Stand Conditions Associated with Tree Regeneration in Sierran Mixed-Conifer Forests

Andrew N. Gray, Harold S. J. Zald, Ruth A. Kern, and Malcolm North

Abstract: Fire suppression has significantly increased canopy cover, litter depth, and stem density in many western forests, altering microsite conditions that affect tree seedling establishment. We conducted studies in a mixed-conifer forest in the Sierra Nevada, California, to determine relationships between established understory trees and microsite quality, and to examine the effect of fire intensity and shrub cover on seedling establishment. Most of the conifer species were found on microsites with relatively high soil moisture and relatively low direct solar radiation. All species had greater frequency under shadier conditions except for Jeffrey pine, which was found on drier, more open microsites. Although seedlings were more abundant on mineral soil than expected, intact litter and forest floor was not a barrier to establishment. Mortality of planted seedlings was high, particularly in exposed areas. Although shrub cover may initially aid survival, few conifer saplings were present in shrub-dominated patches, possibly because shrubs can be aggressive competitors for soil moisture. The lack of regeneration, logs, or snags in many openings suggest that large gaps are hostile environments for tree seedlings. Results suggest that reductions in shrub cover may benefit tree establishment, but increasing understory light and decreasing surface soil moisture through canopy cover reductions may not. FOR. SCI. 51(3):198–210.

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OVER THE LAST CENTURY, fire suppression has dramatically changed forest composition and structure in many forest types throughout the western United States (Cooper 1960, Kilgore 1973, Agee 1993). Within the Sierra Nevada's most common forest type, mixed conifer (Helms 1995), forests had less tree canopy cover during presettlement disturbance regimes, with greater dominance by large open-grown pines (Parsons and DeBenedetti 1979, Helms and Tappeiner 1996). Fire suppression and the harvest of large pines is believed to have changed tree species composition and forest structure, with increased abundance of under-story and mid-story shade-tolerant firs and incense cedars, increased canopy cover, and reduced gap size and abundance (Kilgore 1973, Parsons and DeBenedetti 1979, Weatherspoon et al. 1992, Ansley and Battles 1998). The increased density and layering of these forests makes them more susceptible to high-intensity crown fires that were probably less common during the presettlement fire regime (Kilgore 1973, McKelvey et al. 1996). In recent decades, policy on National Forests in the Sierra Nevada has attempted to shift from fire suppression to applying an understanding of presettlement fire regimes using a combination of prescribed burning and thinning treatments (SNEP 1996).

The future composition, structure, and function of Sierran mixed-conifer forest will be highly dependent on the response of tree regeneration to management practices. Despite the importance of regeneration, it is not clear how within-stand structural and environmental conditions, along with inter- and intra-specific competition, control tree establishment and growth in these forests. Thinning and burning treatments reduce overstory canopy cover and tree density, changing light, soil moisture, and nutrient levels in the understory. Past studies of mixed-conifer regeneration have provided valuable information about stand-level response to different silvicultural treatments (e.g., Fowells and Stark 1965, Stark 1965, Lilieholm et al. 1990, Oliver and Dolph 1992), or the detailed response of a few species (e.g., Tappeiner and Helms 1971, Radosevich 1984). Better information on the comparative behavior of different species to specific within-stand microsite conditions should aid managers when planning silvicultural or fuel-reduction prescriptions.

Seedling establishment is a critical life history stage

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when tree survival and growth is most sensitive to the microsite environment and the resources available. Light competition is often considered the primary limiting resource for tree regeneration and growth in the Sierra (e.g., McDonald 1976, Van Pelt and Franklin 2000), but belowground resources, particularly soil moisture, are important as well (Fowells and Stark 1965, Tappeiner and Helms 1971, Royce and Barbour 2001). In the Mediterranean climate of the southern Sierra Nevada, almost all soil moisture is derived from the winter snowpack (Major 1990). Soil moisture levels decline rapidly during the summer drought, leading to soil moisture deficits even at high elevations (Parker 1994). Soil depth may influence tree establishment by determining the volume of soil available for water storage from melting snow, but substrate may also be important. Although an organic litter layer is often a barrier to seedling establishment, coarse woody debris can be an important substrate for tree regeneration in some forest types (Harmon and Franklin 1989, Gray and Spies 1997) and well-decayed logs can act as moisture reservoirs during summer droughts (Maser and Trappe 1984). Within the shallow soil layer used by small seedlings, mixed-conifer tree species are able to deplete moisture to different minima, but can be less effective at extracting water from dry soil profiles than shrubs (Royce and Barbour 2001).

Shrubs have generally been considered a problem for tree establishment in the Sierra, particularly in response to silvicultural treatments, by depleting soil moisture and reducing light levels (Fowells and Stark 1965, Radosevich 1984, Tappeiner and McDonald 1996). Shrub density can increase dramatically through sprouting or seedling establishment in response to reductions in overstory canopy cover and fire intensity (Tyler 1995). However, several authors have suggested that shrubs may be able to enhance seedling survival by ameliorating temperature extremes, sharing of ectomycorrhizal fungi, or enriching available soil nitrogen (Tappeiner and Helms 1971, Sparling 1994, Dunne and Parker 1999, Horton et al. 1999, Oakley et al. 2003). Although regeneration dynamics will significantly affect mixed-conifer restoration efforts, we still have only a limited understanding of the importance of edaphic conditions, substrate quality, and shrub competition on seedling establishment and growth.

The objectives of this article were to: (1) determine the relationships between different species of naturally-established tree seedlings and light, soil moisture, canopy cover, shrub cover, and forest substrate conditions, and (2) experimentally examine the effects of fire intensity, shrub composition and cover, and microenvironment (soil moisture, soil and air temperature) on seedling growth and survival. We conducted our research in a mixed-conifer forest, which, similar to much of the Sierra Nevada, had not experienced fire in over a century (Fiegener 2002). We worked in an old-growth forest to avoid complications from effects of prior management and to concentrate on the relationships between variable mixed-conifer conditions and regeneration. Burning and thinning treatments were completed in our microsite regeneration study area in 2001 and we will follow the effects of these widely-used restoration methods in future research.

Methods

Site Description

The study was conducted in Sierran mixed-conifer forest at the Teakettle Experimental Forest (36°58′ N, 119°02′ W), 80 km East of Fresno in the Kings River Ranger District of the Sierra National Forest, California (North et al. 2002). Elevation ranges from 1,900 to 2,600 m and slopes range from 15 to 60%. Soils are dominated by Dystric and Lithic Xeropsamments of loamy sand to sandy loam textures (USDA Forest Service and Soil Conservation Service 1993) derived from granitic rock, with exposed weathered and unweathered rock common throughout the study area. The climatic regime is Mediterranean, with the annual precipitation of 125 cm falling almost entirely as snow between Nov. and Apr. The mixed-conifer forest was dominated by white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.) and incense-cedar (*Calocedrus decurrens* (Torr.) Florin). However, the largest trees were sugar pine (*Pinus lambertiana* Dougl.) and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf). Red fir (*Abies magnifica* A. Murr.), California black oak (*Quercus kelloggi* Newberry), and bitter cherry (*Prunus emarginata* [Dougl. ex Hook.] D. Dietr.) were also present in small quantities in the overstory (i.e., trees at least 5 cm dbh).

Regeneration Microsites

Seedling composition and abundance, and associated environmental and forest structure data, were collected on 18 replicated 4-ha plots during the summers of 1998, 1999, and 2000. Replicates were selected for similarity in overstory composition and structure, based on cluster and semivariogram analyses of sample plots across the Experimental Forest (North et al. 2002). In six of the plots, 49 grid points were established on a 25 $\times$ 25-m spacing, whereas in the remaining 12 plots, 9 grid points were established on a 50 $\times$ 50-m spacing. These systematically-placed points sampled a wide range of conditions, from ridgetops and mid-slopes to riparian areas.

All trees <5 cm dbh were tallied on 3.5-m radius (38.5 m^2) plots centered on each grid point ($n = 402$), for a total sample area of 1.55 ha. Seedling plots were divided into quadrants and individuals of each species were counted by size class. The size classes were: 5–50 cm in height (termed "seedlings"), 50–137 cm, and >137-cm tall and less than 5 cm dbh (the latter two classes are termed "saplings"). The tallest seedling or sapling of each species in each quadrant was measured and the substrate it was rooted in was classified as either litter, forest floor, woody debris, mineral soil, or rock.

All trees ≥5 cm dbh within each replicate plot were mapped with a surveyor's total station. Grid point coordinates were used to identify trees within 12.6-m radius (500 m^2) to calculate basal area and tree density for each point.

The solar radiation environment above each point was estimated using digital photographs taken with a Nikon Cool Pix 950 camera with a Nikkor FC-E8 0.21X fisheye converter. Images were taken in black and white at dawn or dusk with uniformly cloudless sky conditions. Digital images were analyzed using SCANOPY software (Régent instruments Inc., Quebec, Quebec, Canada). Estimated radiation variables were indirect site factor (ISF) and direct site factor (DSF), or the estimated proportion of indirect and direct radiation compared to an open site at the same latitude, respectively. Images were processed before the radial distortion of the fisheye lens was described (Frazer et al. 2001), but the relatively small errors are not expected to affect our within-stand comparisons greatly. Volumetric soil water content in the top 15 cm of soil in mid-Oct. 1998 and mid-May 1999 was estimated once for each time period at each point using time domain reflectometry (TDR, model 1502C, Tektronix Inc., Beaverton, OR) with permanently-installed 30-cm probes inserted at an angle (Gray and Spies 1995). Additional mid-summer measurements taken with a different TDR machine proved unusable. Nevertheless, the May sample captured soil moisture conditions at the beginning of the growing season, and the Oct. sample captured conditions of high drought stress at the end of the growing season. Cover of shrubs and herbs by species, coarse woody debris by decay class, mineral soil, and rock was estimated, and litter depth at five random locations was measured, in 1.78-m-radius (10 m^2) plots around each grid point.

Fire and Shrub Effects

Experimental plots were established to investigate the effects of fire intensity and shrub cover on tree regeneration. Nine 10 × 10-m plots were established, three each with no burn (control) treatment, light burn (no added fuels, some foliage burned), or hot burn (fuels added before burn, resulting in nearly complete foliage burned off and some stems charred). Each plot had little or no overstory tree canopy cover, and encompassed one patch each of similarly dense whitethorn ceanothus (*Ceanothus cordulatus* Kellogg) and greenleaf manzanita (*Arctostaphylos patula* Greene), with the remaining area being bare ground. Shrub patches measured 4–10 m^2 before being burned. Plots were burned in Oct. 1999.

White fir and sugar pine seedlings obtained from the USFS nursery at Placerville, CA (1 year old, bare root) were planted in each of the three patch types—open, ceanothus, and manzanita, 15 seedlings per patch, at ~30-cm spacing, in May 2000 and watered daily for 1 week to promote establishment. Because of high seedling mortality during the summer 2000 growing season, the experiment was restarted by planting new seedlings in Oct. 2000. This timing was chosen because it was after fall rains had saturated the soil and allowed seedling establishment at a time of little evaporative demand. Each seedling was mapped and measured to follow individual growth and survivorship.

Volumetric soil water content was monitored at each burn by patch treatment location ($n = 27$) at biweekly intervals throughout May-Sept. 2001 and 2002 with permanent probes sampling two depths (0–15 and 0–45 cm) using TDR. Soil temperature 10 cm below the surface and air temperature 30 cm above the surface were monitored continuously in each of the 27 treatment combinations and replicates using HOBO H8 temperature/external temperature data loggers (Onset Computer Corporation, Pocasset, MA).

Analysis

Separate multiple regression models were developed to evaluate the importance of environmental, substrate, and shrub cover variables (Table 1) on the distribution of each species of understory tree. Because seedling density is affected by many factors in addition to site suitability (e.g., seed production and predation), the independent variable used was the odds ratio of tree frequency (hereafter referred to as "frequency"), expressed as the number of quadrants occupied by a species over the number of quadrants per grid point (four). Logistic regression was applied using a nominal model, where the response function was the logits of the

Table 1. Environmental variables used in the analysis of regeneration microsites at systematic grid points, and their means and standard deviations ($n = 402$).

Variable code	Mean (SD)	Definition
DSF	0.297 (0.168)	Direct site factor (proportion)
ISF	0.292 (0.108)	Indirect site factor (proportion)
GSF	0.297 (0.157)	Global site factor (= 0.5 * ISF + 0.5 * DSF)
OCT98	8.64 (3.79)	Volumetric soil moisture from sample in mid-Oct. 1998 (%)
MAY99	16.5 (5.35)	Volumetric soil moisture from sample in mid-May 1999 (%)
SOILH$_2$O	12.6 (4.28)	Mean of OCT98 and MAY99 (%, ln-transformed)
LITTDPTH	4.47 (4.59)	Depth of litter and/or forest floor (cm)
LITTER	72.1 (27.7)	Cover of litter and forest floor (%)
CWD	8.40 (16.6)	Cover of coarse woody debris ≥ 10 cm diameter (%)
SOIL	4.61 (15.6)	Cover of mineral soil (%)
SHRUB	14.0 (25.8)	Cover of all shrubs except RIRO (%)
RIRO	0.36 (2.68)	Cover of Sierra gooseberry (*Ribes roezlii*) (%)
BAHA	62.5 (54.4)	Basal area of trees ≥ 5 cm dbh (m^2/ha)
TPH	431 (337)	Density of trees ≥ 5 cm dbh (n/ha)

gridpoint frequencies, and the probability distribution was binomial (GENMOD procedure, SAS Institute, 1999). Models were built by running regressions for each species on all independent variables individually, starting with the most significant variable (evaluated with the likelihood ratio Type III F-test value), and adding additional significant ($P < 0.05$) variables. Multicollinearity could introduce errors into the assessment of important independent variables, and was minimized by avoiding large changes in the estimated regression coefficients when an independent variable was added. This was done by using a conservative cutoff level of correlation between new variables and those already in the model of $r > 0.25$, and looking for wide confidence intervals (calculated with Wald tests) for the regression coefficients representing important explanatory variables. Although a coefficient of determination cannot be calculated in logistic regression, a somewhat comparable statistic, proportional reduction in deviance (PRD) was calculated using the deviance of the fitted model and the deviance of a null model with only an intercept fitted. The effect of the variables in the models on the estimated frequency provides a better assessment of their importance. This effect was assessed by setting values of all variables other than the one of interest to the average of the data set, and varying the values of the variable of interest to assess the amount of difference required to double the measure of frequency (as back-calculated from the logits).

Ordination with nonmetric multidimensional scaling (NMS) (Kruskal 1964, McCune and Grace 2002) was applied as a complementary method to evaluate patterns of species composition and the importance of environmental variables on those community patterns within a single analysis. NMS is a robust method of multivariate data reduction where no assumptions are required about normality of data or linearity of relationships. Based on ranked distances, NMS tends to linearize the relation between environmental gradients and community composition. Euclidean distance measures were used among tree species in *n*-dimensional ordination space. A random starting configuration was used for the iterations of the ordination, with 15 runs conducted with real data, and 30 with randomized data. Dimensionality of the data set was assessed by including additional dimensions that reduced the final stress by 5 or more (on a 0–100 scale). Two dimensions were used in the final solution. A Monte Carlo test using 141 iterations for the final solution indicated that the ordination was significantly different from random ($P = 0.0323$). The solution was stable, because stress declined rapidly with additional iterations and eventually settled at a stable low stress level (McCune and Grace 2002). Environmental variables with an $r^2 \geq 0.05$ with either axis were included in the joint plot.

TDR trace data were converted to volumetric soil content using an equation for low carbon-content soils (Gray and Spies 1995), which is very similar to the polynomial equation by Topp et al. (1980) used in most automated TDR soil moisture devices. Both soil moisture dates were similarly important for most of the logistic regression models, so moisture values were averaged over the two time periods (Oct. 1998 and May 1999) and log-transformed to avoid excessive influence of outlier observations on the logistic model deviance. A global site factor was calculated from ISF and DSF by assuming a 50:50% contribution of direct and indirect radiation to total radiation, which is a commonly used empirical average based on seasonal changes in solar declination, cloudiness, and atmospheric transmissivity (e.g., Canham et al. 1990). Summed shrub variables excluded Sierra gooseberry (*Ribes roezlii* Regel), which occurs on very different sites from the other shrub species (North et al. in press). The influence of shrub cover at each gridpoint was further examined by classifying cover levels as none, moderate, or high (0, 1–49, and 50–100% cover, respectively), and testing for differences in seedling frequency and environmental measurements with least-square means tests within logistic regression and analysis of variance (ANOVA), respectively.

Seedling survival, soil moisture, and temperature data from the fire and shrub effects experiment were analyzed with a repeated-measures split-plot ANOVA (GLM procedure, SAS Institute 1999). The arcsin–square-root transformation was applied to survival proportions before analysis. Least-square means tests on significant effects were applied to assess significant differences among means, keeping experiment-wise error rates to $P < 0.05$ in a procedure analogous to Fisher's protected LSD. Because of missing temperature data resulting from intermittent data-logger failure, only two replicates were used for the analyses of temperature response, instead of three. Hypotheses tested in these analyses included: (1) There is no significant difference in seedling survival, soil moisture, or air and soil temperature by burn intensity, shrub patch, or their combination across all dates sampled; and (2) There is no significant difference between species' seedling survival by burn intensity, shrub patch, or their combination across all dates sampled.

Results

Regeneration Microsites

White fir was the most abundant understory tree species, followed in descending order by incense cedar, red fir, bitter cherry, sugar pine, California black oak, and Jeffrey pine (Table 2). Examining just the conifers (because the hardwoods rarely attained overstory tree size), relative densities of species in the understory were often different from relative densities (expressed as either basal area or trees per hectare) in the overstory (Figure 1). Relative density of incense cedar in particular was much greater in the understory than in the overstory. Red fir regeneration was abundant, but primarily in the seedling size class. Relative density of saplings was similar to the relative density in the overstory. White fir relative densities were comparable in the overstory and understory. Relative densities of understory pines were substantially lower than relative densities in the overstory, particularly for Jeffrey pine. For all overstory species on the 72 ha of sample plots, density was 403.7 trees/ha, and basal area was 57.2 m^2/ha.

Frequency of understory trees (seedlings and saplings combined) was most strongly associated with microclimate

Table 2. Number of gridpoints (out of 402) where understory trees were found, density for seedlings (>5 and <50 cm tall) and saplings (≥50 cm tall and <5 cm dbh), and for saplings alone, at Teakettle Experimental Forest.

Species	Code	Grid points present (n)	Seedlings + saplings		Saplings only	
			(n/ha)	(%)	(n/ha)	(%)
Abies concolor	ABCO	172	1202	53.5	179	41.8
Abies magnifica	ABMA	22	281	12.5	9	2.1
Calocedrus decurrens	CADE	106	568	25.3	111	25.8
Pinus jeffreyi	PIJE	10	10	0.4	4	0.9
Pinus lambertiana	PILA	51	54	2.4	17	3.9
Prunus emarginata	PREM	19	100	4.4	88	20.5
Quercus kelloggii	QUKE	18	32	1.4	21	4.8
Total			2247	100	428	100

variables (Table 3), although the amount of the deviance explained by these models (PRD) varied among species. The amount of each variable required to double the estimated frequency is a more meaningful assessment of the importance of the variables in the model than PRD. For example, an increase in soil moisture (SOILH$_2$O) of 4.5% is expected to double the frequency of red fir, but an increase of 12% would be needed to have the same effect on white fir, which is unlikely because that amount is more than twice the standard deviation for that variable (Table 1). Frequencies of all species except Jeffrey pine and bitter cherry were positively associated with increasing soil moisture levels. Responses to both sample dates were similar for most species, so average moisture was used in the final models shown. Both fir species were negatively associated with direct solar radiation, DSF, whereas Jeffrey pine was positively associated with indirect radiation, ISF. Substrate cover entered into several of the models, with cover of litter and forest floor positively associated with frequencies of white fir, red fir, sugar pine, and black oak, whereas cover of mineral soil was negatively associated with bitter cherry. Total shrub cover was negatively associated with frequency of incense-cedar and sugar pine, but positively associated with frequency of cherry. Some variables were relatively highly correlated with each other, suggesting potential alternate variables of importance, e.g., ISF and DSF (r = 0.78), ISF and shrub cover (r = 0.32), and ISF and litter cover (r = −0.32).

The importance of environmental variables differed among size classes of the same species. Direct radiation was negatively associated with frequency of white fir and incense-cedar in the seedling size class, but was not as important as litter cover or shrub cover for the same species in

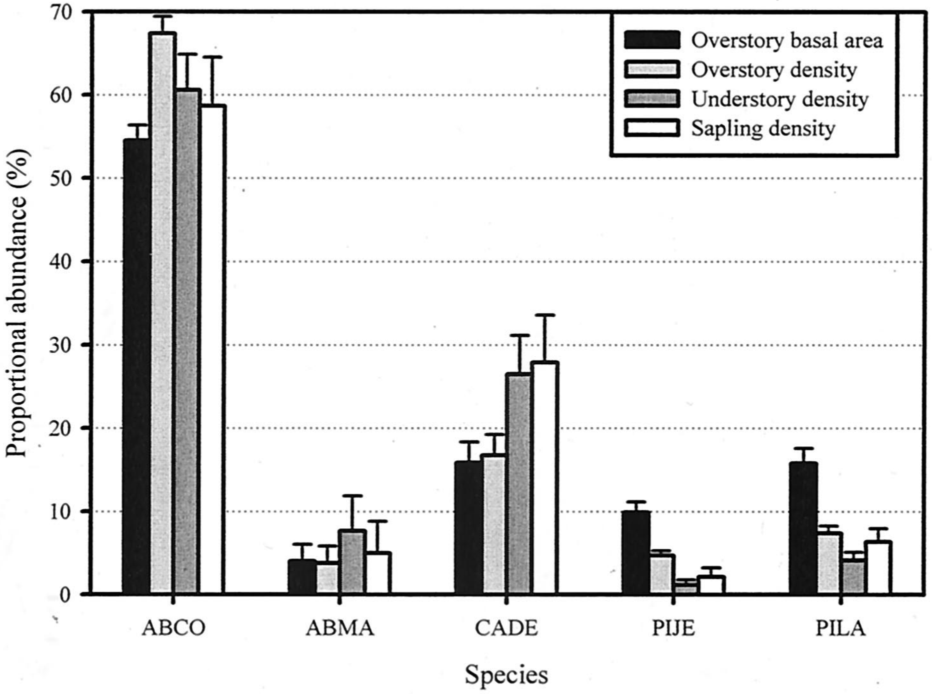

Figure 1. Comparison of proportional abundance of different conifer species for overstory trees (≥5 cm dbh), all understory trees (≥5 cm tall and <5 cm dbh), and for saplings only (≥50 cm tall and <5 cm dbh). For each variable, e.g., overstory basal area, the proportion of the total in a plot made up by each species was calculated. Means and standard errors across plots (weighted by the different numbers of grid points per plot for understory trees) are shown (n = 18). See Table 2 for species codes.

Table 3. Important environmental variables associated with the frequency of seedlings and saplings identified by logistic regressions for each species, the proportional reduction in deviance of each model, and the amount of change in the variable value that results in a positive doubling of the estimated frequency.

Species	Independent variables*	Parameter estimates	F value	$P > F$	Odds doubling
Abies concolor	DSF	−2.85	23.3	<0.0001	−0.25
PRD = 0.14	LITTER	0.0167	20.1	<0.0001	42
	SOILH_2O	1.21	13.2	0.0003	12
Abies magnifica	SOILH_2O	1.91	20.7	<0.0001	4.5
PRD = 0.11	DSF	−4.31	19.3	<0.0001	−0.16
	LITTER	0.0159	7.0	0.0087	44
Calocedrus decurrens	SOILH_2O	2.21	42.1	<0.0001	4.3
PRD = 0.11	SHRUB	−0.0125	7.3	0.0074	−60
Pinus jeffreyi	ISF	9.38	59.6	<0.0001	0.075
PRD = 0.14					
Pinus lambertiana	LITTER	0.0242	24.5	<0.0001	29
PRD = 0.10	SHRUB	−0.0228	17.3	<0.0001	−30
	SOILH_2O	1.14	9.7	0.0020	9
Prunus emarginata	SOIL	−0.296	14.0	0.0002	−2.4
PRD = 0.06	SHRUB	0.0113	7.0	0.0083	62
Quercus kelloggii	LITTER	0.0206	12.5	0.0005	34
PRD = 0.05	SOILH_2O	1.22	8.2	0.0045	7.8

* See Table 1 for abbreviations.

the sapling size class (Table 4). Soil moisture, however, was important for both size classes.

The NMS ordination (Figure 2) represented 96% of the variation in the data set, with axis 1 accounting for 70% and axis 2 for 26%. The first axis was related to DSF and litter cover, whereas the second axis was related to soil moisture. Red fir tended to be found in the shadiest areas of the forest. White fir, sugar pine, and incense-cedar were similarly found in areas that were more open than where red fir was found, with incense-cedar frequency greatest on the wettest sites. Bitter cherry and Jeffrey pine were found in drier and more open locations, with Jeffrey pine found at the highest light levels. Plots with no understory trees tended to be the driest and most exposed. Black oak seemed to occur in intermediate locations compared to the other species. The environmental variables with the strongest correlations with the ordination axes were the soil moisture variables, with the Oct. sample and average of both dates having a greater correlation than the May sample.

The logistic analysis of understory tree frequencies in relation to grouped shrub cover levels (0, 1–49, >50%) confirmed the negative association for incense-cedar and sugar pine, and the positive association for bitter cherry with increasing shrub levels shown in Table 3. The analysis and separation of means tests also detected a positive association between Jeffrey pine and high shrub cover levels ($F_{2,399} = 10.4$, $P < 0.0001$), and an association between black oak and moderate shrub cover levels ($F_{2,399} = 10.9$, $P < 0.0001$). Both direct and indirect light levels increased with grouped shrub covers ($F_{2,397} = 12.8$, $P < 0.0001$ and $F_{2,397} = 19.2$, $P < 0.0001$, respectively) in the ANOVA and separation of means analyses. Soil moisture levels in Oct.

Table 4. Separate analyses for seedlings and saplings of species with sufficient sample size of important environmental variables associated with frequency, the proportional reduction in deviance of each model, and the amount of change in the variable value that results in a positive doubling of the estimated frequency.

Species	Independent variables*	Parameter estimates	F value	$P > F$	Odds doubling
Seedlings					
Abies concolor	DSF	−4.20	35.7	<0.0001	−0.17
PRD = 0.14	SOILH_2O	1.36	14.1	0.0002	8.4
	LITTER	0.0132	10.1	0.0016	53
Calocedrus decurrens	SOILH_2O	2.10	35.8	<0.0001	4.6
PRD = 0.11	DSF	−1.77	6.6	0.0109	−0.42
Pinus lambertiana	SOILH_2O	1.61	20.5	<0.0001	5.4
PRD = 0.10	LITTER	0.0227	18.7	<0.0001	31
Saplings					
Abies concolor	LITTER	0.0205	26.1	<0.0001	34
PRD = 0.07	SOILH_2O	0.808	5.6	0.0186	18
Calocedrus decurrens	SOILH_2O	2.51	63.0	<0.0001	3.4
PRD = 0.16	SHRUB	−0.0158	9.1	0.0027	−45
Pinus lambertiana	ISF	−6.58	24.3	<0.0001	−0.11
PRD = 0.06					

*See Table 1 for abbreviations.

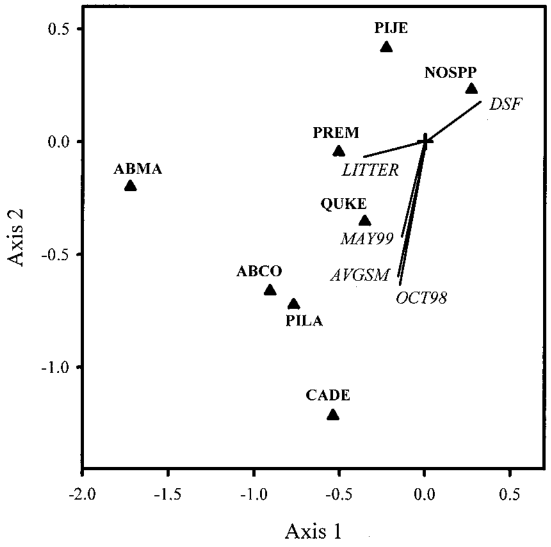

Figure 2. Segregation among tree species in ordination space and joint plot of significant environmental variables from Nonmetric Multidimensional Scaling analysis of species frequency. Species are designated with codes and symbols, environmental variables with lines and italics. See Table 2 for species codes and Table 1 for other abbreviations.

did not differ among shrub groups ($F_{2,393} = 1.2$, $P < 0.30$), but were significantly higher in points without shrubs than in the two groups with shrubs in May ($F_{2,384} = 8.04$, $P < 0.0004$). Litter and forest floor was not as thick in the points with shrubs than in the group without ($F_{2,399} = 3.36$, $P < 0.036$).

Most of the measured seedlings and saplings (65% for all species taken together) were found growing on intact forest floor (Figure 3). Approximately equal numbers of understory trees were found growing on loose litter or mineral soil (16% each), whereas very few were found growing on decayed wood or rock (1% each). These proportions of substrates occupied by understory trees were significantly different from the proportional cover of available substrates recorded on the gridpoints ($\chi^2_{\text{df}=3} = 39.2$, $P < 0.001$). Although the proportional abundance of litter and forest floor was very similar to their use as rooting substrates, the proportional abundance of mineral soil was much lower (5%), and the abundance of decayed wood and rock higher (8 and 6%, respectively), than their use as rooting substrates. Differences among species in use of rooting substrates was not great, although bitter cherry and black oak tended to be rooted in litter more than the other species, and red fir was rooted in mineral soil more than the rest.

Fire and Shrub Effects

Mortality of seedlings planted in the shrub patch and burn treatments was high and began early in the first growing season, with a survival rate of only 2.2% overall at the end of the second growing season. Species survival rates of 0.6% for white fir and 3.8% for sugar pine were significantly different ($F_{1,30} = 5.79$, $P = 0.0225$) (Figure 4). The burn $*$ date interaction was significant ($F_{6,108} = 16.3$, $P < 0.0001$), with survival in the bare, exposed hot burns significantly lower than survival in the other treatments early in the first growing season (spring 2001), but not at the end of the second growing season. The patch $*$ species $*$ date interaction was also significant ($F_{6,108} = 2.66$, $P = 0.0191$), again primarily caused by differences early in the first growing season, and no difference at the end of the second

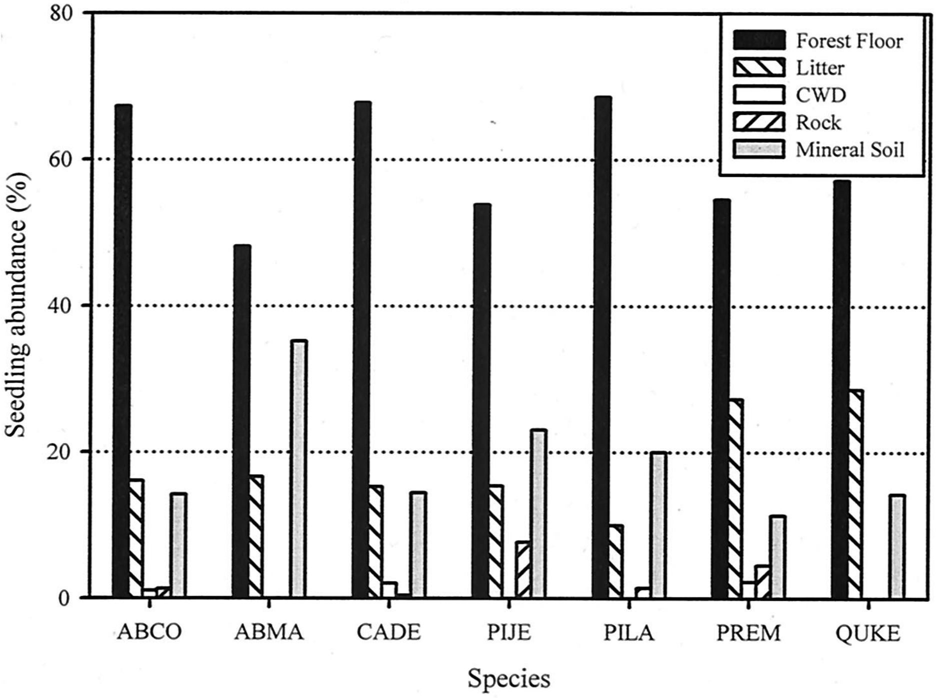

Figure 3. Abundance of seedlings found on different rooting substrates, expressed as a percentage of all seedlings found. See Table 2 for species codes.

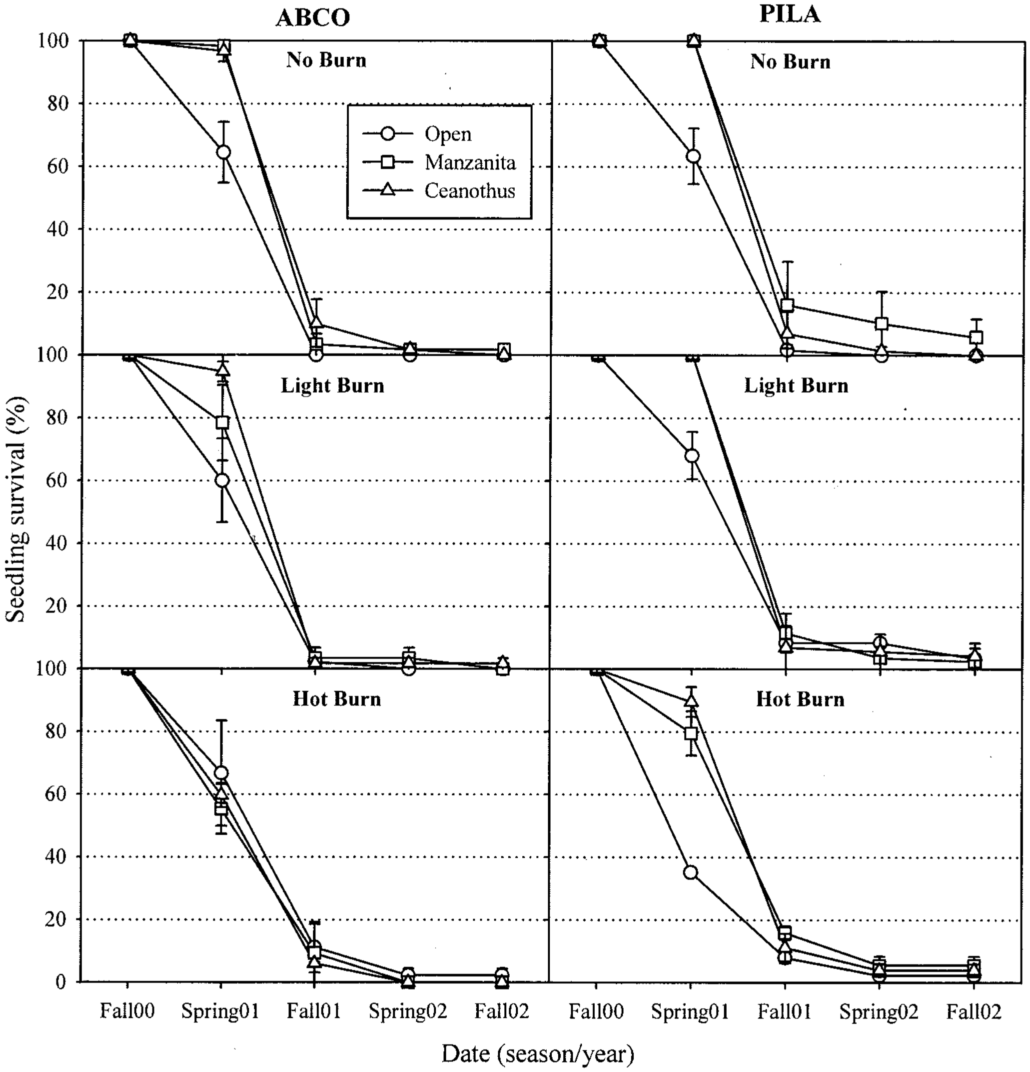

Figure 4. Trends in mean survivorship (with standard errors) for white fir (left side) and sugar pine (right side) by burn treatment (top to bottom) and shrub cover (n = 3).

growing season. Separation of means indicated that survival of sugar pine was greater than survival of white fir in ceanothus and manzanita patches, but not in open patches, and that survival of both species was greater in the shrub patches than in the open patches. The low numbers of surviving seedlings (particularly of white fir), and their uneven distribution across treatment combinations, precluded statistical analyses of seedling growth. Results may indicate important trends, however, with diameter growth of sugar pine seedlings greatest in the hot-burn treatments, whereas the greatest height growth was in the no-burn treatment, followed by hot and light burn (Table 5).

Soil moisture trends and statistical results were similar for both depths, so only the results for the 0–45-cm depth are presented. A rapid seasonal drawdown of soil moisture was evident, with volumetric moisture levels reaching 8–9% by early July and remaining low (Figure 5A). Soil moisture differed significantly among burn treatments by date ($F_{32,286}$ = 1.92, P = 0.0030), caused by higher soil moisture in unburned plots than in burned plots early in both growing seasons, and no differences among treatments in mid to late summer. A separate analysis on the change in soil moisture between the earliest and latest sample of each growing season indicated that the greater change in soil moisture in the unburned plots was not significant ($F_{2,12}$ = 4.35, P = 0.0680). Soil moisture during late summer in the unburned plots tended to be higher in the open patches than under the shrubs (e.g., means and standard errors of 8.55 [0.49], 7.94 [0.24], and 7.78 [0.27], for open, manzanita, and ceanothus patches in Aug. 2001, respectively), but the shrub terms were not significant in the repeated measures ANOVA.

Soil temperature was not significantly different among treatments. Because seasonal trends are similar to those of air temperature, soil temperature results are not shown. The seasonal trends for air temperature were similar among years, although mean monthly air temperatures increased dramatically from Apr. to May in 2001, compared to 2002 (Figure 5, B and C). The burn * date and patch * date interactions were significant ($F_{48,177}$ = 3.36, P < 0.0001

Table 5. Mean change in diameter from Sept. 2001 to Sept. 2002 and height from May 2001 to Sept. 2002 of sugar pine seedlings in the fire and shrub effects experiment.

Treatment	Diameter change (mm)	Height change (cm)
No burn	0.7 (0.49)*	5.8 (1.9)*
Light burn	0.6 (0.11)	1.4 (0.4)
Hot burn	0.9 (0.13)	3.0 (0.7)

* Standard errors in parentheses.

and $F_{43,177} = 2.57, P < 0.0001$, respectively). Separation of means indicated that air temperatures in the light-burn treatments were significantly higher than in the hot-burn and unburned treatments during mid-summer, but not during winter. Similarly, air temperatures were significantly different in mid-summer among all patch types, with open > manzanita > ceanothus, but not during winter.

Discussion

The high density of the shade-tolerant and fire-intolerant white fir and incense-cedar in the mixed-conifer forest understory, in contrast to the density of fire-resistant sugar pine and Jeffrey pine, was consistent with findings in other fire-suppressed forests in the Sierra and the west in general (Cooper 1960, Kilgore 1973, Helms and Tappeiner 1996). The abundance of California black oak was fairly typical of mixed-conifer forest, but few studies report the abundance

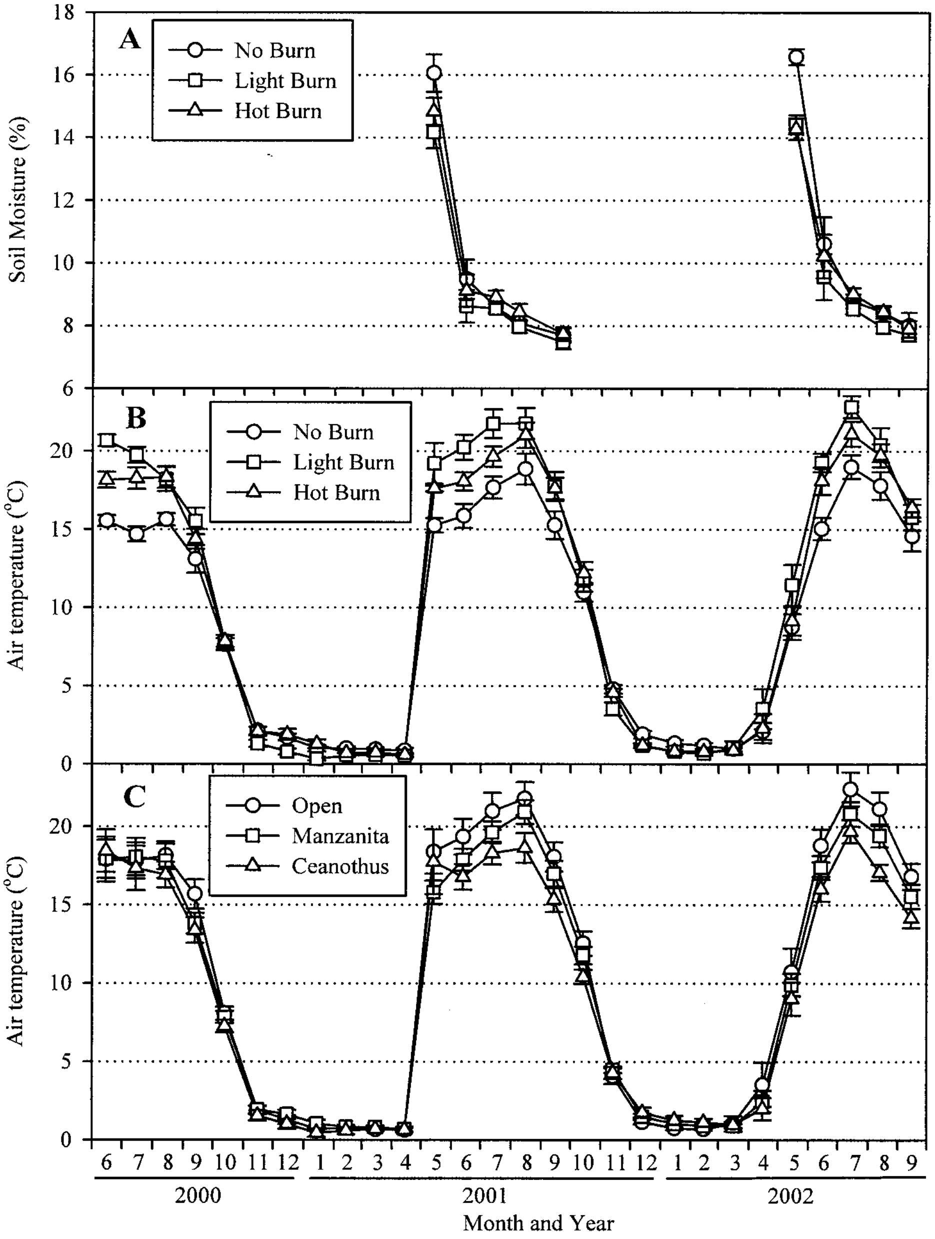

Figure 5. Trends of monthly means and standard errors in: (A) soil moisture from 0–45 cm depth by burn treatment, (B) air temperature at 30 cm aboveground by burn treatment, and (C) air temperature at 30 cm aboveground by shrub patch type ($n = 3$).

or distribution of bitter cherry. Density of red fir in the understory was high, but only in the seedling size class, and its distribution was localized on a small number of plots. Sugar pine is apparently able to persist in the understory of fire-suppressed forests (Parsons and DeBenedetti 1979, Ansley and Battles 1998). Although density of understory sugar pine was not high, it was relatively well distributed across the sample plots in this study. Density of Jeffrey pine in the understory was quite low and localized in relation to the overstory. The lower relative density of pines in the understory compared to the overstory—given comparable species mortality rates—suggests potential long-term decline of pines in undisturbed forests, as was found in one long-term study (Ansley and Battles 1998).

The environmental conditions recorded at microsites where established seedlings and saplings are found do not necessarily reflect the conditions present when those trees became established, or the conditions during critical periods affecting tree survival. No exogenous disturbances have occurred at Teakettle Experimental Forest for at least several decades (North et al. 2002). However, light, moisture, and substrate conditions can be expected to change gradually over time in response to overstory tree growth, and more dramatically in localized areas in response to tree mortality. The conifer understory tree populations we studied were dominated by trees in the 5–50-cm height class, so conditions on the majority of grid points are not expected to have changed much since establishment. This is less certain for the larger sapling size classes. Although differences found in environmental associations between seedlings and saplings may be the result of differences in optima for establishment compared to growth, they may also be the result of changes in sapling environments since establishment. Many factors besides environment affect seedling and sapling distributions, including seed dispersal, seed predation, herbivory, and disease. Thus, grid points without seedlings could have been empty for a great variety of reasons, whereas the occupied grid points presumably were within some range of environmental tolerances when the trees became established. The unoccupied grid points did differentiate from those where species were found in the ordination, which suggests some association with environment.

The rooting substrates on which understory trees were found in this study differed from their availability. There was an apparent preference for mineral soil as a substrate, but the abundance of seedlings on the forest floor, and the positive association between litter and white fir, sugar pine, and black oak, was surprising. Forest floor materials can be a barrier for establishment, dry out quite rapidly, and reach very high temperatures under direct solar radiation (Haig et al. 1941, Isaac 1943, Gray and Spies 1997). In a study of mixed-conifer species regeneration response to logging, Stark (1965) found lower survival on mineral soil than on forest floor, and attributed the cause to variation in compaction and composition of the bare-soil category. Very few understory trees in this study were found rooted on coarse woody debris. In contrast, decayed wood can be important for regeneration in the Pacific Northwest, apparently by providing abundant moisture and locations raised above the surrounding understory vegetation (Harmon and Franklin 1989, Gray and Spies 1997). It is possible that only particular species are able to exploit this resource. The genera most commonly associated with "nurse log" regeneration in North America, *Tsuga*, *Picea*, and *Betula* (Harmon et al. 1986), are not found in Sierran mixed-conifer forests. Alternatively, decayed wood in mixed-conifer forests may not retain much moisture through the long summer drought. Preliminary analyses indicated that volumetric water content of decayed wood in the forests used in this study were usually the same as the soil water content by the end of the summer (Dr. Jim Marra, University of Washington, Apr. 7, 2003).

Soil moisture and solar radiation were important environmental variables associated with frequency of understory tree species. The positive association between soil moisture and frequency of most species and the correlation of soil moisture with the species ordination suggests that lack of moisture may be an important limiting factor for regeneration in mixed-conifer forests. Our study found incense-cedar associated with high-moisture microsites, Jeffrey pine with low-moisture microsites, and the other conifers in areas of intermediate moisture availability. Studies in drier Ponderosa pine (*Pinus ponderosa* P.& C. Lawson) forest types attribute successful regeneration to infrequent years with relatively abundant summer precipitation (e.g., Cooper 1960, White 1985), but studies of regeneration in mixed-conifer forests have generally focused on regeneration success in relation to overstory shade (e.g., Fowells and Stark 1965, McDonald 1976). Nevertheless, Sierran mixed-conifer forests are known to transpire a large portion of the annual precipitation, and deplete soil moisture to depths of several meters (Arkley 1981), so it is likely that within-stand microsites with relatively abundant moisture are important for regeneration.

Soil moisture at seedling rooting depth was higher in unburned plots than in burned plots, but the difference was short-lived, because soil moisture in the seedling rooting zone became uniformly low by mid-July. Soil moisture was significantly higher at gridpoints without shrubs than those with shrubs. Similarly, by late summer the soil moisture levels in the burn experiment tended to be higher in the open patches of bare ground than within the ceanothus or manzanita patches. In this Mediterranean climate, with most of the precipitation delivered as snow, soil moisture availability to tree seedlings is dependent on the water-holding capacity of the soil and competition from other vegetation. In early postfire years before accumulation of forest floor and litter, seedlings germinating in exposed burned areas may have the advantage of release from competition, but apparently an even greater disadvantage of low soil moisture and increased air temperatures. Seedlings germinating in the shade of ceanothus or manzanita shrubs must compete for soil moisture, especially later in the summer, but, at least initially, may have the advantage of shading and potentially higher survivorship of young seedlings, as suggested by sugar pine in the unburned manzanita patches.

The negative association between direct solar radiation and the frequency of red fir, white fir, and incense-cedar seedlings, and the frequency of sugar pine in similar environments, suggests the importance of desiccation in understory mortality. Direct radiation on dry surfaces leads to high temperatures and high vapor pressure deficits, to a much greater extent than from indirect radiation alone. Mortality of planted seedlings was higher in the exposed areas (burned treatments and open patches in the unburned treatments) early in the first growing season in the fire effects study, which coincided with the early onset of high air temperatures. Seedlings are highly susceptible to desiccation, and must establish sufficient root depth in time to acquire soil moisture as surface layers dry out (Haig et al. 1941). Snow tended to melt earlier in exposed areas in this study than in closed-canopy areas. The greater abundance of litter and forest floor in closed-canopy areas may have also acted as a barrier to heating and evaporation in the upper soil layers. Although shade is usually viewed as necessary for successful regeneration of Sierran mixed-conifer forests, growth of established seedlings usually benefits from light levels that may be lethal to initial establishment (Fowells and Stark 1965, McDonald 1976, Tappeiner and McDonald 1996). Sugar pine, Jeffrey pine, and California black oak tend to be less shade-tolerant as they mature (Minore 1979, Stuart and Sawyer 2001) and probably would require relatively high light levels to attain overstory status.

Shrubs are a potential source of shade that may aid tree seedling establishment when overstory tree canopy cover is low (Tappeiner and Helms 1971). However, shrubs often suppress tree regeneration and growth in managed forests (Lanini and Radosevich 1986, Tappeiner and McDonald 1996). Shrub cover was not as important as other microsite variables in explaining understory tree frequency, but was negatively associated with frequency of incense-cedar and positively associated with frequency of bitter cherry, and to a lesser degree, with Jeffrey pine and California black oak. Most of the shrub cover consisted of whitethorn ceanothus, a shrub that grows symbiotically with N-fixing *Frankia* bacteria, and tended to occur in discrete patches in areas with relatively low tree canopy cover and low soil moisture. Bitter cherry, which was often found in the middle of dense ceanothus patches, tends to be an early-successional species (Oakley and Franklin 1998) that may require relatively high levels of N to establish. Although overall survival in the shrub and fire effects experiment was low, there was a tendency for greater initial survival of planted seedlings in shrub patches than in open areas. Nevertheless, whitethorn ceanothus and greenleaf manzanita have been found to deplete soil moisture more rapidly, and to a greater extent for the latter, than associated Sierran tree species (Royce and Barbour 2001). Tree seedling water potential in midsummer has been shown to decline with increasing shrub volume in stands with many of the same species (Lanini and Radosevich 1986).

The role of shrubs in relation to tree regeneration in the mixed-conifer stands we studied is still inconclusive, in part because it is not yet clear whether shrubs tended to occupy inherently drier, more-exposed sites than most seedlings did, or whether the shrubs created those conditions that were detrimental to seedling establishment. There was an abundance of large ($>$0.2 ha) openings in these stands that were not occupied by either shrubs or trees. Although hydraulic redistribution of soil water is a potential mechanism for maintaining relatively high soil moisture levels in closed-canopy areas (Brooks et al. 2002), analyses of overstory and understory tree water isotope ratios indicate that is not occurring at our site (Agneta Plamboeck, University of California–Berkeley, Jan. 23, 2003). It is possible that large openings, either dominated by shrubs or bare mineral soil, or gaps created by recent fire with their relatively high levels of direct solar radiation and low levels of soil moisture, may persist as areas that are hostile to tree regeneration.

Patchy canopies, forest patches containing shade-tolerant and -intolerant species, and open forest gaps (bare ground and shrub-dominated sites $>$0.2 ha) suggest that mixed-conifer forests in the Southern Sierra Nevada are not "gap-phase" systems (Van Pelt and Franklin 2000, North et al. 2004). It is not clear whether stand-scale disturbances increase belowground resource abundance and subsequent regeneration, or whether tree regeneration in apparently unsuitable patches only occurs during infrequent wet summers (Cooper 1960). These forests may still be responding to the lack of fire as a disturbance. Frequent fire may have limited stem density and reduced the importance of soil moisture as a limiting factor. With increased tree densities after more than a century of fire suppression, and increases in tree size, moisture may have become very limited and led to mortality in inherently drier sites that are currently maintained as openings. Nevertheless, there is little evidence of snags and logs from prior trees in the openings. We do not know what created or maintained these large, persistent gaps, but such large openings are unusual in productive old-growth forests elsewhere. In coastal Pacific Northwest old-growth forests, for example, gaps $>$0.05 ha are rare (Van Pelt and Nadkarni 2004), it is the relatively small gaps ($\sim$0.01 ha) that appear to be stable (Spies et al. 1990), and light levels rarely exceed 0.2 of that in the open (Gray et al. 2002), whereas the mean for those measures in this study was 0.3.

Basic information on comparative regeneration behavior of mixed-conifer tree species may help managers predict how sites will respond to prescribed fire and thinning, and possibly identify sites that do not require treatment. Although it is not clear to what extent sugar pine and Jeffrey pine dominated the overstory of Sierran mixed-conifer forests prior to fire suppression, this study suggests that regeneration is low relative to current overstory composition. The low survival rates and low frequency of seedlings in high-light openings, coupled with the relative shade tolerance of sugar pine, suggests that relatively low levels of canopy disturbance may be sufficient to maintain or increase the abundance of this species in mixed conifer. Increasing the abundance of Jeffrey pine, which was found in more exposed microsites, may be complicated by shrubs that are aggressive competitors for limited soil moisture. Prescribed fire might be one option for reducing shrub cover and facilitating regeneration of Jeffrey pine.

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