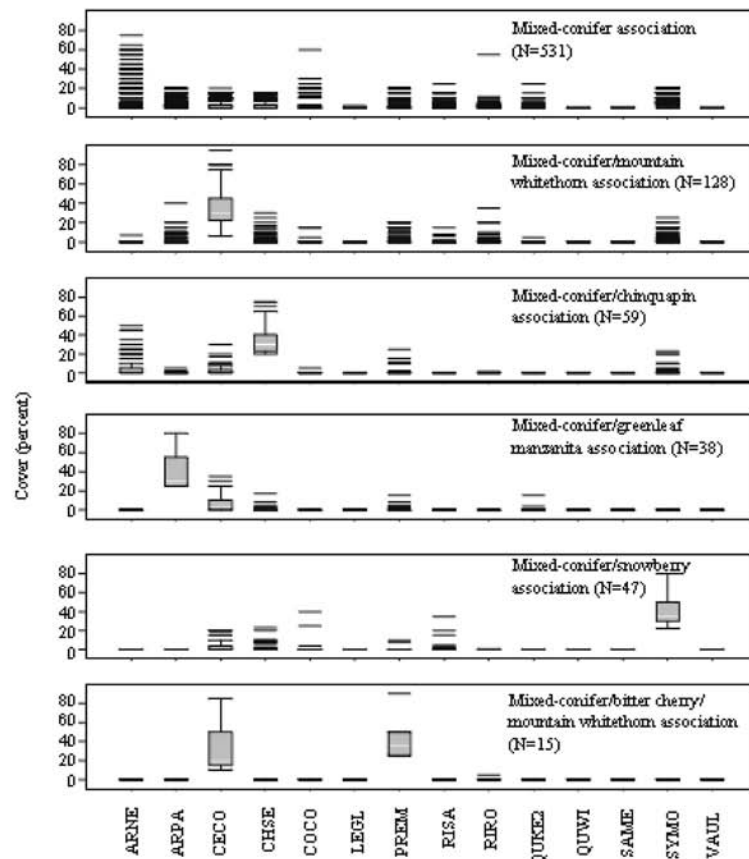
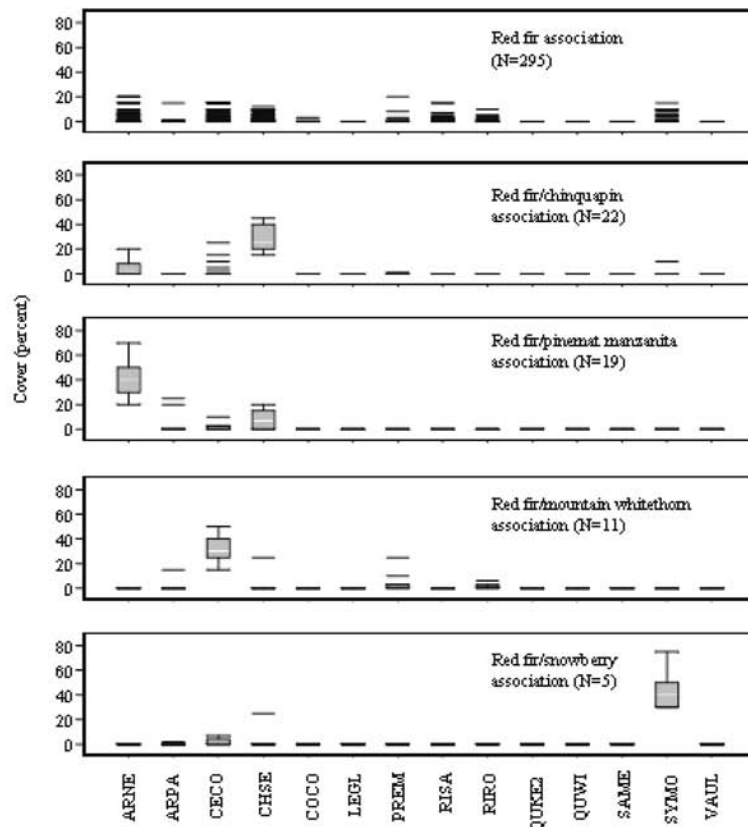


Figure 20—Distribution of percent cover of each shrub species within the five plant associations of the red fir forest type. Box plots show minimum, 1st quartile, median, 3rd quartile, maximum, and outliers. Shrub species acronyms on the x-axis are listed in *appendix B*.



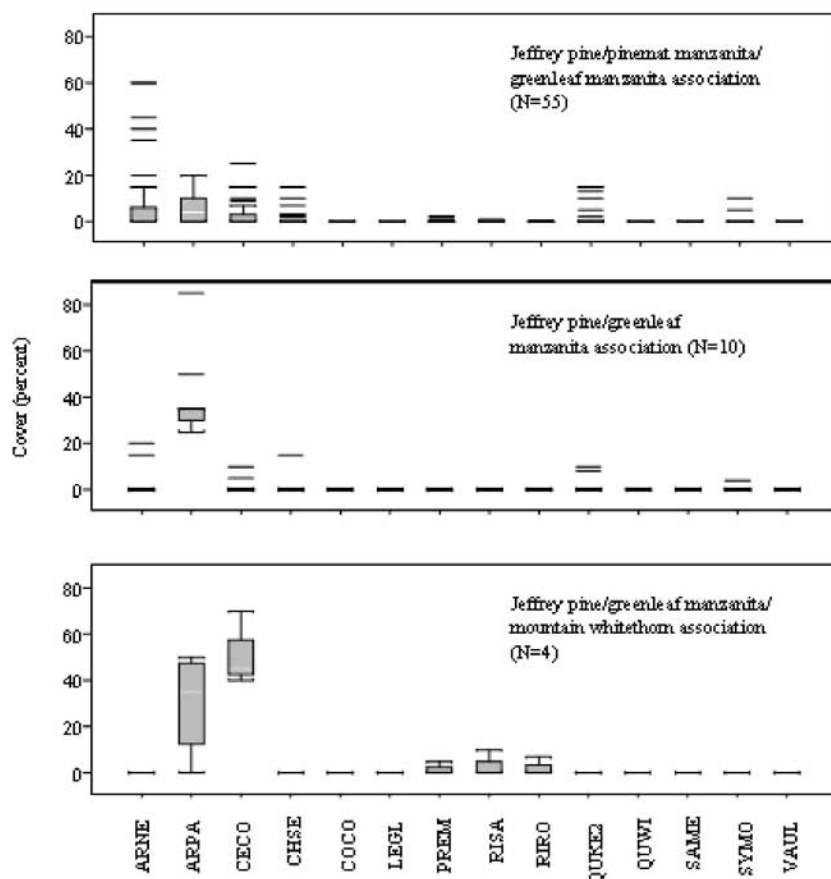


Figure 21—Distribution of percent cover of each shrub species within the three plant associations of the Jeffrey pine forest type. Box plots show minimum, 1st quartile, median, 3rd quartile, maximum, and outliers. Shrub species acronyms on the x-axis are listed in *appendix B*.

Other Forest Types

Plots that were not classified as mixed-conifer, red fir, or Jeffrey pine were dominated by either lodgepole pine (N=6), black oak (N=1), or did not have any trees (N=18) (*fig. 17*). Lodgepole pine is relatively uncommon within Teakettle, and the plots classified within this forest type are exclusively at higher elevations. Red fir also accounted for a large proportion of the basal area in plots classified in the lodgepole pine forest type (*fig. 18*). Two plots within the lodgepole pine forest fell within meadows and therefore had a unique composition of herbs and were classified to reflect this (*fig. 17*).

Eighteen plots did not have trees and were further classified on the basis of rock cover or shrub and herb composition (*fig. 17*). Three plots were in moist meadows, three were in dry meadows at upper elevations (dominated by *Astragalus bolanderi*), and the remainder were in shrub fields dominated either by pinemat manzanita (N=3), or combinations of greenleaf manzanita, mountain whitethorn, and bush chinquapin (N=5; *fig. 17*).

Black oak is uncommon within Teakettle—only one plot was classified in this forest type (*fig. 17*).

Comparisons and Distributions of Forest Types

The red fir and mixed-conifer forest types have much greater snag basal area (*fig. 22*) and log volume (*fig. 23*) than the other forest types, probably because they are on more productive sites.

The lodgepole pine and treeless vegetation types had much greater herb cover than the other forest types (*fig. 24*). The lodgepole pine plots were located exclusively in mesic meadows, and the low canopy cover of the treeless areas provides sunlight for understory herbs.

Figure 22—Snag basal area for five of the forest types classified at Teakettle. Plots in the red fir and mixed-conifer forest types had significantly greater snag basal than the other forest types ($p=0.001$), but were not significantly different from one another ($p=0.786$). Box plots show minimum, 1st quartile, median, 3rd quartile, maximum, and outliers. The black oak forest type ($N=1$) is not shown.

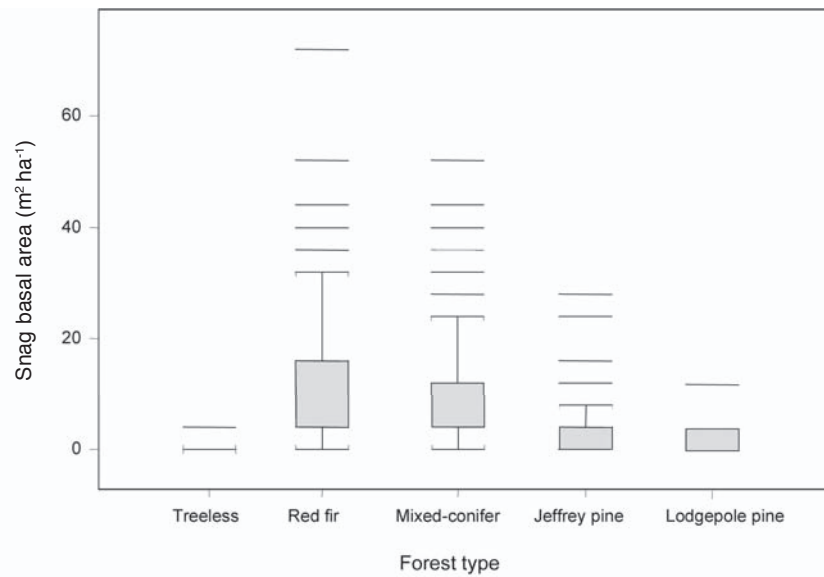


Figure 23—Log volume for five of the forest types classified. Plots in the red fir and mixed-conifer forest types had significantly greater log volume than the other forest types ($p=0.001$), but were not significantly different from one another ($p=0.67$). Volume was calculated using the formula: $V=L(A_1 + A_2)/2$ where V is the volume, L is the length, and A_1 and A_2 represent the area of each end of the log (Harmon and Sexton 1995). Box plots show minimum, 1st quartile, median, 3rd quartile, maximum, and outliers. The black oak forest type ($N=1$) is not shown.

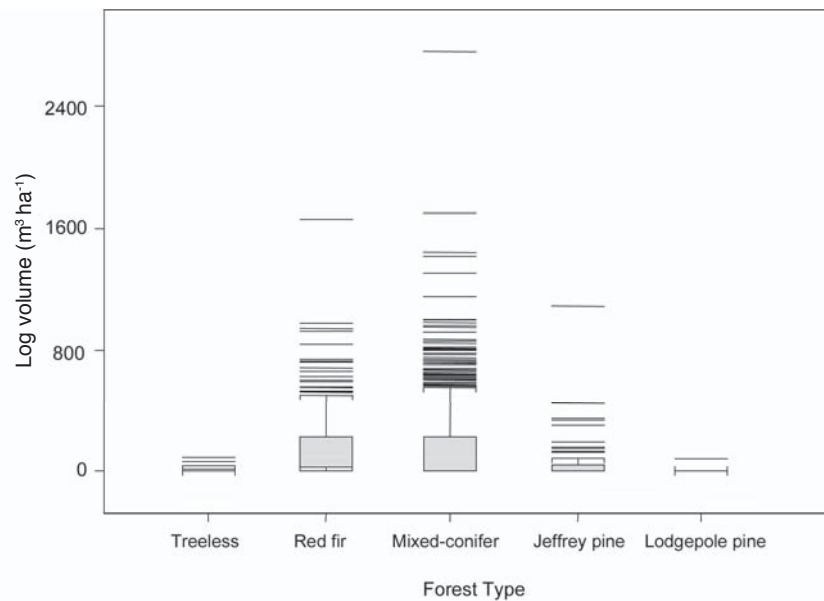
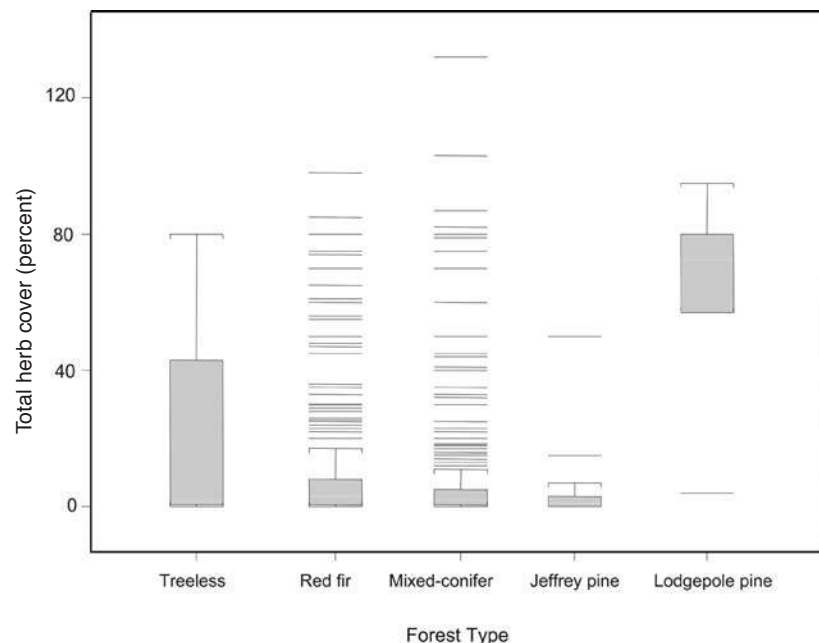


Figure 24—Distribution of total herb cover for five of the forest types. Because herb cover on a plot was calculated for each species individually, total cover values may exceed 100 percent. Box plots show minimum, 1st quartile, median, 3rd quartile, maximum, and outliers. The black oak forest type ($N=1$) is not shown.



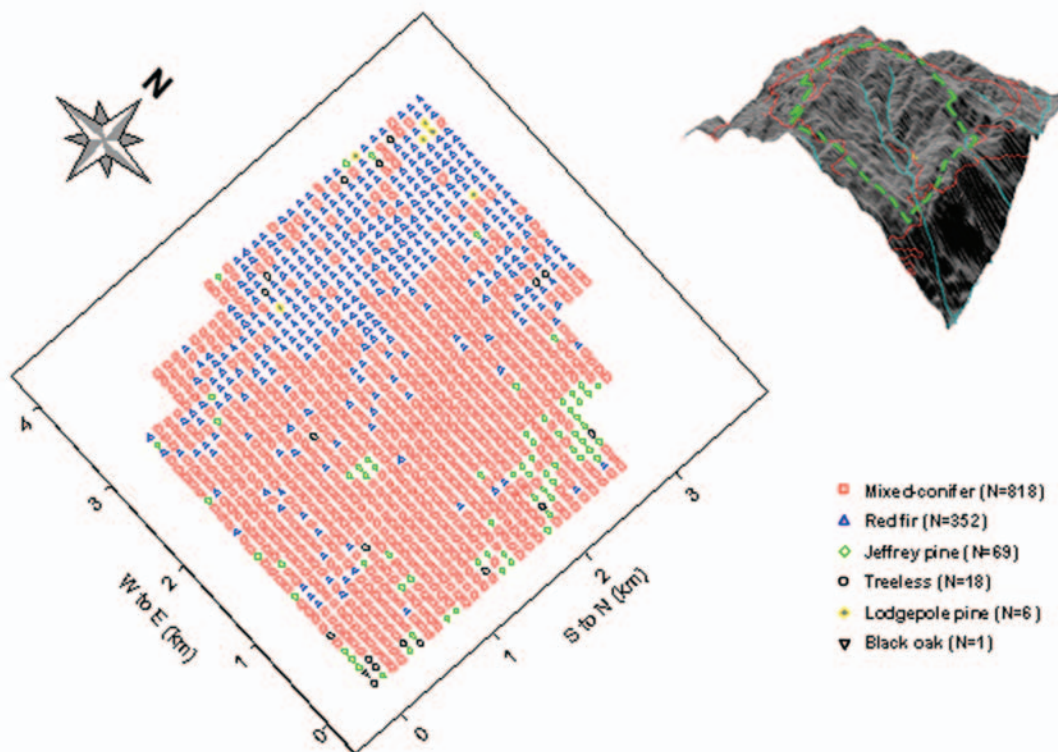


Figure 25—Spatial distribution of the six forest types classified at Teakettle, including the treeless series. The mixed-conifer forest dominates the lower elevations, while the red fir is most common at higher elevations.

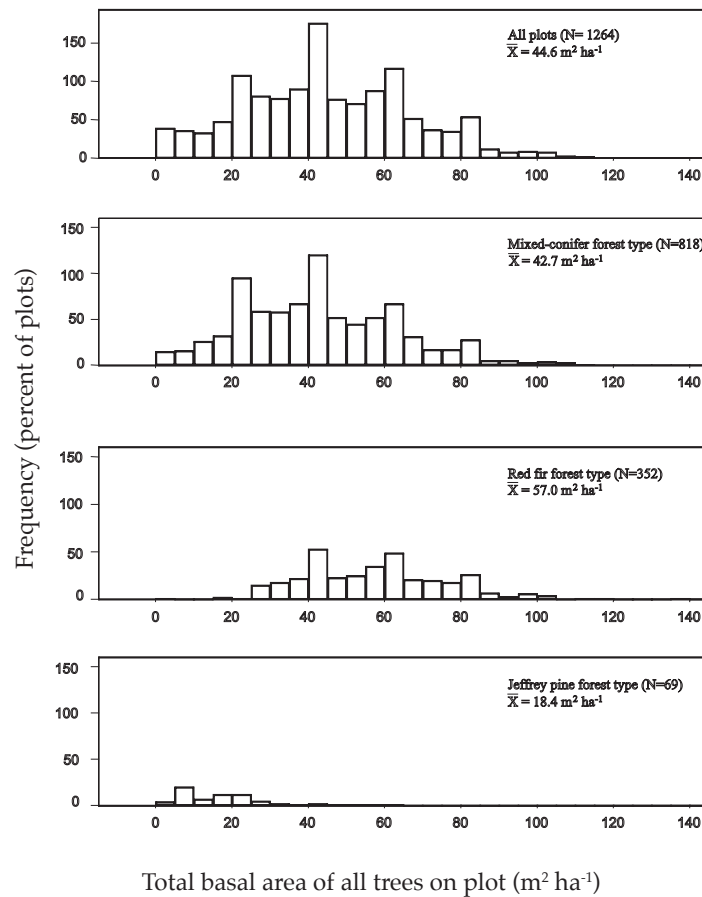
The distribution of each forest type within Teakettle largely follows the main elevational gradient of the forest (*fig. 25*). Although the Jeffrey pine, black oak, and treeless vegetation types occur at generally the same elevation as the mixed-conifer, the distribution of these forest types is largely a function of soil depth and topography as they are restricted to the more xeric and exposed sites with shallow soils. The lodgepole pine type is found at the same elevations as the red fir forests, but only in the most mesic sites.

Comparisons with Existing Classifications of Mixed-Conifer and Red Fir Forests

Teakettle old-growth forests appear representative of old-growth elsewhere in the Sierra Nevada, with similar basal area values from mixed-conifer forests in the northern Sierra (Fites 1993) and red fir forests in the southern Sierra (Potter 1998). Total tree basal area within Teakettle ranged from 0 to 136 m² ha⁻¹ with a mean of 44.6 m² ha⁻¹ (*fig. 26*). The dense closed-canopy forests in the red fir forest type had the greatest average basal area, while the Jeffrey pine forest had the lowest average basal area (*fig. 26*).

Our classifications of these forest types are generally consistent with those of other authors, although our fine-scale sampling has produced more associations than reported elsewhere. For example, Fites (1993) describes the mixed-conifer/chinquapin and the mixed-conifer/snowberry plant associations, but we recognize three other mixed-conifer plant associations as well (*fig. 17*). We also found more red fir in mixed conifer at Teakettle than described elsewhere (Barbour 1988, Rundel and others 1977). Red fir within Teakettle's mixed conifer is largely restricted to riparian areas where low temperatures and snowpack lingering until late spring may allow it to be successful at this elevation (Royce and Barbour 2001a,b). Potter (1998) describes the red fir, Jeffrey pine, and lodgepole pine forest types, but our analysis produced distinct subdivisions within each of these types (*fig. 17*). These differences likely stem from differences in sampling extent and intensity. We intensively surveyed a relatively small area and produced a detailed data set, while most previous classifications have been at a larger spatial scale and lower sampling intensity.

Figure 26—Frequency distributions of tree basal area for all plots within Teakettle and for each of the three main forest types classified.



Intensive Measurements of Mixed-Conifer and Red Fir Forests

After our survey of the entire forest, we intensively measured the mixed-conifer and red fir forest types at a finer scale, using fixed-radius plots (*fig. 9*).

Dominance in the mixed-conifer forest type is shared by five major tree species, while the red fir forest is composed exclusively of red and white fir (*fig. 27*). Mean stem density and basal area of live trees and snags was greater in red fir than the mixed-conifer forest (*fig. 27*). Density of live trees and snags >75 cm dbh was 39 and 11 stems/ha, respectively, in mixed conifer, and 43 and 13 stems/ha in red fir (*fig. 27*). On average, Jeffrey pine and sugar pine are the largest trees, with mean dbh of 53 and 47 cm, respectively, and have the highest proportion of individuals greater than 75 cm dbh in mixed conifer (*table 6*).

Canopy cover has a wide range of values in mixed-conifer, while in red fir forests it is usually between 45-80 percent (*fig. 28*). Red fir forests are generally much more homogenous, while mixed-conifer forests tend to be naturally heterogeneous with patches of closed canopy forest alternating with open gaps and shrubs.

Mixed conifer's patchy nature highlights a sampling problem we detected when comparing the prism-point, fixed-radius plot and stem-map data sets. The prism point estimate of tree basal area for the intensively sampled plot area was 46.4 m²/ha, the fixed radius plots was 61.3 m²/ha, and the stem map was 60.6 m²/ha. The stem map estimate is probably very close to the actual value since it measures every tree ≥ 5 cm dbh. The prism point estimate undervalues basal area by 23 percent. The problem may be that prisms rely on line of sight to tally trees as "in" or "out" (determined by their size and distance from the observer). In a highly patchy forest, fewer trees may be tallied because line of sight is limited

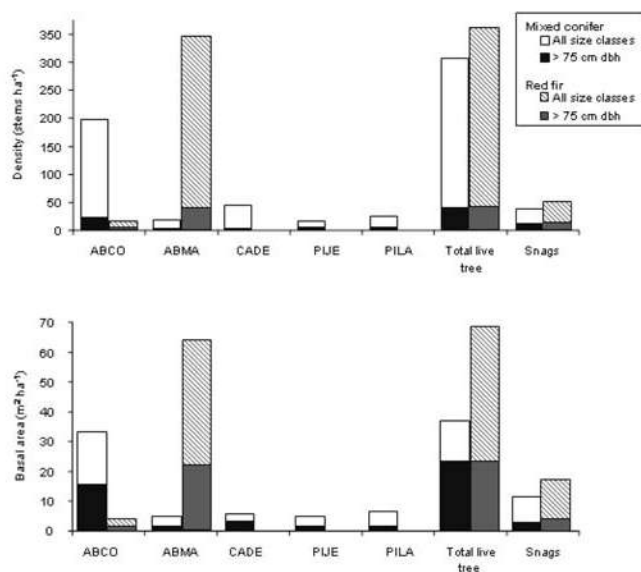


Figure 27—Mean density and basal area of dominant tree species and snags from the intensive survey of the mixed-conifer and red fir portions of the forest. Tree species acronyms are listed in *appendix B*.

Table 6—Size characteristics of the dominant tree species from intensive surveys within the mixed-conifer and red fir forest types.

Species	Mean DBH (cm)		Maximum DBH (cm)		Proportion of stems > 75 cm DBH (percent)	
	Mixed conifer	Red fir	Mixed conifer	Red fir	Mixed conifer	Red fir
White fir	37	47	188	114	11	17
Red fir	41	35	175	201	17	11
Incense cedar	36	—	192	—	10	—
Jeffrey pine	53	—	186	—	29	—
Sugar pine	47	—	216	—	20	—
Snags	55	51	237	175	29	23

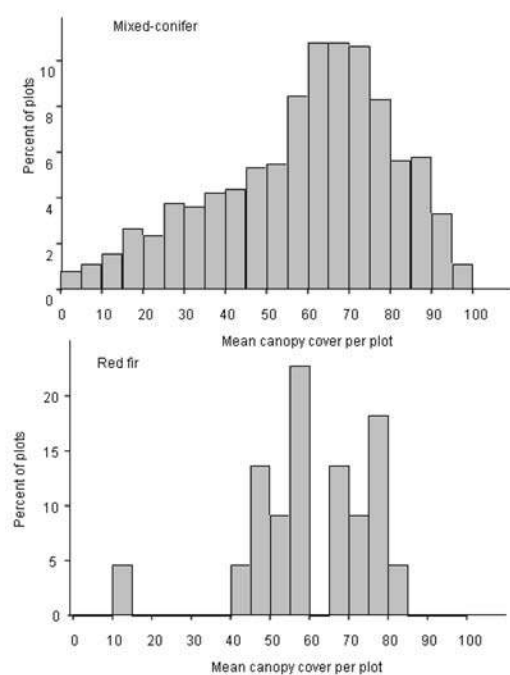


Figure 28—Mean canopy cover distribution for plots intensively surveyed within the mixed conifer and red fir portions of the forest. Means were derived from five readings taken with a moosehorn device within each plot as described in the text.

in tree clusters or, where unobstructed in gaps there are few trees. Although the mean tree basal area calculated from the fixed-radius plots was consistent with the stem map value, its standard deviation ($11.2 \text{ m}^2/\text{ha}$) was high. Values range from $0\text{--}111.6 \text{ m}^2/\text{ha}$ depending on the patch condition where each plot was taken. We calculated the number of $1/20 \text{ ha}$ plots needed to estimate a mean basal area within $3 \text{ m}^2/\text{ha}$ of the stem map value ($\alpha = 0.05$ and $\beta = 0.9$) as 19 plots. With this high sample size requirement, many forest inventories in mixed conifer may not produce accurate estimates of mean basal area. An 8.4 ha stem map shows how variable tree distribution can be (fig. 29). There are clusters of shade-tolerant white fir and incense cedar, widely spaced large Jeffrey and sugar pine, and frequent tree gaps. Mixed conifer's variable stem distribution is an inherent characteristic of its complex structure that makes it difficult to accurately measure of appropriately scale management activities (North and Oakley 2003).

Mixed-Conifer Patch Conditions

Mixed-conifer forests do not have continuous canopy cover, and vegetation is highly variable across small distances. The heterogeneous conditions of mixed conifer were analyzed to describe its different patch conditions. Based on cluster analysis of the data from the 402 gridpoints within the 18 plots selected for the Teakettle Experiment, we found four distinct patch types (closed canopy forest, mountain whitethorn patches, open gaps, and shallow soil/rock outcrops) that dominate 97 percent of the plots in the mixed-conifer forest (table 7). Preliminary microclimate and soil sampling measurements indicate these patch types have distinct resource conditions. For example, soil moisture is higher and microclimate conditions more moderate in closed canopy patches relative to gaps where surface temperatures can reach 60°C , (Ma and others 2002a) and available forms of nitrogen are concentrated in mountain whitethorn patches (Oakley and others [In press]). The apparent spatial partitioning of nitrogen, moisture, and light in different patch conditions makes successional dynamics difficult to predict in mixed conifer. The dynamics of this pattern and its response to fire and thinning disturbance have become a focal research question for the Teakettle Experiment.

Ecological Components of Mixed Conifer

Vegetation conditions directly structure microclimate, soil nutrients, and habitat structure, which in turn are fundamental influences on ecosystem productivity and diversity. Efforts to understand the pattern and scale of mixed-conifer forest have influenced the field design and structured the sampling stratifications for the Teakettle Experiment. The following sections describe conditions and species found in mixed conifer that are influenced by the pattern and composition of the forest.

Canopy Arthropods

Forest arthropods account for 70–80 percent of the vascular plant and animal species in forest ecosystems (Schowalter 2000). Because of their small size, short life spans, and high reproductive rates, arthropods are highly responsive to changes in environmental conditions, especially changes in host plant condition and density (Coley and others 1985, Mattson 1980, Mattson and Haack 1987, Schowalter and others 1986, 1999). Many species are capable of changes in density of several orders of magnitude within 1–3 years and can substantially alter forest conditions through their effects on plant growth and survival.

The capacity for insects to respond to and effect changes in ecosystem conditions has been demonstrated recently in the southern Sierra Nevada. An outbreak of the Douglas-fir tussock moth in and surrounding Kings Canyon and Sequoia National Parks during 1997–98 caused virtually complete defoliation of understory firs (Schowalter 2000). Such an extensive outbreak would probably not have

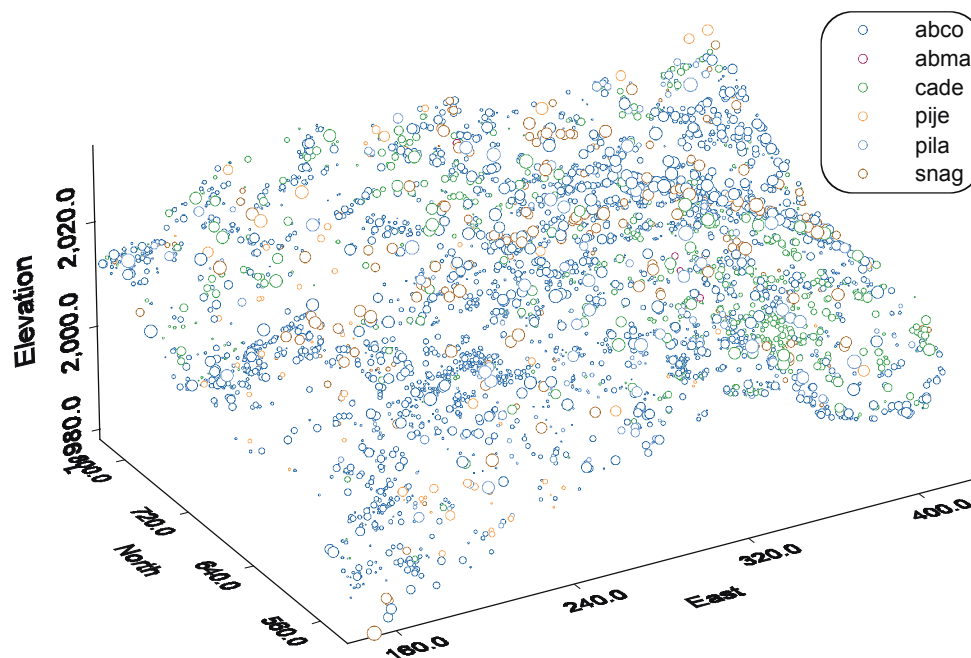


Figure 29—Stem map (8.4 ha) of Teakettle's mixed-conifer forest showing patchy distribution of stems and tree basal area. Circle size is proportional to tree DBH. Abbreviations in the legend are listed in *appendix B*.

Table 7—Characteristics of the four principal patch types within mixed conifer. Within a row, a bold value is significantly different from the other values ($p < 0.05$). Maximum soil surface temperature and moisture values were collected in early June. Values with NM were not measured.

Characteristics	Closed canopy	Shrub	Open canopy	Rock/shallow soil
Percent of mixed-conifer area	68.0	13.0	11.0	5.0
Canopy closure (percent cover)	79.0	44.0	32.0	30.0
Mountain whitethorn (percent cover)	2.0	64.0	3.0	2.0
Litter depth (cm)	5.4	3.6	0.7	2.3
Rock (percent cover)	1.6	0.6	1.1	32.0
Coarse woody debris (percent cover)	9.3	6.8	3.0	7.6
Nitrate ($\mu\text{g N/g}$)	0.8	8.1	2.2	NM
Max. soil surface temp. ($^{\circ}\text{C}$)	28.4	47.2	59.8	NM

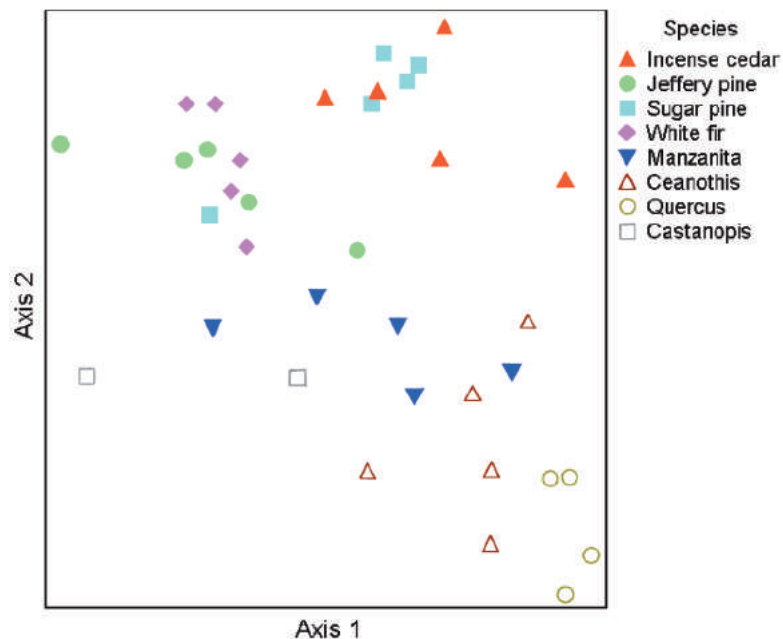
been supported in the relatively open-canopy pine and mixed-conifer forests that dominated this area before fire suppression. Moth-induced fir mortality reduces stem density toward more historic conditions (Schowalter 2000); however, the high density of standing dead trees also exacerbates the risk of catastrophic wildfire.

At Teakettle, 2 years of pre-treatment data were collected on tree- and shrub-associated arthropod communities during 1998-1999 in a subset of the plots for the Teakettle Experiment. About 100 taxa have been recorded on four overstory conifer species and three understory tree and shrub species. Data show that distinct arthropod communities occur on the different plant species, especially between overstory conifers and understory shrubs (*table 8, fig. 30*) and likely will respond differentially to thinning and fire treatments due to changes in host plant condition and density.

Table 8—Canopy and shrub invertebrate taxa with significant indicator values ($P < 0.05$). The indicator value is a product of a taxon's abundance on a particular plant species relative to its abundance on all plant species, and that taxon's frequency of occurrence in the sample units on each plant species. The result is given as a percentage of perfect indication (i.e., 100 percent) (Dufrêne and Legendre 1997).

Taxon	Indicator value	P value
Herbivores		
Geometrids (inchworms)	76	0.001
Lymantriids (tussock moth)	53	0.009
Unidentified Lepidopteran	50	0.038
Curculionids (weevils)	53	0.011
Aphids	61	0.010
Cicadlids (leafhoppers)	50	0.002
Membracids (treehoppers)	50	0.010
Unidentified Homoptera	37	0.044
Thrips	40	0.001
False spider mites	78	0.001
Predators		
Aradids (flat bugs)	60	0.009
Neuroptera (snakeflies)	85	0.001
Chacidoids (parasitic wasps)	80	0.001
Therid spiders	48	0.022
Detritivores		
Psocoptera (barklice)	51	0.026
Oribatid 4	36	0.051

Figure 30—Nonmetric dimensional scaling diagram of invertebrates by host plant species. Although there is some overlap, the general clustering of points indicates invertebrate communities tend to be distinct in different tree and shrub species.



Soil and Coarse Woody Debris Microarthropods

Microarthropod diversity and abundance were compared in soils sampled underneath closed canopy forest, in open gaps, and from coarse woody debris (CWD) in small gaps. Results represent a sub-sample of 36 soil and CWD cores taken in July of 1998. Microarthropods were extracted from soil and CWD cores taken at 8 cm depth by using high-gradient arthropod extraction (Moldenke 1994). Soil bulk density and gravimetric moisture content were also measured for each core

(fig. 31). Only decay class IV logs (Maser and others 1988) were selected for CWD sampling. All individuals from the suborders Prostigmata and Mesostigmata were pooled by suborder.

Oribatid mites were the most abundant group of soil microarthropods collected (table 9, fig. 31). Oribatid species richness in CWD and closed-canopy patches was higher than in gaps (fig. 32). Gaps were generally depauperate in terms of species richness and abundance, although two taxa (*Eremaeus* sp. 1 and *Oppia/Oppiella* morph) were more abundant in gaps than in the other patch types (table 9). Low soil moisture and low soil organic matter content, as suggested by the high bulk density (fig. 33), likely limit microarthropod activity in gaps relative to the other patch types. Abundance in closed canopy soils is likely related to higher substrate quality of litter and higher soil moisture content present underneath the canopy. Bulk density is lowest in CWD; however, the substrate quality is relatively poor compared to litter. The high moisture holding capacity of CWD likely maintains microarthropod abundance and species richness.

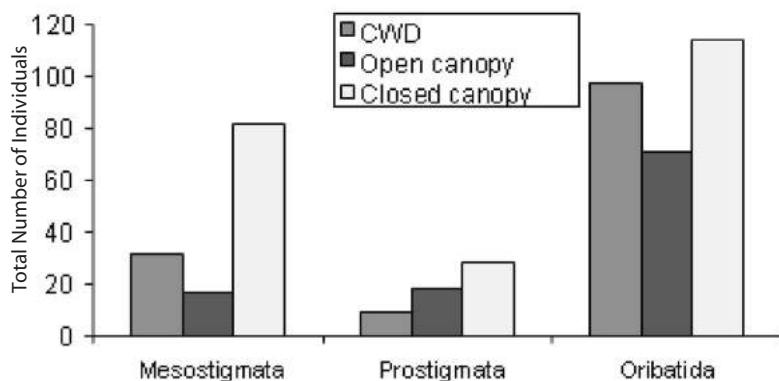


Figure 31—Acari abundance in three patch types. CWD refers to coarse woody debris.

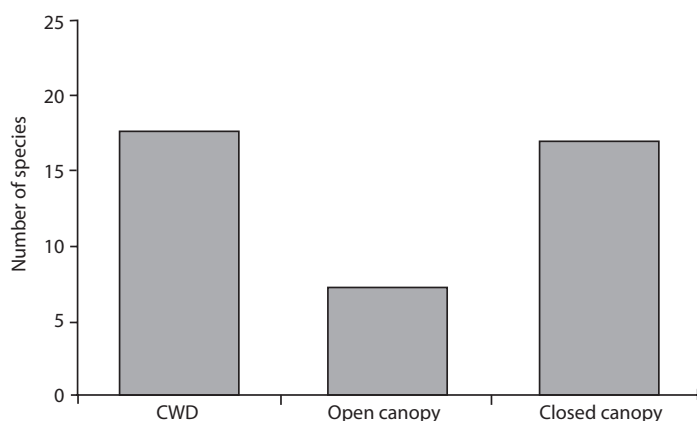


Figure 32—Oribatid species richness. CWD refers to coarse woody debris.

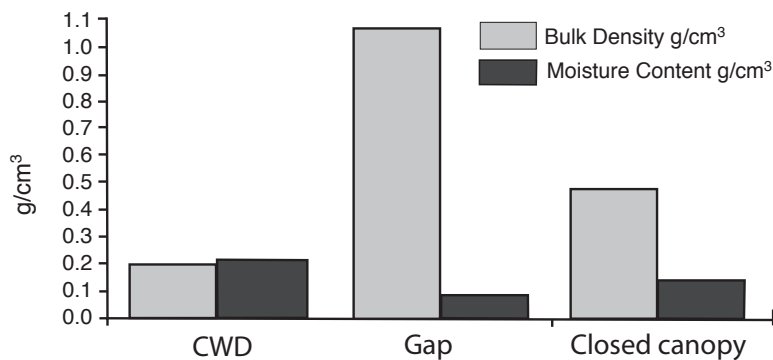


Figure 33—Large differences in bulk density and moisture content between patch types suggest organic matter content and moisture correlate with microarthropod diversity and abundance.

Table 9—*Acari abundance.*

Acari (mites) taxon	CWD ¹	Open canopy	Closed canopy	Total
<i>Mesostigmata</i>	32 ²	17	82	131
<i>Prostigmata</i>	9	18	28	55
<i>Oribatida</i>				
<i>Achipteria</i> imm	1	0	10	11
<i>Caenobelba</i> sp 1 med 600 µm	1	0	2	3
<i>Caenobelba</i> sp 2 sm 250 µm	3	0	6	9
<i>Caenobelba</i> sp 3 lg 750 µm	0	0	1	1
<i>Ceratozetes</i> sp 1 sm	1	0	0	1
<i>Ceratozetes</i> sp 2	2	0	0	2
<i>Ceratozetes</i> sp 3 med	0	0	1	1
<i>Crotonioidea</i> sp. 1	0	0	1	1
<i>Damaeioidea</i> unk	3	0	0	3
<i>Eremaeus</i> sp1 sm 600 µm	2	26	19	47
<i>Eremaeus</i> sp2 lg	0	0	14	14
<i>Eupterotegaeus</i> sp. 1	0	8	3	11
<i>Liacarus</i> sp1	0	0	1	1
<i>Liacarus</i> sp2	0	0	2	2
<i>Nanhermannia</i> imm	1	0	0	1
<i>Nanhermannoid</i> sp1	1	0	0	1
<i>Nanhermannoid</i> sp2 thinner	1	0	0	1
<i>Nanhermannoid</i> sp3stout	1	0	0	1
<i>Oppia</i> 300 µm	2	0	0	2
<i>Oppia</i> / <i>Oppiella</i> 300 µm	44	1	23	68
<i>Oppia</i> / <i>Oppiella</i> 225 µm	18	21	5	44
<i>Oribatella</i>	1	1	8	10
<i>Pterogasterine</i> sp 1.	0	0	1	1
<i>Pterogasterine</i> sp 2.	2	0	1	3
<i>Pthiracarus</i> sp 1	3	1	6	10
<i>Scheloribates</i> 400 µm	0	0	1	1
<i>Scheloribates</i> lg	1	0	0	1
<i>Scheloribates</i> med	0	0	0	0
<i>Scheloribates</i> sm	1	0	2	3
unk immature sp2 morph	0	0	3	3
unk mite 8 imm	8	4	4	16
unk <i>Oppioidea</i> < 200 µm	0	9	0	9
Total	97	71	114	
unk immature amorphic	7	157	53	217

¹ CWD refers to coarse woody debris.² Values represent the total number of individuals for all samples.

Breeding Bird Richness and Density

From 1985 through 1992, territorial bird densities were estimated using spot mapping (Anonymous 1970) on a 42-ha plot in the Teakettle Experimental Forest. The plot has been characterized as old-growth at the mixed conifer to red fir transition (Purcell and others 1992). Spot mapping involves repeated samples of all species in an area during the breeding season and produces a map of the number of bird territories and their spatial locations. The plot, 650 m on each side, was divided into a grid with transects marked at 50-m intervals. Three to four observers sampled the plot each year, completing 12 visits between May 18 and June 28. Only the most skilled observers available were selected for censusing after completing training on the songs and calls of Sierra Nevada forest birds. For each visit, the starting point was randomly located and alternate transects were walked until the whole plot was covered. Locations of all species seen or heard were mapped, including behaviors and movements of birds. Emphasis was on contemporary contacts (two or more simultaneous detections of same species individuals) and territorial interactions such as counter-singing, to help segregate territories of different males. Locations of nests were also noted. After all 12 visits were completed, territories were delineated for each species based on clusters of registrations and territorially significant interactions (table 10).

Although plot size, observer and analyst variability (Verner and Milne 1990), and habitat heterogeneity over a study plot can contribute to variability in territory numbers for many species, much of the fluctuation in these data is likely due to annual variability in species numbers. Fox sparrows and golden-crowned kinglets were the two most abundant species in all years. Dark-eyed juncos and hermit warblers were the next most abundant species, with dark-eyed juncos ranking third or fourth in 6 of the 8 years, and hermit warblers ranking third or fourth in 5 of 8 years. Nearly half of the species depend on trees for nesting substrates, using a variety of tree species and locations within trees. About one quarter of the species are cavity nesters. A relatively large number of primary cavity nesters occur here. These species, also known as excavators, excavate their own cavities in trees, snags, and logs. Secondary cavity nesters, or non-excavators, largely depend on cavities provided by excavator species, and at Teakettle they have low diversity. Species for which nesting was never verified are listed as visitors. Visitors include species with territories larger than the size of our study plot or that forage over large areas (e.g., sharp-shinned hawk, Cooper's hawk, northern goshawk, violet-green swallow), nocturnal species that are rarely seen during daylight hours and are thus not suitably censused by this method (e.g., northern saw-whet owl), vagrants that occur outside their normal breeding habitat (Wilson's warbler) or current range (Swainson's thrush), species that move upslope after breeding at lower elevations (e.g., house wren, orange-crowned warbler), and nomadic species (red crossbills).

Table 10—Number of territories for birds observed at Teakettle from 1985-1992 within a 42 ha survey plot.

Common name	Scientific name	Mean number of territories (S.D.)	
Primary cavity nesters			
Red-breasted Sapsucker	<i>Sphyrapicus ruber</i>	2.9	(0.9)
Hairy Woodpecker	<i>Picoides villosus</i>	1.4	(0.9)
White-headed Woodpecker	<i>Picoides albolarvatus</i>	4.0	(1.0)
Northern Flicker	<i>Colaptes auratus</i>	1.1	(0.6)
Pileated Woodpecker	<i>Dryocopus pileatus</i>	0.9	(0.4)
Red-breasted Nuthatch	<i>Sitta canadensis</i>	17.9	(3.5)
Secondary cavity nesters			
Northern Pygmy-Owl	<i>Glaucidium gnoma</i>	0.4	(0.4)
Mountain Chickadee	<i>Poecile gambeli</i>	9.8	(3.1)
Other cavity nesters			
Vaux's Swift	<i>Chaetura vauxi</i>	0.1	(0.2)
Brown Creeper	<i>Certhia americana</i>	7.8	(3.7)

Common name	Scientific name	Mean number of territories (S.D.)	
Tree nesters			
Band-tailed Pigeon	<i>Columba fasciata</i>	0.2	(0.3)
Calliope Hummingbird	<i>Stellula calliope</i>	0.3	(0.5)
Olive-sided Flycatcher	<i>Contopus cooperi</i>	0.1	(0.2)
Western Wood-Pewee	<i>Contopus sordidulus</i>	0.5	(0.7)
Hammond's Flycatcher	<i>Empidonax hammondi</i>	14.8	(5.1)
Cassin's Vireo	<i>Vireo cassinii</i>	2.4	(3.7)
Warbling Vireo	<i>Vireo gilvus</i>	1.8	(1.8)
Steller's Jay	<i>Cyanocitta stelleri</i>	3.1	(2.2)
Common Raven	<i>Corvus corax</i>	0.6	(0.3)
Golden-crowned Kinglet	<i>Regulus satrapa</i>	40.8	(20.8)
Hermit Thrush	<i>Catharus guttatus</i>	5.3	(2.2)
American Robin	<i>Turdus migratorius</i>	2.8	(1.2)
Yellow-rumped Warbler	<i>Dendroica coronata</i>	11.4	(6.0)
Hermit Warbler	<i>Dendroica occidentalis</i>	20.6	(13.1)
Western Tanager	<i>Piranga ludoviciana</i>	11.7	(5.0)
Purple Finch	<i>Carpodacus purpureus</i>	0.1	(0.2)
Cassin's Finch	<i>Carpodacus cassinii</i>	0.3	(0.4)
Pine Siskin	<i>Carduelis pinus</i>	1.1	(1.7)
Evening Grosbeak	<i>Coccothraustes vespertinus</i>	1.1	(0.9)
Shrub nesters			
Dusky Flycatcher	<i>Empidonax oberholseri</i>	16.6	(3.3)
MacGillivray's Warbler	<i>Oporornis tolmiei</i>	10.8	(4.6)
Green-tailed Towhee	<i>Pipilo chlorurus</i>	0.6	(0.7)
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	1.1	(0.2)
Ground nesters			
Mountain Quail	<i>Oreortyx pictus</i>	3.3	(1.8)
Winter Wren	<i>Troglodytes troglodytes</i>	2.6	(1.5)
Townsend's Solitaire	<i>Myadestes townsendi</i>	2.9	(2.1)
Nashville Warbler	<i>Vermivora ruficapilla</i>	3.6	(3.6)
Fox Sparrow	<i>Passerella iliaca</i>	47.4	(17.3)
Dark-eyed Junco	<i>Junco hyemalis</i>	21.3	(5.5)
Other nesters			
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	0.8	(1.1)
Brown-headed Cowbird	<i>Molothrus ater</i>	1.2	(0.4)
Visitors (possible nesters)			
Sharp-shinned Hawk	<i>Accipiter striatus</i>	--	--
Cooper's Hawk	<i>Accipiter cooperii</i>	--	--
Northern Goshawk	<i>Accipiter gentilis</i>	--	--
Red-tailed Hawk	<i>Buteo jamaicensis</i>	--	--
Blue Grouse	<i>Dendragapus obscurus</i>	--	--
Northern Saw-whet Owl	<i>Aegolius acadicus</i>	--	--
Swainson's Thrush	<i>Catharus ustulatus</i>	--	--
Yellow Warbler	<i>Dendroica petechia</i>	--	--
Wilson's Warbler	<i>Wilsonia pusilla</i>	--	--
Spotted Towhee	<i>Pipilo maculatus</i>	--	--
Chipping Sparrow	<i>Spizella passerina</i>	--	--
Red Crossbill	<i>Loxia curvirostra</i>	--	--
Visitors			
American Kestrel	<i>Falco sparverius</i>	--	--
Black Swift	<i>Cypseloides niger</i>	--	--
White-throated Swift	<i>Aeronautes saxatalis</i>	--	--
Anna's Hummingbird	<i>Calypte anna</i>	--	--
Clark's Nutcracker	<i>Nucifraga columbiana</i>	--	--
Violet-green Swallow	<i>Tachycineta thalassina</i>	--	--
White-breasted Nuthatch	<i>Sitta carolinensis</i>	--	--
House Wren	<i>Troglodytes aedon</i>	--	--
Western Bluebird	<i>Sialia mexicana</i>	--	--
Orange-crowned Warbler	<i>Vermivora celata</i>	--	--
Black-throated Gray Warbler	<i>Dendroica nigrescens</i>	--	--
Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	--	--
Lesser Goldfinch	<i>Carduelis psaltria</i>	--	--
Lawrence's Goldfinch	<i>Carduelis lawrencei</i>	--	--

Snag Survey

Snags are an important habitat feature of coniferous forests, and many wildlife species depend on them for foraging, nesting, denning, roosting, and resting. In 1988, in conjunction with the breeding bird survey, a study was initiated at Teakettle to examine species, size, density, turnover of decay classes, and use by birds of snags in a mixed-conifer/true-fir transitional forest. On the 42 ha plot, all snags were tagged in every other grid square, resulting in a 21 ha sample. Snags were revisited every other year from 1991 through 1997, and new snags were tagged as they appeared.

White fir snags were numerically dominant, followed by red fir, Jeffrey pine, sugar pine, and incense cedar (fig. 34). There are a high number of large-diameter snags, which are important to wildlife because of their longevity (Raphael and Morrison 1987) and use by cavity-nesting birds (Bull 1986, Zarnowitz and Manuwal 1985). Over all diameter classes, snags in decay classes 1 and 2 (Cline and others 1980) were most abundant (fig. 35). Smaller-diameter snags were predominantly found in decay classes 1 or 2, while large-diameter snags were more often class 4. In Teakettle's unmanaged old growth conditions, there was an average of nearly 20 snags >54 cm dbh per ha (fig. 35).

Of cavity nests found in live or dead trees, more than half of the nests of the following species were found in snags: red-breasted sapsuckers (*Sphyrapicus ruber*), hairy woodpeckers (*Picoides villosus*), white-headed woodpeckers (*Picoides albolarvatus*), northern flickers (*Colaptes auratus*), mountain chickadees (*Poecile gambeli*), and red-breasted nuthatches (*Sitta canadensis*).

Northern Flying Squirrels and Truffles

The northern flying squirrel (*Glaucomys sabrinus*) is an important component of the trophic structure in mixed conifer because it relies on truffles for 80 to 90 percent of its diet (Maser and others 1985, McKeever 1960), and it is the principle prey of the California spotted owl (*Strix occidentalis occidentalis*) (Laymon 1988, Verner and others 1992). Results from two field seasons of trapping and radio telemetry work indicate flying squirrel densities at Teakettle (0.64 squirrels/ha \pm std 0.98) are lower than reported in other western forests (Carey and others 1992). Flying squirrel density is positively correlated with shrub cover and number of large snags (dbh > 100 cm; $p = 0.02$). Squirrel densities are also significantly ($p = 0.04$) higher in trapping grids closer to streams than in upland grids. Den locations are predominantly (74 percent) in large snags (mean dbh = 107 cm) or trees with dead tops and are found close to streams (mean distance 50 m).

Fecal analysis of the northern flying squirrel's diet indicates truffles are a principle food source. The most common truffle genera in fecal samples by season are: *Rhizopogon* spp (96 percent early summer and 92 percent late summer), *Melanogaster* spp (88 percent and 16 percent), *Leucophleps* spp (68 percent and 0 percent), and *Gauteria* spp (36 percent and 76 percent). These species were also common in truffle samples collected in quadrats as part of a separate study at Teakettle. Several truffle species, most notably *Hysterangium* spp., were common in the quadrats, but uncommon or absent in fecal samples.

For 4 years, truffles at Teakettle were sampled monthly during snow-free periods (May to October) in 50 four m² plots (North 2002). Dry weight biomass of all truffles by month was 0.2 kg/ha in May, 2.4 kg/ha in June, 2.2 kg/ha in July, 0.4 kg/ha in August, 0.3 kg/ha in September, and 0.1 kg/ha in October. Sampling was split between upland and riparian areas. Riparian areas have 62 percent and 400 percent more biomass and species richness of truffles, respectively, than upland areas, and truffles persist longer in riparian plots (through all 5 months of sampling, compared to 3 months on upland areas). A total of 32 different species have been collected.

Figure 34—Number of snags per ha by species for 6 surveys from 1988 to 1997. See appendix B for common names of species.

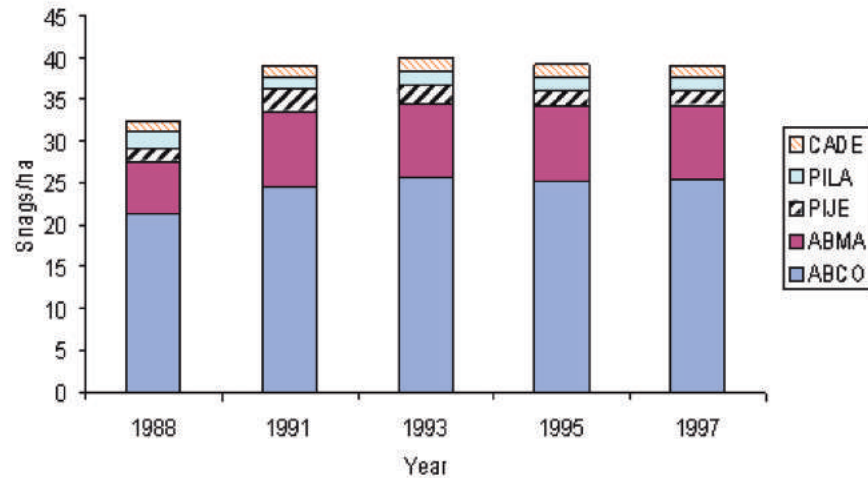
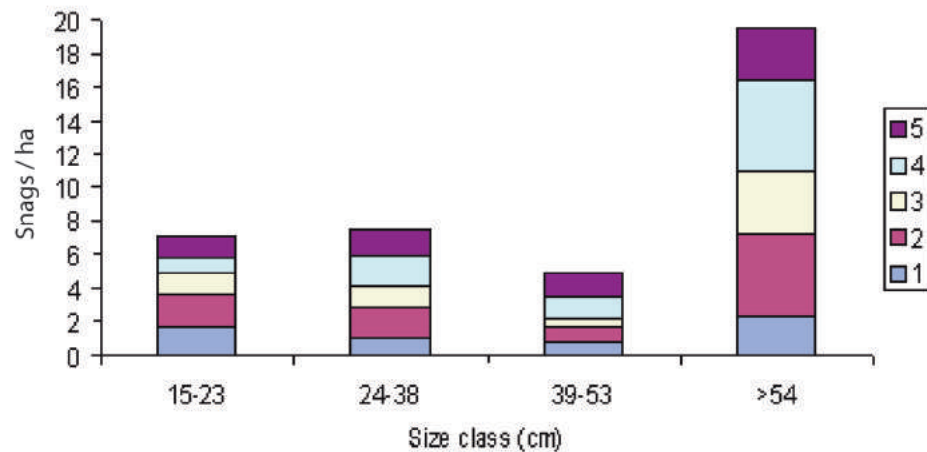


Figure 35—Number of snags per ha by 4 size and 5 decay classes in 1997. Decay classes are based on Cline and others (1980).



Lichens

Although often overlooked, lichen epiphytes can be an important ecological component of forests. In old-growth forests of the Pacific Northwest, lichens are known to contribute significantly to biomass production and nutrient cycling, and play a critical role in the food webs of invertebrates and vertebrates alike (FEMAT 1993). In spite of such importance, we know little about Sierra Nevada lichen community composition or response to the widespread management practice of mechanical thinning. We do know that lichens are highly susceptible to changes in microclimate and habitat destruction (Gilbert 1977), making them especially vulnerable to forestry practices (Renhorn and others 1997).

One particular concern is the effect management practices may have on lichens as a source of winter food and nesting material for small mammals. The California Spotted Owl (*Strix occidentalis occidentalis*) relies on the northern flying squirrel (*Glaucomys sabrinus*) for most of its diet (USDA 1993). Lichen epiphytes constituted more than 90 percent of flying squirrel diet in January through May in red and white fir forests of northeastern California (McKeever 1960), and were the predominant food of flying squirrels from December through June in northeastern Oregon (Maser and others 1985). Three other regional species listed by the Forest Service as “sensitive”—the northern goshawk, marten, and fisher (USDA 1993), are also principal predators of flying squirrels (Powell 1993, Wells-Gosling 1985) and Douglas’ squirrels (Carey 1991, Hargis and McCullough 1984). Both of these prey use lichen epiphytes in nest construction (Carey 1991, FEMAT 1993, Hayward and Rosentreter 1994).

Table 11—The more conspicuous lichens of the Teakettle Experimental Forest.¹

Species	Habitat	Observations
<i>Ahtiana sphaerospora</i> (Müll. Arg.) Goward	Epiphytic	On uppermost boles and branches of conifers
<i>Bryoria fremontii</i> (Tuck.) Brodo & D. Hawk.	Epiphytic	Common on red fir sprays
<i>Dermatocarpon reticulatum</i> H. Magn.	Epilithic	On granite boulders
<i>Hydrothyria venosa</i> J. L. Russell ²	Aquatic	Common in streams
<i>Hypogymnia imshaugii</i> Krog	Epiphytic	Common on fir and pine, especially decorticated branches
<i>Letharia columbiana</i> (Nutt.) J.W. Thomson	Epiphytic	Common on higher branches of fir and pine
<i>L. vulpina</i> (L.) Hue	Epiphytic	Dominant on fir and pine boles; also found on higher branches
<i>Melanelia elegantula</i> (Zahlbr.) Essl.	Epiphytic	Common on fir and pine, especially decorticated branches

¹ Vouchers are in the herbarium of Tom Rambo, Department of Environmental Horticulture, University of California, Davis.

² Red-listed by the California Lichen Society

Although lichen and epiphyte communities of the Teakettle Experimental Forest are dominated by two species of *Letharia* (table 11), another common lichen epiphyte, *Bryoria fremontii*, may have more important ecological linkages. As a winter survival food for northern flying squirrels, *Bryoria's* abundance may be particularly important when seasonal snowpack makes the squirrel's main food, truffles, unavailable.

The lichen research at Teakettle is focused on the growth response of *B. fremontii* to the thinning treatments. The study will examine how the silvicultural treatments affect canopy microclimate conditions, and how those in turn may influence the growth response of *B. fremontii*. The research will also determine which tree species and habitat conditions are most important for establishment and growth of *Bryoria*, and improve our knowledge of epiphyte ecology in Sierra Nevada red fir and mixed-conifer forests.

Pathogens and Insects at Teakettle

Pathogens and insects ("pests") at Teakettle Experimental Forest have been censused in 12 four-ha plots (table 12). Pest species have been grouped into three functional groups that may contribute to gap formation and stand heterogeneity: dwarf mistletoe, root disease, and bark beetles. A single agent, however, rarely causes tree mortality. Pest complexes (e.g., root diseases/bark beetles; dwarf mistletoe/bark beetles, or root diseases/dwarf mistletoe/bark beetles), sometimes in conjunction with abiotic stress factors (e.g., drought), are often responsible for mortality (Ferrell 1996, Filip and Goheen 1982, Lundquist 1995, Worrall and Harrington 1988). Although both root disease and dwarf mistletoe can and do kill trees directly, most often the final cause of death is bark beetles attacking trees stressed by these diseases (Goheen and Hansen 1993, Paine and Baker 1993). The chronic nature of tree mortality in disease gaps may provide sufficient habitat to support resident bark beetle populations (Goheen and Hansen 1993). These low-level populations of beetles may then serve as focal points for large-scale bark beetle outbreaks during years when forests are subjected to exogenous stresses such as drought (Goheen and Hansen 1993, Mattson and Haack 1987, Waring, 1987). In the Sierra, mature trees rarely die solely from predisposing factors such as drought or competition (Rizzo and others 2000, Waring and others 1987). In the absence of pest pressure, most trees can survive through droughts unless the drought is very extended (Waring 1987).

Table 12—Pathogens and insects identified to date in Teakettle's mixed-conifer forest

Host	Pest	
<i>Abies concolor</i> (white fir)	<i>Arceuthobium abietinum</i> f. sp. <i>concoloris</i> (dwarf mistletoe)	(ab) ¹
	<i>Melampsorella caryophyllacearum</i> (broom rust)	(b)
	<i>Heterobasidion annosum</i> (root disease)	(ab)
	<i>Phaeolus schweinitzii</i> (root disease)	(ab)
	<i>Echinodontium tinctorium</i> (trunk rot)	(b)
	<i>Scolytus ventralis</i> (bark beetle)	(ab)
	<i>Orygia pseudotsugata</i> (Douglas fir- tussock moth)	(b)
<i>Abies magnifica</i> (red fir)	<i>Arceuthobium abietinum</i> f. sp. <i>magnificae</i> (dwarf mistletoe)	(ab)
	<i>Melampsorella caryophyllacearum</i> (broom rust)	(b)
	<i>Heterobasidion annosum</i> (root disease)	(ab)
	<i>Echinodontium tinctorium</i> (trunk rot)	(b)
	<i>Scolytus ventralis</i> (bark beetle)	(ab)
	<i>Orygia pseudotsugata</i> (Douglas fir- tussock moth)	(b)
<i>Calocedrus decurrens</i> (incense cedar)	<i>Phoradendron juniperinum</i> subsp. <i>libocedri</i> (true mistletoe)	(b)
	<i>Gymnosporangium libocedri</i> (broom rust)	(b)
	<i>Oligoporus amarus</i> (trunk rot)	(b)
	no major insects	
<i>Pinus jeffreyi</i> (Jeffrey pine)	<i>Arceuthobium campylopodum</i> (dwarf mistletoe)	(ab)
	<i>Elytroderma deformans</i> (needle cast)	(b)
	<i>Dendroctonus jeffreyi</i> (bark beetle)	(a)
	<i>Dendroctonus valens</i> (bark beetle)	(b)
	<i>Ips</i> spp. (bark beetles)	(b)
<i>Pinus lambertiana</i> (sugar pine)	<i>Cronartium ribicola</i> (white pine blister rust)	(a)
	<i>Dendroctonus ponderosae</i> (bark beetles)	(a)
	<i>Dendroctonus valens</i> (bark beetles)	(b)
	<i>Ips</i> spp. (bark beetles)	(b)

¹ **a** is major cause of mortality, and **b** is primarily cause of growth loss; may cause mortality under certain conditions

At Teakettle, white fir, red fir, and Jeffrey pine are each infected by a host-specific species of dwarf mistletoe, and incense cedar is attacked by a species of true mistletoe. Dwarf mistletoe generally doesn't kill fir directly (Parmeter and Scharpf 1963). The parasite will infect both tree branches and stems, which then can be colonized by wood decay fungi leading to breakage at the point of infection (Parmeter and Scharpf 1963). *Arceuthobium campylopodium* is one of the most damaging forest pests in the western United States, and Jeffrey pine is considered one of the most susceptible pines (Hawksworth and Wiens 1996). While infection can predispose trees to attack by bark beetles, *A. campylopodium* can occasionally kill trees directly.

The primary root disease at Teakettle is *Heterobasidion annosum*. Two host-specialized forms are found in the Sierra Nevada: the "pine-type" primarily infects *Pinus* spp., *Juniperus* spp., and incense-cedar; the "fir-type" is common on *Abies* spp. and giant sequoia (Harrington and others 1989, Otrosina and others 1992). To date, surveys have identified only the fir-type of *H. annosum* at Teakettle. After tree death, *H. annosum* is capable of living as a saprobe, slowly decaying the underground root wood for a number of years (Stenlid and Redfern 1998). Because of this saprobic phase, the fungus can infect regenerating trees within a gap.

Each of the major conifer species, except for incense-cedar, has a fairly host-specific bark beetle associated with it. *Scolytus ventralis*, which attacks both red

and white fir, is the only beetle that attacks more than one host on the site. Of the three most common beetles found at Teakettle, *Dendroctonus ponderosae* and *D. jeffreyi* are considered primary bark beetles, while *S. ventralis* is considered to be a less aggressive or secondary bark beetle (Paine and others 1997, Raffa and others 1993). Primary beetles are near-obligate parasites that attack and kill trees by mass colonization, while secondary beetles are considered to be facultative parasites that mostly colonize very stressed or dead trees (Raffa and others 1993). Outbreaks of secondary beetles may kill healthy trees, but these outbreaks are usually less extensive compared to the primary bark beetles (Paine and others 1997).

White pine blister rust (*Cronartium ribicola*) is infecting sugar pine at Teakettle, but its impact appears to be largely confined to smaller seedlings and saplings (Maloney 2000). To date, large overstory pine mortality has not been observed and cone-bearing branches appear to die before the fungus has had a chance to reach the bole. Comprehensive surveys suggest blister rust is limited to moist areas and patches of *Ribes* at Teakettle (Maloney 2000).

Mycorrhizae

Preliminary analysis of the underground mycorrhizal community associated with white fir suggests that species richness is very high at Teakettle. In July 1999, 72 soil cores (2 cm diameter by 40 cm depth) were taken across Teakettle and stratified by depth. Mycorrhizal root tips were isolated from the soil, and 90 species-level taxa were identified by molecular analysis. Frequency across the plots was combined with dry biomass of the mycorrhizal root tips to give a relative importance value for each taxon (fig. 36). The community is relatively even and is less dominated by a few species than other forest systems. The data gathered so far, however, may underestimate richness because at the time of sampling, the organic layer of the soil was very dry, and very little ectomycorrhizal activity was seen. Although there are few clear dominants and many infrequent species, *Cenococcum geophilum* was the most important taxon. It is one of the most ubiquitous species worldwide and seems to have increased importance in harsh environments. A russuloid taxon, which has not been identified to species, was also very frequent but not very abundant. Members of the Russulaceae are commonly dominant in California's mature and old-growth forests. The availability of many mycorrhizal host species coupled with the heterogeneity of the environment are potential key components of species richness and will be examined in future research.

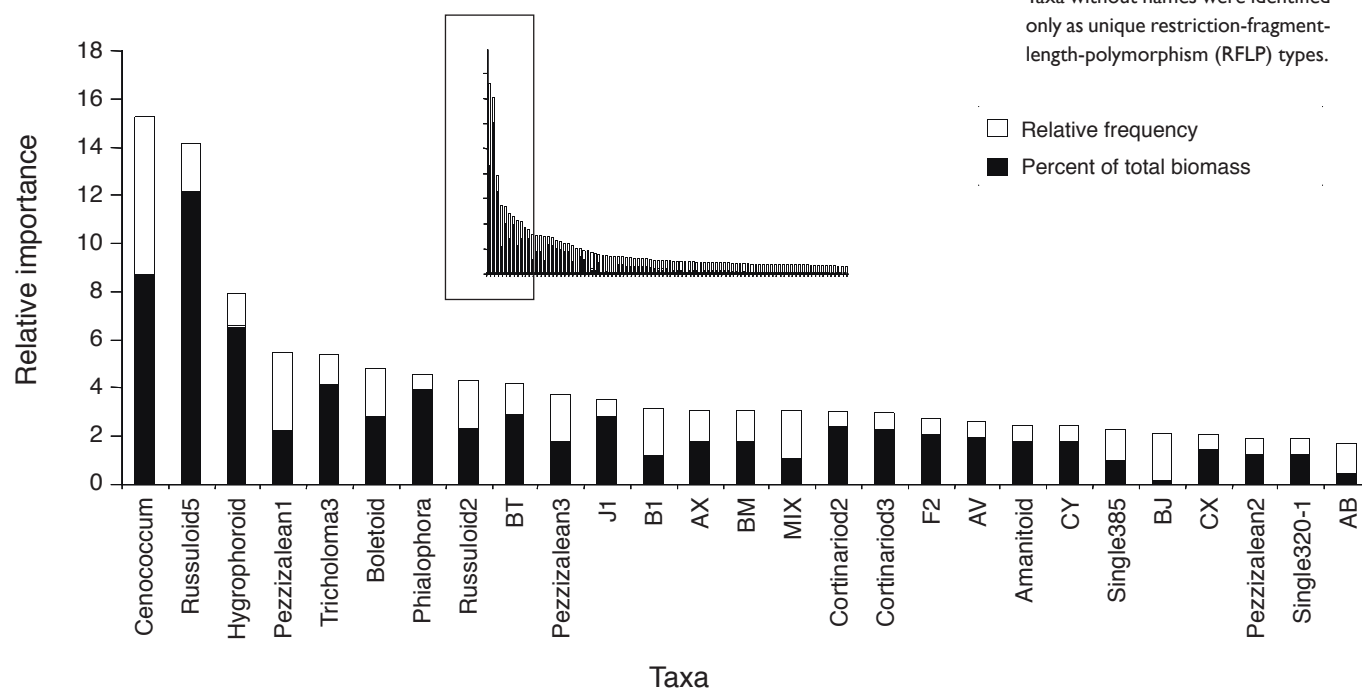
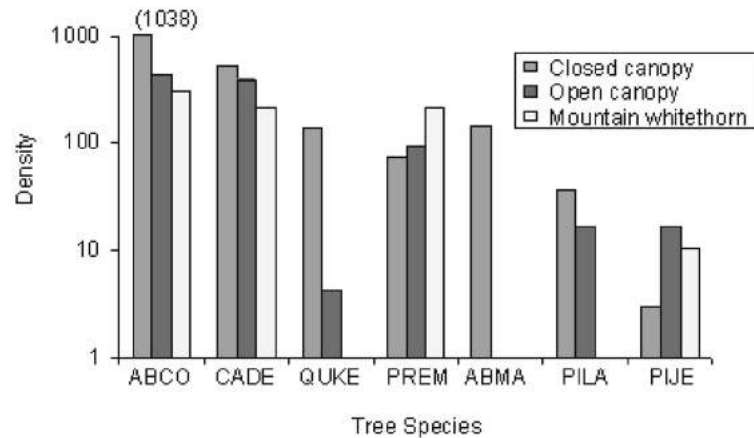


Figure 36—Mycorrhizal community of white fir with taxa ranked by importance. The main chart only shows the most common taxa inside the box of the inset graph and excludes the many taxa that were much less frequent and abundant. Taxa without names were identified only as unique restriction-fragment-length-polymorphism (RFLP) types.

Figure 37—Density of tree seedlings and saplings (>5 cm tall and <5 cm dbh) per hectare by species and patch type. Note that the y-axis is logarithmic. Tree species acronyms on the x-axis are listed in *appendix B*.



Tree Seedlings and Soil Moisture

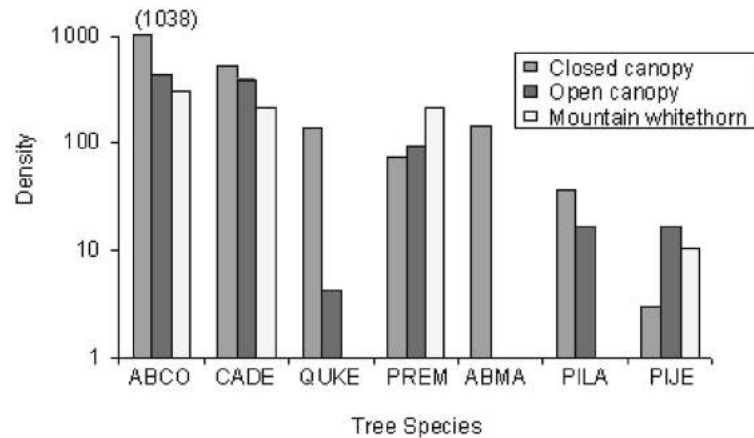
To date, tree seedlings and saplings (trees >5 cm tall and <5 cm DBH) were systematically surveyed in 25 m² plots established at 268 of the 402 gridpoints. The survey found the following species in declining order of abundance: white fir, incense cedar, black oak, bitter cherry, red fir, sugar pine, and Jeffrey pine. Regeneration varies by patch type: most species were most abundant in closed-canopy forest and had fewer individuals in gaps and the least in mountain whitethorn patches (*fig. 37*). The exceptions were bitter cherry, which was most abundant in snowberry patches; Jeffrey pine, which was most abundant in open areas; and black oak, which was most abundant in bedrock-dominated areas (not shown).

Monthly snow-free measurements of soil moisture have been collected for two years at the 402 gridpoints within the 18 plots of the Teakettle Experiment (*appendix A*), using time-domain reflectometry (Gray and Spies 1995). Soil moisture is measured in the upper soil layer (0-15 cm) at all gridpoints, and additionally between 0-45 cm at nine points in each plot. Pre-treatment measurements of soil moisture found a constant rate of drying of soils in the upper 45 cm during the growing season. Volumetric moisture values soon after snowmelt (mid-May) average 18 percent (with a range of 12-33 percent), and decline to 14 percent (6-47 percent) by early July, and to 10 percent (5-28 percent) by October. The high variability of moisture is likely caused by differences in topography and depth to bedrock and is probably important in determining the location and speed of vegetation response to disturbance.

Summary

The Teakettle Experimental Forest encompasses several forest communities typical of the western slopes of the Sierra Nevada. Forest composition appears to be strongly influenced by elevation, topography and soil depth. Between 1,900 and 2,300 m, mixed-conifer forest predominates, although red fir is locally common along riparian corridors that may be cold air drainages. Jeffrey pine is dominant on ridge tops with shallow soil. Red and white fir dominate tree density and basal area at Teakettle, but Jeffrey and sugar pine are often the largest individuals and are good indicators of drier and warmer mixed-conifer conditions. Mixed conifer is a forest of high contrast with open patches having high soil surface temperatures and low soil moisture, and closed-canopy forest with a relatively deep litter layer and lower understory light levels. Distinct shrub patches are common and the most dominant shrub, mountain whitethorn, may be an important resource island of available nitrogen in these forests.

Figure 37—Density of tree seedlings and saplings (>5 cm tall and <5 cm dbh) per hectare by species and patch type. Note that the y-axis is logarithmic. Tree species acronyms on the x-axis are listed in *appendix B*.



Tree Seedlings and Soil Moisture

To date, tree seedlings and saplings (trees >5 cm tall and <5 cm DBH) were systematically surveyed in 25 m² plots established at 268 of the 402 gridpoints. The survey found the following species in declining order of abundance: white fir, incense cedar, black oak, bitter cherry, red fir, sugar pine, and Jeffrey pine. Regeneration varies by patch type: most species were most abundant in closed-canopy forest and had fewer individuals in gaps and the least in mountain whitethorn patches (*fig. 37*). The exceptions were bitter cherry, which was most abundant in snowberry patches; Jeffrey pine, which was most abundant in open areas; and black oak, which was most abundant in bedrock-dominated areas (not shown).

Monthly snow-free measurements of soil moisture have been collected for two years at the 402 gridpoints within the 18 plots of the Teakettle Experiment (*appendix A*), using time-domain reflectometry (Gray and Spies 1995). Soil moisture is measured in the upper soil layer (0-15 cm) at all gridpoints, and additionally between 0-45 cm at nine points in each plot. Pre-treatment measurements of soil moisture found a constant rate of drying of soils in the upper 45 cm during the growing season. Volumetric moisture values soon after snowmelt (mid-May) average 18 percent (with a range of 12-33 percent), and decline to 14 percent (6-47 percent) by early July, and to 10 percent (5-28 percent) by October. The high variability of moisture is likely caused by differences in topography and depth to bedrock and is probably important in determining the location and speed of vegetation response to disturbance.

Summary

The Teakettle Experimental Forest encompasses several forest communities typical of the western slopes of the Sierra Nevada. Forest composition appears to be strongly influenced by elevation, topography and soil depth. Between 1,900 and 2,300 m, mixed-conifer forest predominates, although red fir is locally common along riparian corridors that may be cold air drainages. Jeffrey pine is dominant on ridge tops with shallow soil. Red and white fir dominate tree density and basal area at Teakettle, but Jeffrey and sugar pine are often the largest individuals and are good indicators of drier and warmer mixed-conifer conditions. Mixed conifer is a forest of high contrast with open patches having high soil surface temperatures and low soil moisture, and closed-canopy forest with a relatively deep litter layer and lower understory light levels. Distinct shrub patches are common and the most dominant shrub, mountain whitethorn, may be an important resource island of available nitrogen in these forests.

Although Teakettle's mixed conifer is old growth, tree and snag basal area and log volume are low compared to other western old-growth forests. This is probably due to the patchy nature of mixed-conifer ecosystems in the southern Sierra Nevada. Sample plots that fell entirely within a tree group have a basal area and density typical of productive Pacific Northwest old growth, while gap plots may have few if any trees. These gaps have remained at Teakettle despite decades of fire suppression. This gap persistence is unusual in productive forests where trees often colonize available growing space and strongly influence microclimate conditions. The lack of snags and tree regeneration in most of the gaps indicates they have probably been gaps for several decades and do not appear to be shrinking. We do not know what mechanism is maintaining these gaps but suspect that shallow, coarse-textured soils, and high soil surface temperatures are important influences. Soil moisture holding capacity probably significantly influences the location and growth of trees because summer survival largely depends on a site's water reservoirs from the winter snowpack. Some of the forest's gap pattern appears to result from the geomorphic template (i.e., shallow depth to bedrock). Some of the larger gaps, however, have deep soils. Plant colonization in these openings may be limited by the high surface temperatures and lack of shade.

Growing conditions in Sierra forests have high temporal variability with strong seasonal and annual weather changes that affect plant establishment and growth. Almost all precipitation occurs in the winter; and soil moisture available to plants is determined by snow pack depth, the speed at which it melts, and substrate water-holding capacity. Plants with shallow roots may experience drought conditions within a month of being uncovered from the winter snow pack. El Niño and La Niña events produce extreme annual fluctuations in snow conditions. In 1998 after an El Niño winter, snow melted out of Teakettle 8 weeks later than the previous year, and even through October many soil moisture samples did not drop below 20 percent that year. Within the brief 30-year record from nearby Cliff Camp, annual snow depth varied by up to tenfold.

The transition from mixed-conifer to red fir forest produces a fundamental change in forest structure and pattern. On average, red fir forests have higher tree and snag basal area and greater log volume than mixed conifer. Red fir forests are less variable than mixed conifer with fewer gaps, lower tree species richness, and higher canopy cover. The shift from mixed conifer to red fir includes the loss of Jeffrey pine, sugar pine, and incense cedar, but the main transition is from white fir to red fir dominance. The transition may correspond to tree response to snow pack conditions. Several studies found white fir and red fir seedlings have similar ecophysiological requirements during the growing season but that the transition to red fir dominance may relate to snowpack tolerance (Barbour and others 1990, 1991; Pavlik and Barbour 1991). The ecotone between the forests corresponds to the mean freezing level during December to March storms, which is the elevation at which snow pack depth substantially increases over small elevation increases. Royce and Barbour (2001a, b) have suggested that the red fir ecotone can be modeled based on timing of snow pack melt, slope aspect, and soil water storage capacity. The higher number of red fir that we found in cool riparian areas relative to other mixed-conifer forests may be a reflection of these factors. Teakettle's riparian areas have a much deeper snow pack than adjacent upland forest, and during the spring melt, snow often persists for 2 to 3 weeks longer.

As a relatively pristine old-growth forest, Teakettle may serve as a useful standard to gauge the effects of forest management practices in other areas. For example, there has been considerable debate about the number of large trees per acre that would classify a stand as old growth, and whether a stand could have a "surplus" of large trees that could be thinned (USDA 2001). The size criteria often used is 30" dbh (76.2 cm). The density of these trees at Teakettle is fairly high, averaging 39 and 43 stems/ha in mixed conifer and red fir, respectively. These densities suggest big trees are underrepresented by current stand conditions in

most Sierra forests. Furthermore, the scale at which stand structures are measured can skew estimates of basal area and density. Measurements taken in tree clusters will overestimate the number of large trees present across the matrix of gaps and tree groups that characterize mixed conifer.

Much of the information from the Teakettle Experiment studies is preliminary, but all of the research to date indicates high species richness and a complex community that is influenced by patch structure, composition, microclimate, and nutrient conditions.

Plants are the building blocks of terrestrial ecosystems, and their composition establishes a scaffold of structure that influences many ecological processes. The Teakettle Experiment will continue to explore the connection between composition, structure, and function through long-term measurements of the cascading effects of fire and thinning restoration treatments on ecosystem processes in Sierra mixed conifer.

References

- Anonymous. 1970. **Recommendations for an international standard for a mapping method in bird census work**. In: Svensson, S., ed. Bird census work and environmental monitoring. Bull. Ecol. Res. Comm. 9. Stockholm: Swedish National Scientific Research Council; 49-52.
- Barbour, Michael G. 1988. **California upland forests and woodlands**. In: Barbour, Michael G.; Billings, W. D., eds. North American terrestrial vegetation. New York: Cambridge University Press; 131-164.
- Barbour, Michael G.; Berg, Neil H.; Kittel, George F.; Kunz, Michael E. 1991. **Snowpack and the distribution of a major vegetation ecotone in the Sierra Nevada of California**. Journal of Biogeography 18: 141-149.
- Barbour, M. G.; Pavlik, B. M.; Antos, J. A. 1990. **Seedling growth and survival of red and white fir in a Sierra Nevada ecotone**. American Journal of Botany 77: 927-938.
- Barbour, Michael G.; Woodward, Roy A. 1985. **The Shasta red fir forest of California**. Canadian Journal of Forest Research 15: 570-576.
- Belbin, L.; McDonald, C. 1993. **Comparing three classification strategies for use in ecology**. Journal of Vegetation Science 4: 341-348.
- Berg, Neil H. 1990. **Experimental forests and ranges: Field research facilities of the Pacific Southwest Research Station**. Gen. Tech. Rep. PSW-GTR-119. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 67 p.
- Bull, Evelyn L. 1986. **Resource partitioning among woodpeckers in northeastern Oregon**. Moscow, ID: University of Idaho; 109 p. Ph.D. dissertation.
- Bull, Evelyn L.; Parks, Catherine G.; Torgersen, Torolf R. 1997. **Trees and logs important to wildlife in the interior Columbia River Basin**. Gen. Tech. Rep. PNW-GTR-391. Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 55 p.
- Carey, Andrew B. 1991. **The biology of arboreal rodents in Douglas-fir forests**. Gen. Tech. Rep. PNW-GTR-276. Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 46 p.
- Carey, Andrew B.; Horton, Scott P.; Biswell, Brian L. 1992. **Northern spotted owls: Influence of prey base and landscape character**. Ecological Monographs 62: 223-250.
- Cline, Steven P.; Berg, Alan B.; Wright, Harold, M. 1980. **Snag characteristics and dynamics in Douglas-fir forests, western Oregon**. Journal of Wildlife Management 44: 773-786.
- Coley, P. D.; Bryant J. P.; Chapin, F. S., III. 1985. **Resource availability and plant antiherbivore defense**. Science 230: 895-899.
- Davis, Frank W.; Stoms, David M. 1996. **Sierran vegetation: A gap analysis**. In: Sierra Nevada Ecosystem Project: Final report to Congress, Volume II. Wildland Resources Center Report No. 37, University of California, Davis, CA; 671-690.
- Drumm, Mary K. 1996. **Fire history in the mixed conifer series of the Kings River Adaptive Management Area, Sierra National Forest**. Arcata, CA: Humboldt State University; 30 p. M.S. thesis.
- Dufrêne, Michael; Legendre, Pierre. 1997. **Species assemblages and indicator species: the need for a flexible asymmetrical approach**. Ecological Monographs 67: 345-366.
- FEMAT (Forest Ecosystem Management Assessment Team). 1993. **Forest ecosystem management: an ecological, economic, and social assessment**. Washington DC: U.S. Government Printing Office.
- Ferrell, George T. 1996. **The influence of insect pests and pathogens on Sierra forests**. In: Sierra Nevada Ecosystem Project: Final report to Congress, vol. II. University of California, Centers for Water and Wildlands Resources, Davis, California; 1177-1192.
- Fiegenger, Rob. 2002. **A fire history of mixed conifer at the Teakettle Experimental Forest**. Unpublished draft supplied by author.
- Filip, G. M.; Goheen, D. J. 1982. **Tree mortality caused by root pathogen complexes in Deschutes National Forest, Oregon**. Plant Disease 66: 240-243.
- Fites, Jo Ann. 1993. **Ecological guide to mixed conifer plant associations**. USDA Forest Service, Pacific Southwest Region publication.
- Garrison, G. A. 1949. **Uses and modifications for the "moosehorn" crown closure estimator**. Journal of Forestry 47: 733-735.
- Gilbert, O. L. 1977. **Lichen conservation in Britain**. In: Seaward, M. R. D., ed. Lichen ecology. London: Academic Press; 415-436.
- Goheen, D. J.; Hansen, E. M. 1993. **Effects of pathogens and bark beetles on forests**. In: Schowalter, T. D., Filip, G. M., eds. Beetle-pathogen interactions in conifer forests. San Diego: Academic Press; 175-198.
- Graber, David M. 1996. **Status of terrestrial vertebrates**. In: Sierra Nevada Ecosystem Project: Final report to Congress, Volume II. Wildland Resources Center Report No. 37, University of California, Davis, CA; 709-734.

- Gray, Andrew; Spies, Tom. 1995. **Water content measurement in decayed wood and forest soils using time domain reflectometry.** Canadian Journal of Forest Research 25(3): 376-385.
- Hansen, E. M.; Lewis, K. J., editors. 1997. **Compendium of conifer diseases.** St. Paul, MN: American Phytopathological Society.
- Hargis, C. D.; McCullough, D. R. 1984. **Winter diet and habitat selection of marten in Yosemite National Park.** Journal of Wildlife Management 48: 140-146.
- Harmon, M. E.; Sexton, J. 1995. **Water-balance of conifer logs in early stages of decomposition.** Plant and Soil 172: 141-152.
- Harrington, T. C.; Worrall, J. J.; Rizzo, D. M. 1989. **Compatibility among host-specialized isolates of *Heterobasidion annosum* from Western North America.** Phytopathology 79: 290-296.
- Hawksworth, F. G.; Weins, D. 1996. **Dwarf mistletoes: biology, pathology, and systematics.** Agric. Handb. 709. Washington, DC: USDA Forest Service.
- Hayward, G. D.; Rosentreter, R. 1994. **Lichens as nesting material for northern flying squirrels in the northern Rocky Mountains.** Journal of Mammalogy 75: 663-673.
- Keeler-Wolf, Todd. 1990. **Ecological surveys of Forest Service Research Natural Areas in California.** Gen. Tech. Rep. PSW-GTR-125. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 177 p.
- Kuchler, A. W. 1977. **The map of the natural vegetation.** In: Barbour, M. G.; Major, J., eds. Terrestrial vegetation of California. New York: Wiley & Sons; 909-938.
- Laymon, Stephen A. 1988. **Ecology of the spotted owl in the central Sierra Nevada, California.** University of California, Berkeley. Ph.D. dissertation.
- Lundquist, J. E. 1995. **Pest interactions and canopy gaps in ponderosa pine stands in the Black Hills, South Dakota, USA.** Forest Ecology and Management 74: 37-48.
- Ma, Siyan; North, Malcolm; Chen, Jiquan; Jurgensen, Martin; Oakley, Brian. 2002a. **Temporal and spatial variability of air and soil temperature in a Sierra Nevada old-growth mixed conifer forest.** Unpublished draft supplied by author.
- Ma, Siyan; Chen, Jiquan; North, Malcolm; Erickson, Heather; Bresse, Mary; LeMoines, James. 2002b. **Short-term effects of experimental burning and thinning on soil respiration in an old-growth, mixed-conifer forest.** Unpublished draft supplied by author.
- Maloney, Patricia E. 2000. **The role of human and natural disturbances in mixed-conifer forests of the Lake Tahoe Basin and Sierra San Pedro Martir, Baja.** University of California, Davis. Ph.D. dissertation.
- Maser, Chris; Cline, Stephen; Cromack, Kermit, Jr.; Trappe, Jim; Hansen, Eric. 1988. **What we know about large trees that fall to the forest floor.** In: From the forest to the sea: A story of fallen trees. Gen. Tech. Rep. PNW-GTR-229. Portland, OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 25-45.
- Maser, Zane; Maser, Chris; Trappe, Jim. 1985. **Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon.** Canadian Journal of Zoology 63: 1084-1088.
- Mattson, W. J. 1980. **Herbivory in relation to plant nitrogen content.** Annual Review of Ecology and Systematics 11: 119-161.
- Mattson, W. J.; Haack, R. A. 1987. **The role of drought in outbreaks of plant-eating insects.** BioScience 37: 110-118.
- McCune, B.; Mefford, M. J. 1999. **PC-ORD. Multivariate analysis of ecological data, version 4.** Gleneden Beach, OR: MjM Software Design; 237 p.
- McKeever, S. 1960. **Food of the northern flying squirrel in northeastern California.** Journal of Mammalogy 41: 270-271.
- McKelvey, Kevin S; Busse, Matt K. 1996. **Twentieth-century fire patterns on forest service lands.** In: Sierra Nevada Ecosystem Project, Volume II. U.C. Davis, Wildland Resources Center Report No. 37; 1119-1138
- Moldenke, Andrew R. 1994. **Arthropods.** In: Weaver, R. W., ed. Methods of soil analysis: Part 2 microbiological and biochemical properties. Soil Science Society of America Book Series, volume 5, Madison, WI; 517-542.
- North, Malcolm. 2002. **Seasonality and abundance of truffles from oak woodlands to red fir forests.** Gen. Tech. Rep. PSW-GTR-183. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture.
- North, Malcolm P.; Oakley, Brian, B. 2003. **Pattern, scale and plot replication in heterogeneous forests.** Unpublished draft supplied by author.
- Oakley, Brian, B.; North, Malcolm P; Franklin, Jerry F. [In press]. **The effects of fire on soil nitrogen associated with patches of the actinorhizal shrub *Ceanothus cordulatus*.** Plant and Soil.
- Otrosina, W. J.; Chase, T. E.; Cobb, F. W. 1992. **Allozyme differentiation of intersterility groups of *Heterobasidion annosum* isolated from conifers in the western United States.** Phytopathology 82: 540-545.

- Paine, T. D.; Baker, F. A. 1993. **Abiotic and biotic predisposition**. In: Schowalter, T. D.; Filip, G. M., eds. Beetle-pathogen interactions in conifer forests. San Diego: Academic Press; 61-80.
- Paine, T. D.; Raffa, K. F.; Harrington, T.C. 1997. **Interactions among Scolytid bark beetles, their associated fungi, and live host conifers**. Annual Review of Entomology 42: 179-206.
- Parmeter, J. R.; Scharf, R. F. 1963. **Dwarf mistletoe on red fir and white fir in California**. Journal of Forestry 61: 371-374.
- Pausas, Juli G.; Austin, Mike P. 2001. **Patterns of plant species richness in relation to different environments: An appraisal**. Journal of Vegetation Science 12: 153-166.
- Pavlik, Bruce M.; Barbour, Michael, G. 1991. **Seasonal patterns of growth, water potential, and gas exchange of red and white fir saplings across a montane ecotone**. American Midland Naturalist 126: 14-29.
- Potter, Donald A. 1998. **Forested communities of the upper montane in the central and southern Sierra Nevada**. Gen. Tech. Rep. PSW-GTR-169. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 319 p.
- Powell, R. A. 1993. **The fisher life history, ecology, and behavior**. Minneapolis, MN: University of Minnesota Press.
- Purcell, Kathryn L.; Turner, Jennifer G.; Drynan, Douglas A. 1992. **Old-growth coniferous red fir forest transition**. Journal of Field Ornithology 63: 64-65.
- Raffa, K. F.; Phillips, T. W.; Salom, S. M. 1993. **Strategies and mechanisms of host colonization by bark beetles**. In: Schowalter, T. D.; Filip, G. M., eds. Beetle-pathogen interactions in conifer forests. San Diego: Academic Press; 103-128.
- Raphael, Martin G.; Morrison, Michael L. 1987. **Decay and dynamics of snags in the Sierra Nevada, California**. Forest Science 33: 774-783.
- Raven, Peter, H.; Axelrod, Daniel, L. 1978. **Origin and relationships of the California flora**. Sacramento, CA: California Native Plant Society Publication; 134 p.
- Renhorn, K. E.; Esseen, P. A.; Palmqvist, K.; Sundberg, B. 1997. **Growth and vitality of epiphytic lichens 1. Responses to microclimate along a forest edge-interior gradient**. Oecologia 109: 1-9.
- Rizzo, David M.; Slaughter, Gary, W. 2000. **Root disease and canopy gaps in developed areas of Yosemite Valley, California**. Forest Ecology and Management 146: 159-167.
- Royce, Edward B.; Barbour, Michael G. 2001a. **Mediterranean climate effects. I. Conifer water use across a Sierra Nevada ecotone**. American Journal of Botany 88(5): 911-918.
- Royce, Edward B.; Barbour, Michael G. 2001b. **Mediterranean climate effects. II. Conifer growth phenology across a Sierra Nevada ecotone**. American Journal of Botany 88(5): 919-932.
- Rundel, P. W.; Parson, D. J.; Gordon, D. T. 1988. **Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges**. In: Barbour, M. G.; Major, J., eds. Terrestrial vegetation of California. Sacramento, CA: California Native Plant Society; 559-600.
- Schowalter, T. D.; Hargrove, W. W.; Crossley, D. A., Jr. 1986. **Herbivory in forested ecosystems**. Annual Review of Entomology 31: 177-196.
- Schowalter, T. D.; Lightfoot, D. C.; Whitford, W. G. 1999. **Diversity of arthropod responses to host-plant water stress in a desert ecosystem in southern New Mexico**. American Midland Naturalist 142: 281-290.
- Schowalter, Tim D. 2000. **Insect ecology: An ecosystem approach**. San Diego: Academic Press; 483 p.
- SNEP. 1996. **Sierra Nevada Ecosystem Project: Final report to Congress**. Wildland Resources Center Report No. 37. University of California, Davis, CA.
- Stenlid, J.; Redfern, D. B. 1998. **Spread within the tree and stand**. In: Woodward, S.; Stenlid, J.; Karjalainen, R.; Huttermann, A., eds. *Heterobasidion annosum*: Biology, ecology, impact and control. Oxon, U.K.: CAB International; 125-142.
- USDA. 2001. **Sierra Nevada forest plan amendment environmental impact statement**. Volumes I-VI. Pacific Southwest Region, Forest Service, U.S. Department of Agriculture.
- Van Groenewoud, H. 1992. **The robustness of correspondence, detrended correspondence and TWINSpan analysis**. Journal of Vegetation Science 3: 239-246.
- Verner, Jared; McKelvey, Kevin, S.; Noon, Barry, R.; Gutierrez, R. J.; Gould, Gordon, I. Jr.; Beck, Thomas, W. 1992. **The California spotted owl: A technical assessment of its current status**. Gen. Tech. Rep. PSW-GTR-133. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 285 p.
- Verner, Jared; Milne, Kathleen, A. 1990. **Analyst and observer variability in density estimates from spot mapping**. Condor 92: 313-325.
- Wang, Y.; Amundson, R.; Trumbore, S. 1999. **The impact of land use change on C turnover in soils**. Global Biogeochemical Cycles 13: 47-57.
- Waring, R. H.; Cromack, K. Jr.; Matson, P. A.; Boone, R. D.; Stafford, S. G. 1987. **Responses to pathogen-induced disturbance: Decomposition, nutrient availability, and tree vigor**. Journal of Forestry 60: 21-227.

- Waring, Richard H. 1987. **Characteristics of trees predisposed to die.** *Bioscience* 37: 569-574.
- Wells-Gosling, N. 1985. **Flying squirrels gliders in the dark.** Washington, DC: Smithsonian Institution Press.
- Worrall, J. J.; Harrington, T. C. 1988. **Etiology of canopy gaps in spruce-fir forests at Crawford Notch, New Hampshire.** *Canadian Journal of Forest Research* 18: 1463-1469.
- Zarnowitz, Jill; Manuwal, David. 1985. **The effects of forest management on cavity-nesting birds in northwestern Washington.** *Journal of Wildlife Management* 49: 255-263.

Appendix A: The Teakettle Experiment

A fundamental unknown in Sierra Nevada forests is whether thinning and controlled burning can be used to restore the ecological functions of the natural fire regime. In the Sierra, fire has historically been the dominant disturbance driving forest ecosystem composition, structure, and function. Within the last 70 years, however, fire suppression and the selective harvest of large pines have significantly altered ecosystem dynamics. These changes have deflected succession, possibly shifting ecosystem processes outside their historic range of variability. Many Sierra forests are now thickets of shade-tolerant species, which can “ladder” fire into the crowns of the overstory canopy. There is a high probability that these stands will experience a catastrophic burn in which all trees are killed and some of the soil is sterilized. Fire cannot be re-introduced into these forest conditions until stem density and ladder fuels have been reduced. Understory thinning is theorized to mimic mortality from understory burning while reducing the risk of crown fire. Although widely used as a silvicultural tool, the ecological effects of removing stem wood in place of burning it has never been studied in the Sierra Nevada.

Efforts to restore Sierra forests to pre-European conditions have focused on recreating the structure of open “park-like” stands without an equal effort to understand the functional response of basic ecosystem processes. Early reports of Sierra forests indicate some range of variability in forest structure and composition, but in general mixed-conifer forests were less dense and more dominated by large, fire-resistant pines. Paleobotanical evidence suggests frequent fires have influenced Sierra forests and their associated plants, animals, soils and microclimate for several millennia (Raven and Axelrod 1978). Forest managers in the Sierra and many other fire-dominated forests of the western U.S. often assume that recreating forests with a low density of fire-resistant species is restoring the forest ecosystem. Reliance on structural parameters alone to create this “desired” forest condition ignores the crucial effects of disturbance type and intensity on ecosystem function. A desired forest condition can only be used as a measure of ecosystem “health” if the linkages between disturbance, forest structure, and ecological function are understood.

Design

The Teakettle Ecosystem Experiment is based on a full factorial design contrasting two levels of burning and three levels of thinning treatments:

	No Burn	Burn
No thinning treatment	Control	Burn Only
Understory thin	Understory thin/No Burn	Understory thin/Burn
Overstory thin	Overstory thin/No Burn	Overstory thin/Burn

Each treatment unit is a 4 ha plot with three replicates for a total of 18 plots. Baseline data was collected from 1998 to 2000, and response data will be collected for at least 2 years after treatments. Multi-disciplinary research will quantify the effects on all levels of the trophic structure of the ecosystem. The experiment brings together over two dozen scientists and graduate students from nine institutions. Research is coordinated by all studies using the same experimental design, mapping data in the same core area of each plot, and sampling for the same duration. Collaborators have a commitment to sharing data, and scientists are actively involved in data archiving, integration, and project synthesis.

Treatments

Burn treatments will have two levels: no burn and an understory burn. The understory burn will be a controlled fire designed to mimic the historic disturbance regime. The objective will be to contain the flames to a ground fire and avoid overstory crown ignition.

Thinning treatments will contrast three levels of stem reduction: no reduction (present forest conditions), understory thinning (similar to thinning “from below”), and overstory thinning that removes all but a few dominant trees. Understory thinning will follow current guidelines outlined in the California Spotted Owl Report (CASPO) (Verner and others 1992), which limits thinning to trees ≤ 30 in. (76 cm) dbh. CASPO guidelines require thinnings to meet the most restrictive of three conditions: 40 percent canopy cover retention, 40 percent basal area retention or no harvest of trees ≥ 30 in. dbh (CASPO, p. 21). Analysis of plot data gathered at Teakettle indicates the last condition is the most restrictive. Retaining stems ≥ 76 cm dbh will, on average, leave 44 trees/ha with an average dbh of 91 cm. The spatial distribution of the retained trees will be random. Six of the 4-ha plots (24 ha total) will receive this treatment.

The overstory thinning treatment will follow silvicultural practices common prior to the implementation of CASPO. With overstory thinning, all stems are removed except for 18 dominant trees/ha regularly spaced 20-25 m apart. Six of the 4-ha plots (24 ha total) will receive an overstory thinning.

A critical question in the Sierra Nevada is how to use disturbance effectively to restore forest ecosystems after nearly a century of fire suppression. In spite of their widespread use, the different effects of fire and thinning on fundamental ecological processes have not been systematically examined in Sierra mixed-conifer forest. Thinning treatments may mimic fire by reducing ladder fuels, overstocking, and the number of shade-tolerant species, but differ by removing most of the large woody biomass from the site. For decades to centuries after fire, fire-killed trees can continue to play important ecological roles as habitat, sources of nutrients and water, and structural complexity in streams. Fire is also highly variable and often leaves pockets of intact forest. Although thinning may replicate the final stand composition and structure produced by fire, the ecosystem response is unlikely to be the same.

The Teakettle Ecosystem Experiment is a unique opportunity to compare these effects in an old-growth experimental forest in a replicated full factorial experiment. The combination of burning and thinning treatments will provide important insight into how the type of disturbance affects forest composition, structure, and function (for more details see <http://teakettle.ucdavis.edu>).

Appendix B: Plant List

A total of 152 plants found at the Teakettle Experimental Forest, 80 km east of Fresno, California, by scientific name, common name, and abbreviation used in the text. The list is alphabetically sorted by genus and species.

Family	Genus	species	var/ssp	Common name	Abbre. in text
Pinaceae	<i>Abies</i>	<i>concolor</i>		white fir	ABCO
Asteraceae	<i>Achillea</i>	<i>lanulosa</i>		yarrow	
Asteraceae	<i>Achillea</i>	<i>millefolium</i>		yarrow	
Asteraceae	<i>Adenocaulon</i>	<i>bicolor</i>		trail plant	
Asteraceae	<i>Agroseris</i>	<i>retrorsa</i>		spear-leaved agoseris	
Polemoniaceae	<i>Allophylum</i>	<i>integifolium</i>		allopylum	
Asteraceae	<i>Anaphalis</i>	<i>margaritacea</i>		pearly everlasting	
Apocynaceae	<i>Apocynum</i>	<i>androsaemifolium</i>		dogbane	APAN
Ranunculaceae	<i>Aquilegia</i>	<i>formosa</i>		columbine	AQFO
Brassicaceae	<i>Arabis</i>	<i>platysperma</i>	<i>platysperma</i>	rock cress	ARPL
Brassicaceae	<i>Arabis</i>	<i>rectissima</i>	<i>rectissima</i>	bristly-leaved rock cress	
Brassicaceae	<i>Arabis</i>	<i>repanda</i>	<i>repanda</i>	repand rock cress	
Ericaceae	<i>Arctostaphylos</i>	<i>nevadensis</i>		pinemat manzanita	ARNE
Ericaceae	<i>Arctostaphylos</i>	<i>patula</i>		greenleaf manzanita	ARPA
Caryophylliaceae	<i>Arenaria</i>	<i>kingii</i>		sandwort	
Asteraceae	<i>Aster</i>	<i>foliaceus</i>		leafy aster	ASFO
Asteraceae	<i>Aster</i>	<i>occidentalis</i>	<i>occidentalis</i>	western mountain aster	ASOC
Fabaceae	<i>Astragalus</i>	<i>bolanderi</i>		Bolander's locoweed	ASBO
Dryopteridaceae	<i>Athyrium</i>	<i>felix-femina</i>		lady fern	ATFI
Liliaceae	<i>Brodiaea</i>	<i>elegans</i>	<i>elegans</i>	harvest brodeia	
Poaceae	<i>Bromus</i>	<i>ssp.</i>		brome	
Cupressaceae	<i>Calocedrus</i>	<i>decurrens</i>		incense cedar	CADE
Liliaceae	<i>Calochortus</i>	<i>leichtlinii</i>		Leichtlin's mariposa lily	CALE
Portulacaceae	<i>Calyptridium</i>	<i>umbellatum</i>		pussy paws	CAUM
Convulvulaceae	<i>Calystegia</i>	<i>malacophylla</i>		morning glory	CAMA
Brassicaceae	<i>Cardamine</i>	<i>breweri</i>	<i>breweri</i>		

(continues on next page)

Family	Genus	species	var/ssp	Common name	Abbre. in text
Cyperaceae	<i>Carex</i>	<i>athryostachya</i>		slender-beaked sedge	
Cyperaceae	<i>Carex</i>	<i>pachystachya</i>		thick-headed sedge	
Schrophularaceae	<i>Castilleja</i>	<i>spp.</i>		indian paintbrush	
Rhamnaceae	<i>Ceanothus</i>	<i>cordulatus</i>		mountain whitethorn	CECO
Rhamnaceae	<i>Ceanothus</i>	<i>integerrimus</i>		deer brush	CEIN
Rhamnaceae	<i>Ceanothus</i>	<i>prostratus</i>		mahala mat	
Asteraceae	<i>Chaenactis</i>	<i>douglasii</i>		hoary chaenactis	
Rosaceae	<i>Chamaebatia</i>	<i>foliosa</i>		mountain misery	CHFO
Ericaceae	<i>Chimaphila</i>	<i>menziesii</i>		little prince's pine	CHME
Ericaceae	<i>Chimaphila</i>	<i>umbellata</i>		western prince's pine	CHUM
Fagaceae	<i>Chrysopsis</i>	<i>sempervirens</i>		bush chinquapin	CHSE
Onagraceae	<i>Circaea</i>	<i>alpina</i>	<i>pacifica</i>		
Onagraceae	<i>Clarkia</i>	<i>rhomboidea</i>		rhomboid clarkia	
Schrophularaceae	<i>Collinsia</i>	<i>parviflora</i>		small-flowered blue eyed mary	COPA
Orchidaceae	<i>Corallorhiza</i>	<i>maculata</i>		spotted coral root	COMA
Schrophularaceae	<i>Cordylanthus</i>	<i>rigidus</i>	<i>rigidus</i>	bird's beak	
Cornaceae	<i>Cornus</i>	<i>sericea</i>	<i>occidentalis</i>	American dogwood	COSE
Betulaceae	<i>Corylus</i>	<i>cornuta</i>	<i>californica</i>	California hazelnut	COCO
Boraginaceae	<i>Cynoglossum</i>	<i>occidentale</i>		western hounds tongue	CYOC
Asteraceae	<i>Dugaldia</i>	<i>hoopesii</i>			
Poaceae	<i>Elymus</i>	<i>glaucus</i>		blue wildrye	
Onagraceae	<i>Epilobium</i>	<i>canum</i>	<i>latifolium</i>	fireweed	
Onagraceae	<i>Epilobium</i>	<i>ciliatum</i>	<i>glandulosum</i>	fireweed	
Polygonaceae	<i>Eriogonum</i>	<i>nudum</i>		naked-stemmed eriogonum	ERNU
Polygonaceae	<i>Eriogonum</i>	<i>prattenianum</i>			
Polygonaceae	<i>Eriogonum</i>	<i>spergulinum</i>		spurry eriogonum	ERSP
Polygonaceae	<i>Eriogonum</i>	<i>strictum</i>			ERST
Polygonaceae	<i>Eriogonum</i>	<i>umbellatum</i>		sulphur-flowered erogonum	ERUM
Polygonaceae	<i>Eriogonum</i>	<i>wrightii</i>		Wright's eriogonum	
Brassicaceae	<i>Erysimum</i>	<i>capitatum</i>	<i>perenne</i>	western wallflower	ERCA

Family	Genus	species	var/ssp	Common name	Abbre. in text
Rubiaceae	<i>Galium</i>	<i>bifolium</i>		low mountain bedstraw	
Rubiaceae	<i>Galium</i>	<i>trifidum</i>		trifid bedstraw	
Onagraceae	<i>Gayophytum</i>	<i>heterozygum</i>		gayophytum	GAHE
Gentianaceae	<i>Gentianopsis</i>	<i>simplex</i>		fringed gentian	
Geraniaceae	<i>Geranium</i>	<i>richardsonii</i>		Richardson's geranium	GERI
Polemoniaceae	<i>Gilia</i>	<i>leptalea</i>	<i>leptalea</i>	bridge's gilia	
Orchidaceae	<i>Goodyera</i>	<i>oblongifolium</i>		rattlesnake plantain	GOOD
Boraginaceae	<i>Hackelia</i>	<i>mundula</i>		pink stickseed	HAMU
Boraginaceae	<i>Hackelia</i>	<i>velutina</i>		velvety stickseed	HAVE
Saxifragaceae	<i>Heuchera</i>	<i>rubescens</i>		alumroot	
Asteraceae	<i>Helenium</i>	<i>bigelovii</i>		sneezeweed	
Asteraceae	<i>Hieracium</i>	<i>albiflorum</i>		white-flowered hawkweed	HIAL
Asteraceae	<i>Hieracium</i>	<i>horridum</i>		shaggy hawkweed	HIHO
Hypericaceae	<i>Hypericum</i>	<i>anagalioides</i>		tinker's penny	HYAN
Polemoniaceae	<i>Ipomopsis</i>	<i>congesta</i>	<i>congesta</i>	scarlet gilia	
Rosaceae	<i>Ivesia</i>	<i>santolinoides</i>		mouse-tail ivesia	
Juncaceae	<i>Juncus</i>	<i>spp.</i>			
Cupressaceae	<i>Juniperus</i>	<i>occidentalis</i>		western juniper	
Rubiaceae	<i>Kelloggia</i>	<i>galiioides</i>		Kellogg's bedstraw	KEGA
Ericaceae	<i>Ledum</i>	<i>glandulosum</i>		Labrador tea	LEGL
Liliaceae	<i>Lillium</i>	<i>parvum</i>		alpine lily	
Polemoniaceae	<i>Linanthus</i>	<i>ciliatus</i>		bristly-leaved linanthus	LICI
Saxifragaceae	<i>Lithophragma</i>	<i>bolanderi</i>		woodland star	
Saxifragaceae	<i>Lithophragma</i>	<i>campanulatum</i>		woodland star	
Fabaceae	<i>Lotus</i>	<i>crassifolius</i>			LOCR
Fabaceae	<i>Lotus</i>	<i>nevadensis</i>		Sierra nevada trefoil	LONE
Fabaceae	<i>Lotus</i>	<i>oblongifolius</i>		narrow-leaved trefoil	LOOB
Fabaceae	<i>Lupinus</i>	<i>adsergens</i>		Drew's silky lupine	LUAD
Fabaceae	<i>Lupinus</i>	<i>argenteus</i>	<i>heteranthus</i>		
Fabaceae	<i>Lupinus</i>	<i>breweri</i>		Brewer's lupine	

Family	Genus	species	var/ssp	Common name	Abbrev. in text
Fabaceae	<i>Lupinus</i>	<i>fulcratus</i>		California green-stipuled lupine	
Fabaceae	<i>Lupinus</i>	<i>polyphyllus</i>		large-leaved lupine	LUPO
Juncaceae	<i>Luzula</i>	<i>ssp.</i>		woodrush	
Schrophularaceae	<i>Mimulus</i>	<i>guttatus</i>		common large monkey flower	MIGU
Schrophularaceae	<i>Mimulus</i>	<i>tilingii</i>			MITI
Lamiaceae	<i>Monardella</i>	<i>odoratissima</i>		mountain pennyroyal	MOOD
Poaceae	<i>Muhlenbergia</i>	<i>ssp.</i>		muhlenbergia	
Hydrophyllaceae	<i>Nemophila</i>	<i>spatulata</i>		Sierra nemophila	
Apiaceae	<i>Osmorhiza</i>	<i>chilensis</i>		mountain sweet-cicely	OSCH
Apiaceae	<i>Oxypolis</i>	<i>occidentalis</i>		western sweet-cicely	OXOC
Schrophularaceae	<i>Pedicularis</i>	<i>attollens</i>		little elephant's head	
Schrophularaceae	<i>Pedicularis</i>	<i>semibarbata</i>		pine-woods lousewort	PESE
Pteridaceae	<i>Pellaea</i>	<i>bridgesii</i>		Bridge's cliff brake	
Schrophularaceae	<i>Penstemon</i>	<i>azureus</i>	<i>azureus</i>	azure penstemon	PEAZ
Schrophularaceae	<i>Penstemon</i>	<i>newberryi</i>		mountain pride	PENE
Apiaceae	<i>Perideridia</i>	<i>ssp.</i>		yampah	
Hydrophyllaceae	<i>Phacelia</i>	<i>hastata</i>		silverleaf phacelia	PHHA
Hydrophyllaceae	<i>Phacelia</i>	<i>hydrophylloides</i>		waterleaf phacelia	PHHY
Hydrophyllaceae	<i>Phacelia</i>	<i>procera</i>			
Hydrophyllaceae	<i>Phacelia</i>	<i>ramosissima</i>			PHRA
Asteraceae	<i>Phalacroseris</i>	<i>bolanderi</i>			PHBO
Polemoniaceae	<i>Phlox</i>	<i>gracilis</i>			PHGR
Pinaceae	<i>Pinus</i>	<i>contorta</i>		lodgepole pine	PICO
Pinaceae	<i>Pinus</i>	<i>jeffreyi</i>		Jeffrey pine	PIJE
Pinaceae	<i>Pinus</i>	<i>lambertiana</i>		sugar pine	PILA
Pinaceae	<i>Pinus</i>	<i>monticola</i>		western white pine	PIMO
Pinaceae	<i>Pinus</i>	<i>ponderosa</i>		ponderosa pine	PIPO
Orchidaceae	<i>Piperia</i>	<i>unalascensis</i>		rein orchid	
Orchidaceae	<i>Plantathera</i>	<i>leucostachys</i>		white-flowered bog-orchid	

Family	Genus	species	var/ssp	Common name	Abbre. in text
Liliaceae	<i>Polygonum</i>	<i>bistortoides</i>		western bistort	POBI
Rosaceae	<i>Potentilla</i>	<i>drummondii</i>		Drummond's cinquefoil	PODR
Rosaceae	<i>Potentilla</i>	<i>glandulosum</i>		sticky cinquefoil	PODR
Rosaceae	<i>Prunus</i>	<i>emarginata</i>		bitter cherry	PREM
Poaceae	<i>Pseudoroegneria</i>	<i>spicata</i>	<i>spicata</i>		
Dennstaedtiaceae	<i>Pteridium</i>	<i>aquilinum</i>		western bracken fern	PTAQ
Ericaceae	<i>Pterospora</i>	<i>andromeda</i>		pinedrops	PTAN
Ericaceae	<i>Pyrola</i>	<i>asarifolia</i>	<i>asarifolia</i>	bog wintergreen	PYAS
Ericaceae	<i>Pyrola</i>	<i>picta</i>		white-veined wintergreen	PYPI
Fagaceae	<i>Quercus</i>	<i>chrysolepis</i>		canyon live oak	
Fagaceae	<i>Quercus</i>	<i>kelloggii</i>		California black oak	QUKE
Rhamnaceae	<i>Rhamnus</i>	<i>spp.</i>		buckthorn	
Grossulariaceae	<i>Ribes</i>	<i>roezlii</i>		Sierra gooseberry	RIRO
Grossulariaceae	<i>Ribes</i>	<i>sanguineum</i>		red flowering current	RISA
Rosaceae	<i>Rosa</i>	<i>bridgesii</i>			ROBR
Rosaceae	<i>Rubus</i>	<i>parviflorus</i>		timble berry	RUPA
Salicaceae	<i>Salix</i>	<i>lemmonii</i>		Lemmon's willow	
Salicaceae	<i>Salix</i>	<i>spp.</i>		willow	
Ericaceae	<i>Sarcodes</i>	<i>sanguinea</i>		snow plant	
Cyperaceae	<i>Scirpus</i>	<i>microcarpus</i>			
Asteraceae	<i>Senecio</i>	<i>aronicoides</i>		California butterweed	SEAR
Asteraceae	<i>Senecio</i>	<i>triangularis</i>		arrowhead butterweed	SETR
Caryophyllaceae	<i>Silene</i>	<i>lemmonii</i>		Lemmon's campion	
Liliaceae	<i>Smilacina</i>	<i>racemosa</i>		false Solomon's seal	
Liliaceae	<i>Smilacina</i>	<i>stellata</i>		Nuttall's Solomon's seall	SMST
Lamiaceae	<i>Stachys</i>	<i>albens</i>		white hedge nettle	STAL
Brassicaceae	<i>Streptanthus</i>	<i>tortuosus</i>	<i>orbiculatus</i>	mountain streptanthus	STTO
Caprifoliaceae	<i>Symphoricarpos</i>	<i>mollis</i>		creeping snowberry	SYMO
Fabaceae	<i>Trifolium</i>	<i>spp.</i>		clover	

Family	Genus	species	var/ssp	Common name	Abbrev. in text
Ericaceae	<i>Vaccinium</i>	<i>uliginosum</i>		western blueberry	VAUL
Scrophulariaceae	<i>Veronica</i>	<i>serpyllifolia</i>	<i>humifusa</i>	thyme-leaved speedwell	
Violaceae	<i>Viola</i>	<i>glabella</i>		stream violet	
Violaceae	<i>Viola</i>	<i>lobata</i>		pine violet	VILO
Violaceae	<i>Viola</i>	<i>mackloskeyi</i>		Macloskey's violet	
Violaceae	<i>Viola</i>	<i>pedunculata</i>		Johnny-jump-up	
Violaceae	<i>Viola</i>	<i>purpurea</i>			

The Forest Service, U.S. Department of Agriculture, is responsible for Federal leadership in forestry. It carries out this role through four main activities:

- Protection and management of resources on 191 million acres of National Forest System lands;
- Cooperation with State and local governments, forest industries, and private landowners to help protect and manage non-Federal forest and associated range and watershed lands;
- Participation with other agencies in human resource and community assistance programs to improve living conditions in rural areas; and
- Research on all aspects of forestry, rangeland management, and forest resources utilization.

The Pacific Southwest Research Station

- Represents the research branch of the Forest Service in California, Hawaii, American Samoa, and the western Pacific.



The United States Department of Agriculture (USDA) prohibits discrimination in all its programs and activities on the basis of race, color, national origin, gender, religion, age, disability, political beliefs, sexual orientation, and marital or familial status. (Not all prohibited bases apply to all programs.) Persons with disabilities who require alternative means for communication of program information (Braille, large print, audiotape, etc.) should contact USDA's TARGET Center at:

202-720-2600 (voice and TDD)

To file a complaint of discrimination, write:

USDA Director
Office of Civil Rights
Room 326-W
Whitten Building
14th & Independence Avenue, SW
Washington, DC 20250-9410

or call:

(202) 720-5964 (voice or TDD)

USDA is an equal opportunity provider



Federal Recycling Program
Printed on Recycled Paper

United States
Department
of Agriculture
Forest Service

**Pacific Southwest
Research Station**

General Technical Report
PSW-GTR-186

