

Influence of light and soil moisture on Sierran mixed-conifer understory communities

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Received 10 September 2003; accepted in revised form 18 April 2004

Key words: California, NMS ordination, Patch, Plant community, Teakettle Experimental Forest, Understory diversity

Abstract

Sierra Nevada forests have high understory species richness yet we do not know which site factors influence herb and shrub distribution or abundance. We examined the understory of an old-growth mixed-conifer Sierran forest and its distribution in relation to microsite conditions. The forest has high species richness (98 species sampled), most of which are herbs with sparse cover and relatively equal abundance. Shrub cover is highly concentrated in discrete patches. Using overstory tree cover and microsite environmental conditions, four habitats were identified; tree cluster, partial canopy, gap, and rock/shallow soil. Herb and shrub species were strongly linked with habitats. Soil moisture, litter depth and diffuse light were the most significant environmental gradients influencing understory plant distribution. Herb cover was most strongly influenced by soil moisture. Shrub cover is associated with more diffuse light, less direct light, and sites with lower soil moisture. Herb richness is most affected by conditions which influence soil moisture. Richness is positively correlated with litter depth, and negatively correlated with direct light and shrub cover. Disturbance or management practices which change forest floor conditions, shallow soil moisture and direct light are likely to have the strongest effect on Sierran understory abundance and richness.

Introduction

Although the Sierra Nevada occupies only 20% of California's landbase, it contains over 50% of the state's 7000 plus species (Davis and Stoms 1996). Much of the plant diversity is in the understory (Shevock 1996). The southern Sierra, in particular, has the highest species richness and the most endemic and rare species, yet we have little information about the understory communities present (although see Potter 1998) or the site and forest

overstory conditions associated with them. This rich understory may have been severely impacted by the past century of fire suppression. Increases in the density of shade-tolerant trees and overstory canopy cover have increased litter depth, competition for soil moisture, and reduced understory light. These changes may be particularly acute in mixed-conifer forests which historically had a fire return interval of 12–25 years but is now estimated at over 644 years (Skinner and Chang 1996). Understanding the association between site

conditions and the understory community can help identify the current effects of fire suppression, as well as inform managers of the potential impacts from thinning and burning restoration treatments widely used in the Sierra Nevada.

In most forests, understory plant species abundance and richness are strongly influenced by changes in overstory canopy cover resulting from forest disturbance and succession. Studies suggest that initially young stands have high herb and shrub abundance dominated by early seral species (Alaback 1982; Halpern 1988, 1989; Halpern and Spies 1995). In traditional stand development models (e.g., Oliver and Larson 1996), as mature forests age, gaps become more common and old-growth forests are often characterized by variable canopy cover and an understory with higher species evenness and endemism. The mechanisms influencing the old-forest understory community, however, can vary with forest type. In the Pacific Northwest, gaps may foster herb abundance by increasing solar radiation (both direct and diffuse) (Gray et al. 2002) while in northern deciduous forests, gap increases in soil moisture from throughfall precipitation have been associated with herb abundance (Anderson et al. 1969). Herb richness may also be influenced by old forest's high substrate heterogeneity created by variable litter depths and high cover of well-decayed coarse woody debris (Brandini et al. 1988; Harmon 1989; Pausas 1994). Old-growth mixed conifer has distinct gaps, creating a highly variable canopy cover which averages only 65% across a stand (Bonnickson and Stone 1982; North et al. 2002; North et al. 2004). Consequently the forest contains a range of microsites or habitats with distinct light, soil moisture and substrate conditions. This habitat variability may be important for understory species during the prolonged summer drought and high temperatures characteristic of a Mediterranean climate. Fire suppression commonly increases the extent and density of trees (Minnich et al. 1995; Bouldin 1999), reducing microsite variability that may affect the southern Sierra's high species richness and endemism.

In California's Sierra Nevada thinning and prescribed fire are widely applied restoration practices which significantly alter site conditions. Understanding the influence of site conditions on the forest understory can help clarify how changes in forest cover, litter depth or soil moisture hold-

ing capacity may significantly impact this diverse community. We examined the understory community and its abundance in relation to microsite conditions in an old-growth, mixed-conifer forest in the southern Sierra Nevada. Herb and shrub cover by species were compared to overstory canopy cover, soil moisture, litter depth, depth to bedrock, percent cover of coarse woody debris and rock, and indirect measures of understory light. Our objectives were to (1) quantify the alpha, beta and gamma species richness of herbs and shrubs in the mixed-conifer understory; (2) classify the major habitat types organizing understory environmental conditions; (3) identify the plant communities; and (4) infer the most important environmental gradients influencing species distributions.

Methods

Study site

The study was conducted in old-growth forest at the 1300 ha Teakettle Experimental Forest, elevation 1900–2600 m, located 80 km east of Fresno, CA on the north fork of the Kings River (Figure 1). Teakettle's most common soil is a well-drained, mixed, frigid Dystric Xeropsamment, formed from decomposed granite, typical of many southern Sierra forests (Anonymous 1993). Litter depth and depth to bedrock varies across the study area, but all soils are derived from decomposed granite and have similar texture and water percolation rates (North et al. 2002). All sample points in this study were on Cagwin soils, brown gravelly, loamy coarse sand with a mean pH of 5.4. The annual precipitation of 125 cm falls almost entirely as snow between November and April (North et al. 2002).

Within the experimental forest, forest type varies by elevation, grading from mixed-conifer on lower benches to red fir (*Abies magnifica*) on mid-slope, and to red fir and lodgepole pine (*Pinus contorta*) at higher elevations. Approximately 65% of Teakettle's forest is mixed conifer, which characteristically contains white fir (*Abies concolor*), black oak (*Quercus kelloggii*), sugar pine (*Pinus lambertiana*), incense-cedar (*Calocedrus decurrens*), and Jeffrey pine (*Pinus jeffreyi*) (Rundel et al. 1988). As is characteristic of the mixed-conifer

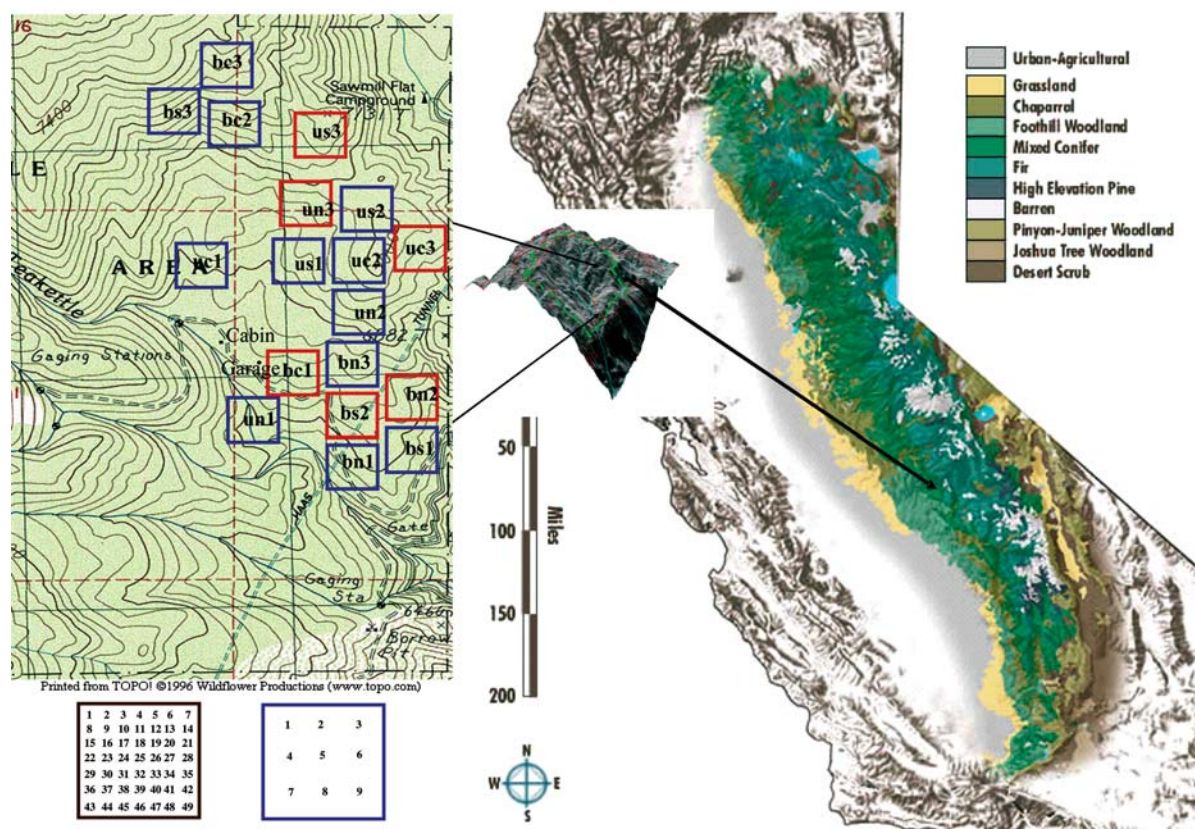


Figure 1. Map of the Sierra Nevada showing general vegetation classifications and the Teakettle Experimental Forest's location in the mixed-conifer zone. The 18 4-ha experimental plots are located in the lower right area of the digital elevation model of Teakettle. Within each of the plots there are either 49 gridpoints on a regular 25 m spacing (the 6 brown bordered plots) or 9 gridpoints on a regular 50 m spacing (12 blue bordered plots) for a total of 402 gridpoints that were sampled.

forest type throughout California, white fir dominates stem density and basal area at Teakettle; however, sugar pine and Jeffrey pine are the largest-diameter and tallest trees (North et al. 2002). Our research focused on a 200 ha contiguous block of mixed-conifer forest.

An analysis of fire scars in Teakettle's mixed conifer indicates that prior to 1865 the fire return interval was 12–17 years (Fiegener 2002). Since 1865, only two small surface fires have burned within the experimental forest. An analysis of tree ages on stumps in experimentally thinned plots at Teakettle (North et al. in press) indicates many trees ≤ 70 cm dbh became established after 1880. Stem maps of aged trees indicate that 20th century fire suppression has increased Teakettle's stem density, particularly of smaller diameter shade-tolerant species such as white fir and incense cedar (North et al. 2004).

Data collection

Within the 200 ha block on the same soil type, 18 replicate 4-ha plots were established for a long-term experiment (Figure 1). Within each plot, permanent gridpoints were mapped and marked using a surveyor's total station. In 12 of the plots, gridpoints were established on a 50×50 m spacing (9 points per plot) and in 6 intensive plots on a 25×25 m spacing (49 points per plot) for a total of 402 sample points. Understory samples should not be autocorrelated because the minimum 25 m separation between adjacent sample points was more than twice the size of the largest understory patches. At each gridpoint, slope and aspect were recorded and the percent cover of all shrub and herb species, coarse woody debris by decay class (Maser et al. 1988) and rock cover were recorded in a 10 m^2 circular plot. Herbs are ephemeral in

Sierran mixed conifer (May–July) and to insure consistency between gridpoint samples, all censuses were completed at the height of herb flowering (late June). Most species were readily identified in the field. Unknowns were collected (outside the plot if possible), pressed, and identified with the Jepson manual (Hickman 1993). Litter depth was averaged from measurements at five random locations. Soil depth was estimated by pounding a rod into the soil in 5 randomly selected locations within 2 m of the gridpoint. We first calibrated this method by selecting 4 stratified locations (closed canopy, shrub, gap and exposed rock) adjacent to but outside the sample area, took 5 probe depths and then dug a soil pit down to bedrock at each location. We noted that cobbles could give shallower probe depths and therefore selected the mean of the three greatest depths as an approximation of depth to bedrock. Volumetric soil water content was estimated for the 0–15 cm layer using time domain reflectometry (TDR; model No. 1502C, Tektronix Inc., Beaverton, OR). TDR probes were inserted 15 cm into the soil profile, left in place, and measurements collected monthly during snow-free months. In our analysis we used a set of measurements from May and October of 1999 which were representative of spring and fall conditions. The May readings are typical of soil conditions immediately after snow melt, as the October readings are before the first rains and provide a good indication of relative drought conditions between sample points. Canopy cover was measured with two methods. A moosehorn – a funnel with a bubble level, a 30° angle of view off vertical and a transparent grid with 100 intersections affixed over the top of the funnel (Garrison 1949) – was used to assess relative canopy cover by species. To assess total canopy cover and understory light, a hemispherical photograph was taken directly over the gridpoint with a digital camera and a Nikkor hemispherical (180° angle) lens. All photographs were taken at dawn or dusk, in black and white, with the top of the picture oriented to true north, using a leveled tripod.

Analysis

Hemispherical photographs were analyzed using SCANOPY software (Regent Instruments). For

each photograph we used four metrics calculated by the program, percent canopy cover and direct, diffuse, and total photosynthetically active photon flux density (PPFD) ($\mu\text{mol s}^{-1} \text{m}^{-2}$). PPFD is calculated from the latitude, longitude, and elevation of the study area and the tracking angle of the sun over the course of a year. We used PPFD values as an approximation of the relative difference in understory light conditions between sample points.

Aspect was transformed to a relative measure of heat load using the equation $(1 - \cos[\theta - 45])/2$ where θ is the azimuth measured from true north (Beers et al. 1966). Slope was not factored in the heat load because all but 8 gridpoints were relatively flat (slope < 15°).

TDR trace measurements were analyzed with an automated algorithm and volumetric water content estimated using the analysis procedure and ‘low-C’ calibration equation from Gray and Spies (1995). Because a calibration for the Teakettle soils has not been developed yet, the actual calculated moisture values may be somewhat biased, but the relative differences among probes should be accurate, since most existing TDR calibration equations have almost identical slopes (Gray and Spies 1995).

Data were divided into two sets: plant cover and environmental variables. The plant cover data set contained cover values for 98 species of herbs and shrubs for each of the 402 gridpoint plots. Environmental variables contained values for percent soil moisture in May and October; direct, diffuse and total PPFD; canopy cover calculated using a hemispherical photograph; percent canopy cover by each of the 6 major overstory tree species using a moosehorn; percent cover of coarse woody debris in decay classes I–III, classes IV–V and total; heat load; percent bare ground; percent rock; depth to bedrock; and litter depth for each gridpoint. Most analyses were completed using PCORD (MjM software design) following guidelines in McCune and Grace (2002).

Using the plant cover data for all 402 plots, alpha (average species richness per plot), beta (total richness/average richness) and gamma (total species) richness; and Shannon’s and Simpson’s diversity indices were calculated. To evaluate the adequacy of the sample size for species presence and abundance, curves for species-area and average distance (the distance between the centroid of

the subsample and the centroid of the whole sample), respectively, were calculated.

Descriptive statistics (mean, standard deviation, skewness, and kurtosis) were first calculated for herb and shrub cover data. The data formed a ‘sparse’ matrix with 93% of the cells containing zero values. All species cover values were highly skewed. Plant cover values were log-transformed, accounting for the lowest nonzero cover value (0.1) by the formula $(\log_{10}(\text{percent cover} + 0.1) - (-1))$ (McCune and Grace 2002).

The distribution of each environmental variable was analyzed and variables with skewness > 1 were log-transformed, accounting for the lowest nonzero value. Because environmental variables had been measured on different scales, each measure was relativized by adjusting values to the standard deviation of each column’s mean value.

Cluster analysis

To analyze how species grouped together within the mixed-conifer community, rare species (encountered < 8 times, present on $< 2\%$ of all plots), were deleted leaving 31 species. Indicator species analysis was used (Dufrene and Legendre 1997) to determine the optimal number of groups for pruning the cluster dendrogram. The 31 understory species were repeatedly clustered using a Sorensen distance measurement and flexible beta linkage ($\beta = -0.25$) into 2–15 groups. For each run, indicator values for each species were summed and the cluster step with the smallest average p -value was selected as the most informative number of clusters (McCune and Grace 2002).

To examine understory habitat conditions, plots with similar environmental variables were grouped. Plots were analyzed with hierarchical cluster analysis using the Sorensen distance measurement and flexible beta linkage ($\beta = -0.25$). The cluster dendrogram was inspected and parsed to 4 groups to retain at least 50% of the data information.

Ordination

Nonmetric dimensional analysis (NMS) was used to investigate indirect gradients influencing species distribution. Seventy plots were identified as out-

liers (% cover > 2 STD) and they were deleted from the ordination analysis. All of these plots lacked any herb or shrub cover. The remaining matrix was still ‘sparse’ and was transformed with Beals smoothing to avoid the ‘zero-truncation problem’ (Beals 1984). NMS was run using the Sorensen distance measure, 6 starting axes, 40 iterations and an instability criterion of 0.00001. The plots in the environmental dataset, identified by habitat type, were reduced to the same 332 plots retained in the plant dataset for the ordination and used as the second data matrix. Using this second data matrix, a joint plot of significant ($r^2 \geq 0.2$) environmental variables was overlaid on the ordination of plots and plant species.

Regression trees

Regression tree analysis was used to identify significant environmental variables associated with total herb and shrub cover, and herb richness. Regression trees are a part of classification and regressions tree analysis, or CART, for continuous dependent variables (Breiman et al. 1984; Moore et al. 1991). As a nonparametric, recursive model, regression trees can sometimes uncover ecological relationships that are difficult to discern with conventional multivariate linear techniques (Vayssières et al. 2000; De’ath 2002). For each of the three regression trees, ‘pruning’ used a minimum node size of 10 and a minimum node deviance of 0.01.

Results

The forest has a rich understory community (high gamma richness), but one in which most species are infrequent (low alpha) and therefore plots are highly heterogeneous (high beta) (Table 1). The herb community has many more species (84) and greater evenness (the most abundant, *Pteridium aquilinum*, only accounts for 11.5% of total herb cover) than the shrub community’s 14 species and strong dominance by *Ceanothus cordulatus* (75% of total shrub cover). Average herb cover is low (2.5%) and highly variable, while shrubs (14.7% cover) are distributed in large, discrete patches. A comparison of total herb and shrub cover found they are significantly negatively correlated

Table 1. Richness, diversity, total herb and shrub cover, and soil characteristics of the mixed-conifer understory community at the Teakettle Experimental Forest.

| | Mean | Standard deviation |
|---------------------------|-------|--------------------|
| Alpha richness | 2.75 | |
| Beta richness | 35.64 | |
| Gamma richness | 98 | |
| Shannon's index (H) | 0.401 | |
| Simpson's index (D) | 0.217 | |
| Herb cover (% cover) | 2.46 | 8.65 |
| Shrub cover (% cover) | 14.73 | 25.7 |
| Litter depth (cm) | 4.41 | 4.52 |
| Rock (% cover) | 5.98 | 18.03 |
| May soil moisture (%) | 19.5 | 3.8 |
| October soil moisture (%) | 8.6 | 5.2 |
| Depth to bedrock (cm) | 122.3 | 65.2 |
| Soil pH | 5.24 | 0.34 |

Soil pH values are from 82 samples points (Heather Erickson unpublished data), as all other values are from 402 sample points.

(Spearman's $r_s = -0.33$, $p < 0.01$) indicating shrubs and herbs usually occupy different sites.

Evaluation of the graphs of the change in the total number of species and the distance between a subsample and the complete sample plotted against the number of samples indicated a species rich community with sparse cover. Two jackknife estimates of total species richness within the sample area, using the projected asymptote of the species presence curve, were 126 and 141 species. With the 10 m² plot used in this study, a large sample size is needed (>200 plots) to estimate all

of the species present and obtain a representative sample of species abundance.

Using measures of canopy cover and the understory environment, there are four distinct understory habitat types (Table 2). The most common (61%) is a mesic, closed-canopy condition which also has high cover of coarse woody debris. A second habitat type (22%) has a more open canopy, drier understory, and well-developed litter layer. A third condition (11%) is a dry gap with shallower soils and without litter or coarse woody debris. A fourth habitat (6%) has rock cover or very shallow soils with little soil moisture.

Using the most common 31 species, four understory plant communities were identified (Table 3). The first community (snowberry) contains 13 species, 8 of which are significant ($p < 0.05$) indicators of that plant community. The second community (pussypaws) has 10 herb taxa with low average cover (0.7%) but high frequency (mean occurrence = 7%). The third community (greenleaf manzanita) is dominated by shrubs (4 of the 5 species) including the two most abundant shrubs at Teakettle, *Ceanothus cordulatus* and *Arctostaphylos patula*. A fourth community (dwarf chinquapin) contains only two species, the shrub *Chrysolepis sempervirens* and *Pyrola asarifolia* (bog wintergreen).

For the NMS ordination the greatest reduction in stress was achieved with two axes. The proportion of variance (the fit between distance in the ordination and the original space) represented by

Table 2. Environmental variables distinguishing four major habitat types within Teakettle's mixed-conifer forest.

| | Habitat types | | | |
|---------------------------------|----------------------|--------------------|----------------------------|----------------------|
| | Mesic, closed canopy | Partial canopy | Dry gap, thin litter layer | Rock or shallow sand |
| % of total samples (# of plots) | 61 (246) | 22 (88) | 11 (44) | 6 (24) |
| Mean October soil moisture (%) | 10.2 ^a | 6.6 ^b | 6.0 ^b | 4.1 ^c |
| Depth to bedrock (cm) | 141.0 ^a | 125.6 ^a | 90.1 ^b | 48.4 ^c |
| % cover CWD | 17.0 ^a | 5.3 ^b | 0.6 ^c | 1.7 ^c |
| Litter depth (cm) | 5.6 ^a | 5.4 ^a | 1.3 ^b | 2.3 ^b |
| Bare ground (%) | 0.9 ^a | 0.2 ^a | 23.7 ^b | 1.7 ^a |
| Rock | 2.0 ^a | 0.1 ^b | 0.3 ^b | 32.4 ^c |
| Canopy cover (%) (Hemi. photo) | 82.0 ^a | 72.1 ^b | 55.0 ^c | 59.4 ^c |
| Direct PPFD | 11.9 ^a | 14.5 ^b | 19.8 ^c | 20.3 ^c |
| Diffuse PPFD | 1.6 ^a | 2.0 ^b | 2.5 ^c | 2.6 ^c |
| Total herb cover (%) | 7.1 ^a | 0.6 ^b | 0.2 ^b | 0.4 ^b |
| Total shrub cover (%) | 8.1 ^a | 47.6 ^b | 12.6 ^c | 15.4 ^c |

The mean total herb and shrub cover for each of the habitats are shown for reference, but they were not used in the cluster analysis determining the habitats. Values within a row with different superscripts are significantly different ($p < 0.05$ using ANOVA and Dunnett's C post-hoc analysis).

Table 3. Four communities of herb and shrub species in Teakettle's mixed conifer determined by indicator species analysis.

| Snowberry | Pussypaws | Greenleaf Manzanita | Dwarf Chinquapin |
|---|--|--|---|
| <i>Symphoricarpos mollis</i> (0.001) | <i>Calyptridium umbellatum</i> (0.001) | <i>Arctostaphylus patula</i> (0.001) | <i>Chrysolepis sempervirens</i> (0.001) |
| <i>Hieracium albiflorum</i> (0.002) | <i>Collinsia parviflora</i> (0.001) | <i>Ceanothus cordulatus</i> (0.001) | <i>Pyrola asarifolia</i> (0.001) |
| <i>Kelloggia galioides</i> (0.006) | <i>Eriogonum nudum</i> (0.001) | <i>Corylus cornuta</i> (0.037) | |
| <i>Poa</i> spp. (0.008) | <i>Galium bifolium</i> (0.001) | <i>Prunus emarginata</i> (0.103) | |
| <i>Osmorhiza chilensis</i> (0.012) | <i>Pedicularis semibarbata</i> (0.001) | <i>Cynoglossum occidentale</i> (0.432) | |
| <i>Ribies roezlii</i> (0.027) | <i>Monardella odoratissima</i> (0.004) | | |
| <i>Pteridium aquilinum</i> (0.029) | <i>Arabis platysperma</i> (0.004) | | |
| <i>Quercus kelloggii</i> (0.042) | <i>Linanthus ciliatus</i> (0.013) | | |
| <i>Silene lemmonii</i> (0.077) | <i>Viola purpurea</i> (0.072) | | |
| <i>Pyrola picta</i> (0.078) | <i>Lupinus fulcratus</i> (0.112) | | |
| <i>Ribies sanguineum</i> (0.132) | <i>Senecio aronicoides</i> (0.267) | | |
| <i>Allophylum intregifolium</i> (0.366) | | | |
| <i>Piperia unalascensis</i> (0.439) | | | |

Each column begins with a community name using the common name for the most significant indicator plant. *p* values, in parentheses, are calculated from a Monte Carlo significance test of the observed maximum indicator value for each species.

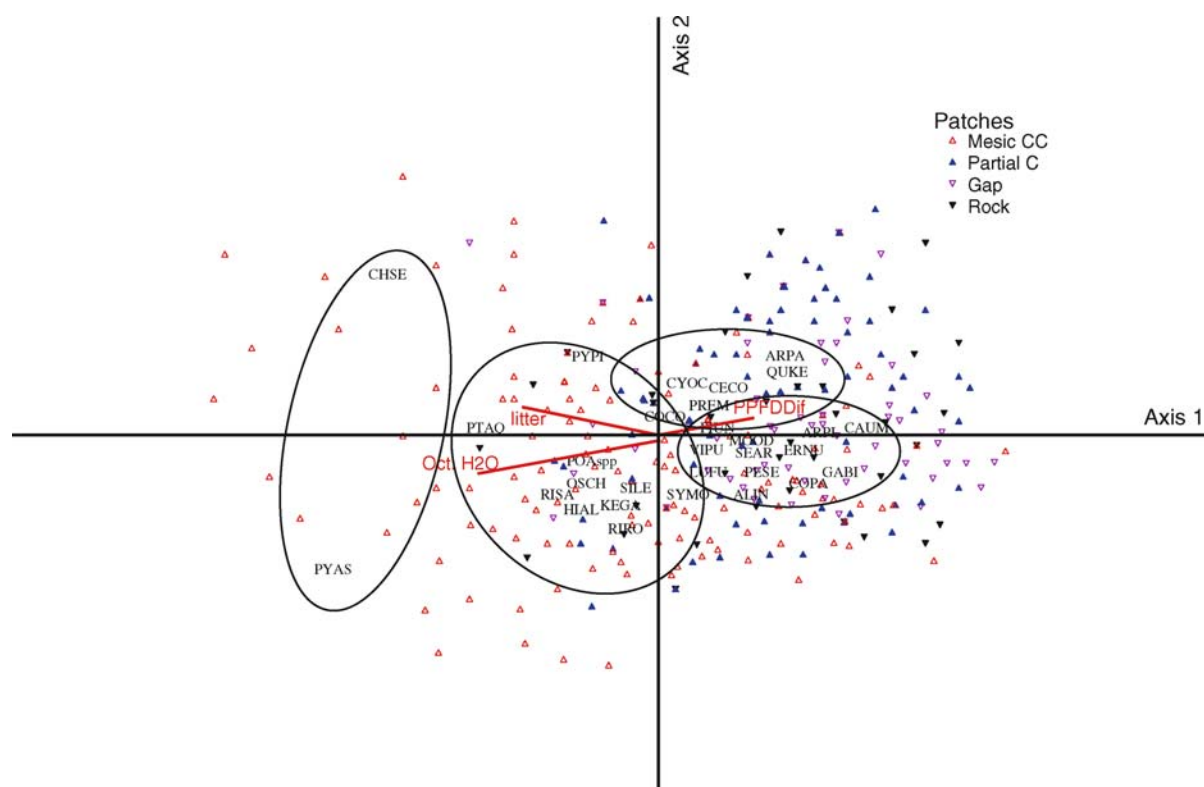


Figure 2. Nonmetric dimensional scaling ordination of the 31 most common plant species (given in four letter code – see Table 3) and the 332 plots which had plant cover. Plots are shown with four symbols indicating their habitat type. The four ellipses enclose core species in the four plant communities identified by indicator species analysis. The joint plot shows the significant environmental variables, the magnitude and direction of their gradient, within the ordination space.

the first and second axes were 0.404 and 0.396, respectively (cumulative = 0.800). The NMS ordination (Figure 2) shows a general correlation

of the species in the snowberry and pussypaws plant communities (Table 3) with microsites identified as mesic, closed-canopy habitats (Table 2).

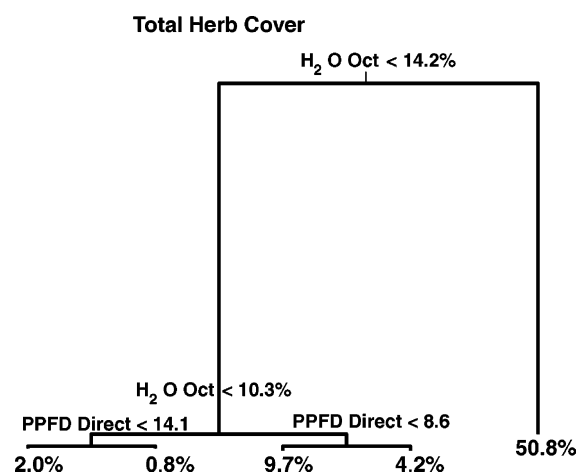


Figure 3. Regression tree analysis of environmental variables associated with total herb cover. The grouping of values in each split is indicated by the direction of the < symbol (e.g., plots with < 14.2% moisture are split off to the left side of the dendrogram in the first split). The length of each branch is proportional to the amount of data variability explained by each split. Terminal values are the average herb cover for all the plots classified in that node.

The 9 herb and 4 shrub taxa in the snowberry community are usually associated with mesic (ex. *Ribes* spp.) or closed-canopy (*Symphoricarpos mollis*) conditions (Potter 1998). The pussypaws community contains species characteristic of drier sandy soils yet still under a mixed-conifer canopy. Shrubs in the greenleaf manzanita community, particularly the dominants *Arctostaphylos patula* and *Ceanothus cordulatus*, are associated with microsites typed as partial-canopy habitats. The two taxa in the dwarf chinquapin community are associated with mesic closed canopy habitat which has a thick litter layer and higher soil moisture. The joint plot of environmental variables identifies October soil moisture, litter depth, and diffuse PPFD as being the most significant environmental conditions associated with the ordination's gradients. Soil moisture and litter depth are associated with more herb species and diffuse light is associated with most of the shrub species.

When total percent cover of herbs is analyzed against environmental conditions using regression trees, soil moisture is the most significant site factor. The highest herb cover (> 50%) is in plots with > 14.2% soil moisture in October (Figure 3). The next highest herb cover (9.7%) is in plots with > 10.3% October moisture and less direct sunlight

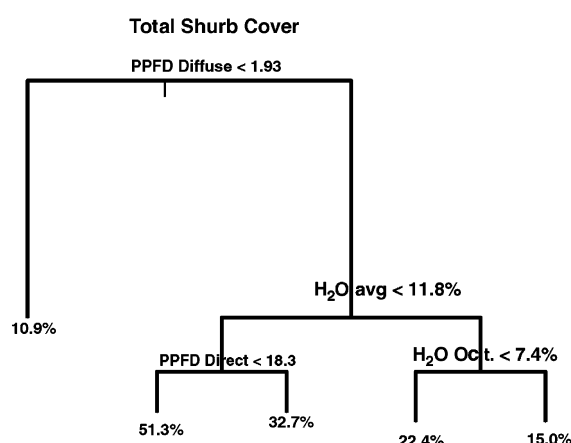


Figure 4. Regression tree analysis of environmental variables associated with total shrub cover. Terminal values are the average shrub cover for all the plots classified in that node.

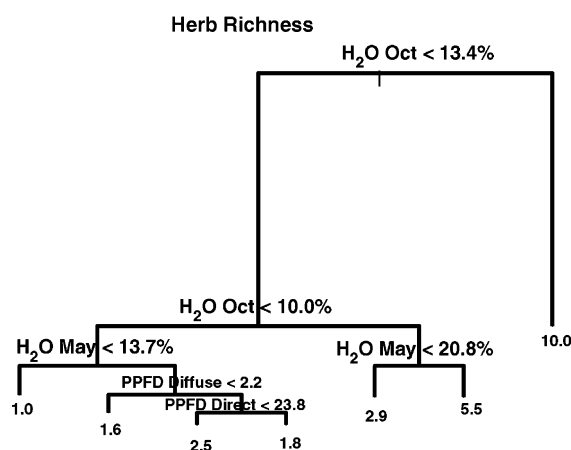


Figure 5. Regression tree analysis of environmental variables associated with total herb richness. Terminal values are the average number of herb species for all the plots classified in that node.

(PPFD < $8.6 \mu\text{mol s}^{-1} \text{m}^2$) (Figure 4). The highest total shrub cover is present with more diffuse light (PPFD > $1.93 \mu\text{mol s}^{-1} \text{m}^2$), less average (May and October) soil moisture, and less direct light (Figure 4). For sites with > 11.8% average moisture, shrub cover is higher on sample points with less October soil moisture (< 7.4%). Total herb richness is associated with higher October soil moisture and to a lesser extent, May soil moisture, more diffuse and less direct light (Figure 5).

Discussion

Covariation of environmental conditions makes it difficult to identify individual gradients that influence understory composition. Surveying the literature, Pausas and Austin (2001) examined patterns of plant richness in relation to nutrients, water, light, temperature, environmental heterogeneity, and disturbance. They found a general tendency for species richness to increase with temperature, water availability and environmental heterogeneity, and decrease with nutrient enrichment. They noted, however, that plant richness is rarely a linear response to changes in these gradients because interactions between these parameters often produce resource limitations. In the prolonged summer droughts characteristic of Mediterranean climates, temperature increases can reduce water availability by increasing evaporative demand. In semi-arid ecosystems in South Africa, plant species richness was negatively correlated to energy availability because higher light environments had less available water (Hoffman et al. 1994). This relation may explain why a statewide analysis of California found the strongest environmental variable associated with plant richness was a positive correlation with precipitation, followed by a negative correlation with temperature (Richerson and Lum 1980).

In forests, environmental variables often covary because they are strongly influenced by structural characteristics such as canopy cover, litter depth and coarse woody debris that change with stand development. At the microsite scale of this study, temperature and light are directly affected by tree canopy cover and their interaction influences soil moisture. Light needed for photosynthesis supplies energy which increases evaporative demand and the potential for moisture stress (Pausas and Austin 2001). Unfortunately we do not have surface temperature measurements at each of our 402 sample points. A study of microclimate at Teakettle, however, found direct PPF_D values were highly correlated with soil surface temperatures which can reach 50 °C during summer months (North et al. 2002). Diffuse PPF_D was not significantly correlated with temperature. There is a broad array of diffuse and direct PPF_D conditions in Sierran mixed conifer because localized stand density ranges from dense tree clusters to large open gaps. In our analyses we separated direct

from diffuse PPF_D because of direct PPF_D's potential to raise surface temperature and have a negative effect on plant establishment and growth, and diffuse PPF_D's potential measure of photosynthetic light and positive effect on plant growth. This PPF_D separation is a rough approximation which may not separate the actual benefit and detriment of light's effect on temperature, photosynthesis and soil moisture.

Patterns of understory richness may be better understood when plants are separated into functional groups (Pausas and Austin 2001; Grimes 2002). In mixed conifer, the key functional distinction is between annual herbs which complete their life cycle shortly after snowmelt, and perennial shrubs which tolerate high temperatures and scarce soil moisture during the long summer drought. Herbs have high richness and evenness, and low frequency. Both richness and total cover are significantly higher on sites which have, on average, > 13% volumetric soil moisture content in October. Herb response to light varies between direct and diffuse PPF_D. Higher cover and richness is associated with less direct light, while diffuse light is a less significant influence on herb richness only. Most of the herbaceous cover is under mesic, closed-canopy habitat in tree clumps characterized by low direct PPF_D and a deeper litter layer. Direct PPF_D and litter depth may be significant influences on the herbaceous community because of their effect on soil moisture. Snow pack melts much earlier and surface soil temperatures are much higher in gaps with direct sunlight (Barbour et al. 1991; North et al. 2002). Litter depth is significantly positively correlated (Pearson coefficient = 0.69, $p < 0.05$) with October soil moisture.

In contrast, shrubs are limited to 14 taxa, cover is highly dominated by *Ceanothus cordulatus*, and shrubs form large contiguous patches. Most shrubs are on the edge of tree clumps and gaps with high levels of diffuse light and low soil moisture. The importance of diffuse light was unexpected as most mixed-conifer shrubs are usually considered to occupy gaps until they are overtopped by conifers. In our study, however, we found they occupy ecotone areas between tree clumps and open gaps.

In the southern Sierra Nevada, old-growth mixed conifer is characterized by canopy gaps, rock outcroppings and a range of soil depths

creating a distinct forest patch pattern. These patches have a wider range of light, temperature, moisture and substrate conditions than most mature forests with continuous canopy cover. This distinct patch pattern likely influences the significant association between habitat and plant community.

In mixed conifer, plant functional type and habitat conditions appear to structure the understory plant community. The greenleaf manzanita community is dominated by drought-tolerant shrubs associated with dry, diffuse-light habitats. Both the snowberry and pussypaw communities are associated with closed-canopy habitat. The ordination suggests all the herbs in the pussypaw community are on slighter drier sites than the herbs and mesic shrubs in the snowberry community. The dwarf chinquapin community is also associated with mesic closed canopy habitat but the ordination suggests both of its taxa, *Chrysolepis sempervirens* and *Pyrola asarifolia* are on sites with high moisture and litter. Both species are common in red-fir forests which have a deeper snow pack and thicker litter layer (Potter 1998; Barbour and Minnich 1999). These more mesic conditions, however, are also common in mixed conifer in riparian and cold drainage areas (North et al. 2002).

Available soil moisture is the most significant influence on understory plant composition. Soil moisture is influenced by several factors including soil porosity, depth to bedrock, litter depth, temperature and plant use. All of our sample points were on granitic Sierran soils, which have similar texture and are typically well-drained (North et al. 2002). While all plots have approximately equal soil moisture immediately after snow melt (i.e., low standard deviation in May values in Table 1), habitat types differ in soil moisture by October (Table 2). The pattern may be due to differences in depth to bedrock and plant functional types between the four habitat types. Closed canopy habitats have the deepest soils and retain the most soil moisture in October while rock or shallow sand habitats have the least soil moisture and shallowest soils. Closed canopy and partial canopy habitats types have comparable litter and soil depths but significantly different October soil moisture, suggesting that some other factor may be responsible for determining fall soil moisture. One explanation may be the high shrub cover in the partial canopy

habitat (48%). The two dominant shrubs, *Arctostaphylos patula* and *Ceanothus cordulatus*, are aggressive competitors for soil moisture and can transpire at much lower soil water potentials than herbs or conifers (Hubbert et al. 2001; Royce and Barbour 2001a, b). The soil moisture difference between partial canopy and gap habitats may be due to a combination of shallow soil and litter depths, and higher temperatures (PPFD direct). A controlled experiment is needed to separate the relative influence of these factors on soil moisture differences between habitats.

Mixed-conifer forests are very patchy creating high resource heterogeneity, a condition often linked to plant community structure (Vila and Sardans 1999; Pausas and Austin 2001). Fine scale differences in water, light and nutrient availability have been correlated with plant diversity (Frelich et al. 2003) and changes in these conditions can affect composition and cover of understory plants (Carson and Pickett 1990). Some studies, however, have suggested low resource quantity more than heterogeneity is associated with higher diversity (Moody and Meentemeyer 2001; Henry et al. 2002). This may not be true in Sierran mixed conifer where the highly diverse herb community occurs when soil moisture is high, and the low-diversity shrub community occupies resource-poor microsites. Temporal changes in water availability and differences between plant functional groups make it difficult to disentangle the effects of resource quantity and heterogeneity on mixed-conifer understory diversity.

Disturbance history can be a strong influence on understory species richness and abundance. Herbs in the mixed-conifer forest may have been reduced in cover and richness by the past decades of fire suppression, if historic increases in tree density have reduced soil moisture. Higher canopy cover produced by fire suppression will reduce understory light, but our analyses suggest this will have less of an effect than competition for soil moisture. The principal water competitors with herbs and shrubs will not be large trees – which usually have relatively deep roots (Arkley 1981; Anderson et al. 1995) – but rather small diameter trees in dense patches (i.e., ‘dog-hair thickets’ of trees < 30 cm dbh).

Mixed-conifer shrubs may be less affected by fire suppression because shrubs can still transpire in very dry conditions when herbs have wilted and

conifers have shut down (Hubbert et al. 2001). Indeed, at Teakettle few herbs and trees are found in shrub patches (North et al. 2002). In the absence of fire over time, shrubs may grow into the large patches observed at Teakettle, possibly checked only by the low light and high temperature environments of tree clumps and open gaps, respectively.

After a century of fire suppression in the Sierra Nevada, prescribed fire and mechanical thinning are being widely applied as restoration techniques. We do not yet know what effects these treatments will have on the understory community. This research, conducted in fire-suppressed old growth, may help identify factors which influence understory richness and abundance. Reductions in shallow soil moisture, litter depth or increases in direct light are likely to have the strongest effect on this highly diverse community.

Acknowledgements

We thank the Sierra Nevada Research Center for providing support for this project. Field work was aided by the technicians at Teakettle during the summer of 2000. We especially thank Harold Zald, PNW Forest Inventory and Analysis, for the depth to bedrock data.

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