Factors Affecting Blue Oak Sapling Recruitment[1]

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Abstract: We used logistic regression to identify environmental and management history factors associated with blue oak (Quercus douglasii*) sapling recruitment. Recent canopy gaps caused by natural mortality or clearing were positively associated with sapling recruitment. Plots with very high or low levels of tree canopy cover were less likely to have saplings than those with intermediate canopy cover levels. Across all locations, and within grazed locations, browsing intensity was negatively associated with sapling presence. Other factors significantly correlated with sapling recruitment include shrub presence, insolation, soil available water-holding capacity, fire, plot altitude, precipitation, and potential evapotranspiration.*

Different interpretations have been offered to explain the apparent flushes of blue oak recruitment that date from the 1850's through the 1890's (McClaran and Bartolome 1989, Mensing 1992, Vankat and Major 1978). Many interrelated ecosystem perturbations date to this period. Settlers and their successors introduced livestock, cut trees and cleared shrubs over large areas, altered fire frequency, hunted deer, and exterminated vertebrate predators. These and other actions also affected understory species composition, rodent populations, soil properties, and other factors. Although many of these factors have the potential to affect blue oak regeneration, the relative importance of these or other factors on current regeneration patterns cannot be determined from fragmentary historical data.

We have shown that the frequency of small blue oak (*Quercus douglasii* Hook. & Arn.) saplings (>1 cm basal diameter, ≤3 cm diameter at breast height [DBH]) varies widely between different blue oak stands (Swiecki and others, these proceedings). Although such saplings tend to be scarce within a stand, their densities within a stand are highly variable (Swiecki and others 1993). In this study, we investigated whether current differences in sapling recruitment within and between blue oak stands are related to site environmental and/or history factors. Because blue oaks typically require at least 10 to 30 years to make the transition from seedling to young tree (McClaran and Bartolome 1989), our study included only locations for which we could obtain 30 years of site history.

Methods

Plot Data

We collected data from 1500 plots, each 0.08 ha, distributed across 15 locations (*table 1*, Swiecki and others, these proceedings). We sampled 100 plots per location except at Pinnacles (99 plots) and Sierra (101 plots). We defined saplings as oaks with a basal diameter of at least 1 cm, and a dbh no greater than 3 cm. Oaks that have a basal diameter less than 1 cm but are greater than 25 cm tall are designated as S0 seedlings. We counted the number of all live and dead saplings within plots and used count classes (0, 1-10, 11-20, etc.) to estimate S0 seedling numbers.

Within each plot we identified canopy and shrub species present and visually estimated total canopy cover, blue oak canopy cover, and the proportion of the plot covered by shrubs, bare ground, herbaceous species, and native bunchgrasses. We rated the severity of current season and chronic browsing and

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Table 1—Study location management history, climate characteristics, and blue oak recruitment

Location	County	Years grazed 1962-1992[1]	Pct of plots burned 1962-1992	Average Insol12[2] (MJ/m^2)	ETdeficit[3] (cm)	Pct of plots with SoilAWC[4] ≥10 cm	Pct of plots with LocAllrecr[5] =1
Wantrup Wildlife Sanctuary	Napa	7	0	6.99	34.1	65	38
Black Butte Lake	Glenn	24, 14	0	7.51	75.3	52	0
Pinnacles National Monument	San Benito	0	78	9.40	78.1	0	52
Sierra Foothills Research & Extension Center	Yuba	30, 30, 10	0	7.77	58.5	64	52
Hopland Field Station	Mendocino	30, 0	5[6]	10.22	10.1	47	0
Sequoia National Park	Tulare	30, 10	25	10.71	57.5	8	22
Dye Creek Preserve	Tehama	30	31	7.62	72.8	9	20
Pardee Reservoir	Amador	30, 0	7	8.75	70.9	14	3
Pozo	San Luis Obispo	30	0	10.70	71.4	84	15
Lake San Antonio	Monterey	27, 3	0	9.82	83.3	83	15
Hensley Lake	Madera	30, 14	0	9.53	102.7	60	0
Henry W. Coe State Park	Santa Clara	0	34	8.60	53.2	71	1
Mt. Diablo State Park	Contra Costa	28, 23	16	7.58	73.3	51	4
California Hot Springs	Tulare	30	5	12.36	50.2	56	7
Jamestown	Tuolumne	28	11	8.52	43.3	78	41

[1] For locations with multiple grazing histories, years for each separate grazing history are listed.
[2] Average of calculated plot December average-day insolation.
[3] Difference between annual reference evapotranspiration (ETo) and average annual precipitation for 1962-1992.
[4] Estimated soil available water-holding capacity in the rootzone.
[5] Binary outcome variable indicating whether or not any live or dead S1-S3 sapling or S0 seedling is in plot.
[6] An additional 23 percent of the plots had burned in 1959.

other factors for each plot (Swiecki and others 1993). We classified plot topographic position using a scale adapted from the USDA Forest Service (Swiecki and others 1990).

We measured plot slope with a clinometer and aspect with a compass. We estimated individual plot elevations from U.S. Geological Survey topographic maps. Plot slope, aspect, altitude, and latitude data were used to calculate clear day potential solar radiation (insolation) for each plot (Rumsey 1993). We obtained information on soil types and depths from published USDA Soil Conservation Service soil surveys and unpublished soil survey data. We used plot observations on apparent soil depth, texture, and rockiness in conjunction with soil survey data to calculate estimates of total soil available water-holding capacity (AWC) for each plot (Swiecki and others 1993).

We obtained management history on grazing practices and tree cutting for the years 1962 through 1992 for each study location from current and former landowners and land managers. It was necessary to extend our tree-cutting history interval back to 1950 because of uncertainty about the date of some tree harvesting at Wantrup. We compiled fire history from 1962 or earlier from historical fire maps. For each location, we calculated reference evapotranspiration (ETo) from published data (Pruitt and others 1987) and compiled rainfall data from the nearest weather station.

Statistical Analyses

We constructed many outcome variables from plot sapling data and more than 100 potential predictor variables from plot environmental and history data (Swiecki and others 1993). We used a variety of data screening techniques to look for correlations between predictor variables before selecting a subset of variables for logistic regression analysis. We used logistic models for binary outcome variables and poisson models for outcome variables that are derived from counts. We developed within-location models, which describe the probability of recruitment at the plot level, for those locations which had sufficient levels of recruitment to allow for model fitting. We also developed all-location models that describe the likelihood of recruitment at the location level, using variables constructed from aggregate data for each location.

Results

Overall location management history details and climate characteristics of the study locations are shown in *table 1*. Stand characteristics and sapling size classes are reported in Swiecki and others (these proceedings), and detailed descriptions of each study location are reported by Swiecki and others (1993).

Within-Location Statistical Models

We constructed logistic regression models for several outcome variables, but only models for the following two variables are discussed here:

Variable Name:	*Model Type*	*Description*
Allrecr	Logistic	Any live or dead S1-S3 sapling or S0 seedling present in plot.
S123seed	Poisson	Count of live and dead seedling-origin saplings in plot.

The models are presented in *table 2*. Models for the S123seed outcome could be developed only for Wantrup, Pinnacles, Sierra, and Jamestown (*table 2*). These four locations, plus Dye Creek and Sequoia, had enough plots with recruitment to allow model building when the more inclusive outcome variable Allrecr was used (*table 2*). Comparisons between predicted and observed recruitment for this outcome are shown in *table 3*. The model for Sequoia was the least successful for predicting plots with recruitment using the P(Allrecr)≥0.5 criterion (*table 3*).

The Poisson models, based on sapling counts, generally had more significant predictor variables than the corresponding logistic models, which are based on the binary outcome variable Allrecr. The logistic and Poisson models may also be unlike because of differences between the outcome variables. For example, Pinnacles had 12 plots with only S0 saplings, which contribute to the differences between the Allrecr and S123seed models. Plots containing only sprout-origin saplings contribute to differences between the Allrecr and S123seed models at Sierra and Jamestown.

For binary predictor variables, an odds ratio (logistic models) or rate ratio (Poisson models) greater than 1 indicates that the outcome is more likely in the presence of a factor than in its absence. For example, the odds ratio of 15 for the binary variable Cut42yr in the Allrecr model for Wantrup indicates that plots cut within the past 42 years were 15 times more likely than uncut plots to have any live or dead S0-S3 recruitment. For categorical variables, model parameters indicate whether an outcome is more or less likely at the lowest level of the factor compared to each other level of the factor. For continuous variables, parameters indicate the incremental change in probability per unit increase (e.g., per meter of altitude). The odds ratio for n meters of elevational change equals the per-meter odds ratio raised to the power n.

Tree Canopy and Canopy Gaps

Total plot canopy cover was a significant predictor of sapling presence at three locations (*table 2*). Two different recodings of the canopy cover variable are used in the final models because the study areas differed markedly in their overall levels of canopy cover. Plots with very high or very low levels of canopy cover were generally less likely to have saplings than plots with intermediate levels of canopy cover (20 to 80 percent).

Some of the plots at Wantrup, Sierra, Dye Creek, and Jamestown fell in areas where trees had been cut for firewood after 1950. Variables indicating that a

Table 2—Predictor variables included in final within-location models

Predictor	Definition	Parameters[1] (95 pct confidence intervals) for outcome variables in final model for location indicated	
		Allrecr[2]	S123seed[3]
Altitude	Plot altitude (m)	Wantrup: 0.981*** (0.971-0.991)	Wantrup: 0.977*** (0.973-0.980) Sierra: 0.987*** (0.983-0.992)
ChrVertBrA	Chronic vertebrate browsing intensity in plot is rated as high	Sequoia: 0.156*** (0.052-0.468) Dye Creek: 0.165*** (0.055-0.494)	
CumGraze	Cumulative grazing score: sum of (months grazed) × (relative stocking) × (season factor) for the period 1962-1992. Relative stocking ranges from 0 (none) to 3 (high). Season factor is 1 for winter and 2 for summer or year-round.	Sierra: 0.991***(0.985-0.997)	
CurrVertBrA	Current vertebrate browsing intensity in plot is rated as high.	Wantrup: 3.22* (0.860-12.0) Jamestown: 0.234** (0.071-0767)	Pinnacles: 1.56*** (1.13-2.14) Jamestown: 0.340**(0.123-0.939)
Cut42yr	Tree cutting has occured in the plot between 1950 and 1992.	Wantrup: 15.0*** (2.98-76.5)	Wantrup: 46.7*** (17.4-175)
GaporCut42	Tree cutting has occurred in the plot between 1950 and 1992, or a canopy gap due to other factors has developed in the plot between 1962 and 1992 (estimated).	Sierra: 6.13*** (1.99-18.9) Jamestown: 3.06* (1.02-9.19)	Pinnacles: 1.17***(1.24-2.36) Jamestown: 1.67 (0.762-3.67)
Insol12	Calculated total daily insolation (MJ/m^{2}) for plot on the average day in December (December 10).	Sierra: 1.27* (0.972-1.66)	Pinnacles: 0.953** (0.912-0.997)
OthCanSpp	Number of tree canopy species other than blue oak in plot.	Sierra: 2.85*** (1.34-6.09)	Wantrup: 0.455*** (0.398-0.521) Sierra: 1.16 (0925-1.45)
Rebum30	Plot has burned at least two times between 1962 and 1992.	Pinnacles: 0.436 (0.157-1.21)	Pinnacles: 0.337*** (0.208-0.586)
ShrubCoverA	Plot shrub cover estimated is >2.5 pct.		Jamestown: 3.73***(1.46-9.52)
ShrubPresent	Shrubs are present within the plot.	Jamestown: 6.45***(1.91-21.8)	Wantrup: 3.23***(2.79-3.75) Pinnacles: 1.49*(.957-2.32) Sierra: 1.85*(0.904-3.79)
SmallTrees	Small-diameter trees (3 to 13 cm DBH)	Sierra: 9.45***(2.48-36.1)	Sierra: 2.19***(1.40-3.43)
SoilAWC	Estimated total available water-holding capacity within the rootzone (cm)	Pinnacles: 1.37**(1.03-1.83) Dye Creek: 1.24**(1.02-1.51)	Wantrup: 0.976***(0.960-0.993) Pinnacles: 1.45***(1.07-1.23)
StandEdgeA	One or more adjacent plots on the sampling grid falls outside of the blue oak stand.	Pinnacles: 0.284**(0.094-0.852)	
TopoPosA	Plot topographic position recoded to 3 classes: (a) hilltop, (b) upper 1/3 hillside, (c) lower 2/3 hillside and low flats		Wantrup: a-b 0.370***(0.183-0.748) a-c 0.965 (0.674-1.38) Pinnacles: a-b 3.27*** (1.83-5.85) a-c 1.35 (0.759-2.41)
TotCanopyA	Tree canopy cover recoded to three classes: (a) ≤2.5 pct, (b) >2.5 pct to 20 pct, (c) >20 pct.	Pinnacles: a-b 4.23*** (1.16-15.5) a-c 5.76*** (1.52-21.8)	
TotCanopyB	Tree canopy cover recoded to three classes: (a) ≤20 pct, (b) >20 pct to 80 pct, (c) >80 pct.	Sierra: a-b 0.349 (0.074-2.10)	Jamestown: a-b 5.50***(1.85-16.3)

[1] Model parameters are odds ratios for Allrecr and rate ratios for S123seed. Parameter values greater than 1 indicate a positive association between the predictor variable and the outcome; values less than 1 signify a negative association. Significance level is denoted by asterisks: * $P \geq 0.10$, ** $P \geq 0.05$, ***$P \geq 0.01$.

[2] Any live or dead sapling or S0 seedling in plot

[3] Count of live + dead seedling-origin saplings in plot.

Table 3–Comparison of the observed Allrecr outcome with the Allrecr outcome predicted by final logistic regression models[1]

Location	Percent of plots correctly classified by model		
	Plots with recruitment	Plots without recruitment	All plots
Wantrup	87	82	84
Pinnacles National Monument	73	64	69
Sierra Foothills Research & Extension Center	75	71	73
Sequoia National Park	0[2]	100	78
Dye Creek	20	92	82
Jamestown	83	80	81

[1] We considered that a positive Allrecr outcome was predicted if the calculated probability of Allrecr ≥ 0.5.

[2] The maximum probability of the Allrecr outcome calculated from the model for this location was 0.39.

canopy gap had developed in the plot within the past 42 years (Cut42yr, GaporCut42) were fairly strong predictors of recruitment at five of the six locations. Prediction of sapling presence by the single variable model for GaporCut42 at Dye Creek (data not shown) was nearly equivalent to that of the final multivariate model (*table 2*).

Grazing and Browsing

Past and current grazing patterns varied between and sometimes within locations (*table 1*). Most locations had been continuously or intermittently grazed from around 1900 or earlier. Pinnacles was unique in that it has not been grazed for at least 62 years. Ten locations had some plots in areas that had been out of grazing for periods ranging from 3 to 35 years. Most locations had been grazed primarily by beef cattle. Hopland has been grazed exclusively by sheep since the 1930's or earlier. Black Butte Lake was grazed primarily by sheep until the 1950's and subsequently by cattle. The study area at Sequoia has been grazed only by horses and mules since the 1940's.

Despite the diversity of grazing histories represented within the study locations, only Sierra had both moderate levels of recruitment and clear differential grazing regimes. At this location, recruitment was more likely to occur in plots with lower cumulative grazing scores (CumGraze predictor variable) (*table 2*). The logistic model shows that saplings were eight to nine times more likely to occur in plots in the nongrazed portion of the study area than in plots in the currently grazed areas.

For other locations, we used ratings of vertebrate browsing damage instead of CumGraze to examine the effects of livestock and deer browsing on the recruitment outcomes. Browsing severity variables were highly collinear with Cumgraze and therefore could not be included in the models for Sierra. Livestock were present at Sequoia, Dye Creek, and Jamestown, and at these locations, plots with high levels of vertebrate browsing damage were less likely to have sapling recruitment (*table 2*). At Wantrup and Pinnacles, which have not been grazed for a number of years, browsing variables were either nonsignificant or showed a positive association with sapling recruitment.

Fire

No fires have occurred in the past 30 years at Wantrup or Sierra, and too few plots have burned at Jamestown to allow consideration of fire in the regression models. Occurrence of a single fire within the past 30 years was not significantly related to the Allrecr outcome for Sequoia or Dye Creek.

At Pinnacles, the occurrence of multiple fires in the past 30 years (Reburn30) was negatively associated with both outcome variables (*table 2*), although the significance level of this variable dropped to *P*=0.111 in the Allrecr final model. Plots that had burned once between 1962 and 1992 were the most likely to have saplings and had the greatest sapling densities:

	Live S1-S3 saplings	
Number of fires 1962-1992[1]:	*Percent of plots*	*Average number per plot*
0	24	0.76
1	55	2.84
2	27	0.62
3	38	0.69

[1] All fires in this interval occurred between 1977 and 1982.

At Pinnacles, the 60 plots that either burned once or did not burn between 1962 and 1992 had 13 saplings in the S2 and S3 size classes. In contrast, the 39 plots that burned two or more times had only one sapling (an S3) larger than the S1 size class.

Vegetation

Final models for four locations showed positive associations between shrub presence or cover and recruitment (*table 2*). The significance levels of variables related to shrub cover were generally much lower in multivariate models than in single variable models, presumably because of correlations between shrub variables and other predictor variables in the models. Although blue oak saplings tended to occur in plots with shrubs, they were seldom found growing through or under shrubs.

At Sierra, the odds of having sapling recruitment within a plot increased with increasing numbers of canopy species (*table 2*). The two most common canopy species other than blue oak at this location were *Q. wislizenii* and *P. sabiniana*, and few plots had more than two canopy species other than blue oak. At Wantrup, sapling counts per plot decreased as the number of canopy species increased (*table 2*). Thirty percent of the plots at Wantrup had between three and six canopy species in addition to blue oak, with the highest numbers of tree species occurring in densely canopied plots along streams and at higher elevations.

The final models for Sierra showed a positive association between small diameter trees (3 to 13 cm DBH) and sapling recruitment. At Pinnacles, plots close to the edge of the stand were less likely to have saplings than those at the interior of the stand. The most common vegetation types beyond the blue oak stand at this location were chaparral and grasslands. No predictor variables related to herbaceous vegetation, including variables related to bunchgrass cover, were significant in the logistic regression models.

Soil and Microclimate

Estimated soil available water capacity (SoilAWC) was positively correlated with recruitment at Pinnacles and Dye Creek, both of which have very droughty soils (*table 1*). Among locations with relatively high soil water holding capacity, SoilAWC was negatively associated with recruitment at Wantrup (*table 2*), and nonsignificant at Sierra and Jamestown.

Topographic position was a significant predictor of the number of saplings per plot in the Poisson models for Wantrup and Pinnacles, but the relationship between recruitment and topographic position differed between these two locations (*table 2*).

At Dye Creek, the single variable model for TopoPosA (not shown) predicted that plots in drainages were almost six times more likely to have recruitment ($P = 0.005$) than plots in the hilltop position. Two locations showed a negative relationship between altitude and recruitment outcomes (*table 2*).

Plot insolation was included as a predictor variable in two of the final logistic regression models. At Pinnacles, a relatively xeric location, plots with more xeric exposures (high Insol12) had fewer saplings than plots with more mesic exposures (*table 2*). However, Insol12 was negatively correlated with TotCanopyA at this location, and whenever both were included in a multivariate model, Insol12 was no longer significant. Models in which TotCanopyA and Insol12 variables were substituted for each other were nearly equivalent. At Sierra, a more mesic site, there was a weak positive association between Insol12 and the Allrecr outcome (table 2). Because there were very few plots with both southerly aspects and steep slopes at Sierra, plot insolation values were generally lower there than at Pinnacles (*table 1*).

All-location Statistical Model

We developed several outcome variables that describe sapling recruitment at the location level. *Table 4* lists the parameters for the final Poisson model for the LocAllrecr outcome. This outcome is the number of plots at a location containing live or dead saplings or S0 seedlings. The LocAllrecr model differs only slightly from a model fitted to counts of plots with live seedling-origin saplings only (Swiecki and others 1993). Only a limited number of factors could be fitted in the all-location model because only 15 data points, one for each location, are used to construct the model. The final model had more variability than expected for a Poisson model.

Table 4–Predictor variables and model parameters for the all-location Poisson regression model for the LocAllrecr[1] outcome

Predictor variables	Description Rate ratio	LocAllrecr (95 pct confidence interval)[2]
AvgInsol12	Average of December average-day insolation (Insol12) for the location (MJ/m^2).	0.778*** (0.678 - 0.893)
LocCurrVertBr	Number of plots in which current vertebrate browsing intensity is rated as high	0.978*** (0.970 - 0.986)
ETdeficit	Difference between annual reference evapotranspiration (ETo) and 1962-1992 average annual precipitation (cm).	1.13*** (1.07 - 1.19)
LocGaporCut	Number of plots in which either (1) tree cutting has occurred in the plot between 1950 and 1992 or (2) a canopy gap has developed in the plot between 1962 and 1992 (estimated) (GaporCut42=1)	1.11*** (1.08 - 1.15)
MaxCanopySpp	The maximum number of canopy species found in any plot at the location.	0.570*** (0.437 - 0.743)
MinPpt2	Lowest 2-year rainfall total (cm) for the location for the period 1962-1992.	1.23*** (1.12 - 1.35)
OneFire30	Number of plots that have burned only one time between 1962 and 1992.	1.06*** (1.04 - 1.09)
SoilAWC≥10cm	Number of plots in which the estimated soil available water-holding capacity is greater than 10 cm.	1.03*** (1.02 - 1.04)

[1] Count of plots containing any live or dead sapling or S0 seedling.

[2] Rate ratios greater than 1 indicate a positive association between the predictor variable and the outcome; ratios less than 1 signify a negative association. Underlined rate ratios show an apparent reversal in the direction of the association between single variable models and the final multivariate model because of collinearity in the multivariate model. Significance level is denoted by asterisks: * $P \geq 0.10$, ** $P \geq 0.05$, *** $P \geq 0.01$.

As indicated in *table 4*, the direction of the effect of some predictor variables is reversed in the final multivariate model relative to the direction they showed in single variable models. This reversal results from including correlated predictor variables in the same model. The net effects of all variables are as shown in the final model, but the effect of an individual predictor variable cannot be inferred from its coefficient in the final model if reversal has occurred.

Three climate-related variables, AvgInsol12, ETdeficit, and MinPpt2 were significant in the final model. Each of these variables was negatively associated with recruitment in its single-variable model, indicating that more xeric locations were less likely to have saplings. Conversely, SoilAWC≥10cm was negatively associated with recruitment in single variable models, indicating that locations with droughtier soils overall had higher levels of recruitment. The net effects of these interrelated variables are as shown in *table 4*.

Predictor variables related to browsing intensity and canopy gaps were significant in the final model (*table 4*) and had effects consistent with those seen in the within-location models (*table 2*). There was also a positive association between LocAllrecr and the number of plots at a location that had burned one time in the past 30 years (OneFire30, *table 4*). Other fire-related variables were nonsignificant. Because of the nonlinear relationship between plot canopy cover and recruitment, and the effects of recent gaps on canopy cover (*table 2*), we did not use average canopy cover as a predictor variable for the LocAllrecr model. Other canopy variables we constructed were not significant in the final model.

In a single variable model, the count of plots at a location containing shrubs was positively correlated with the LocAllrecr outcome (rate ratio 1.023, $P < 0.001$). This predictor variable was not significant in the final multivariate model, even though shrub-related variables were positively associated with sapling recruitment in four within-location models (*table 2*).

Discussion

All final model outcome variables include both live and dead saplings. We considered dead saplings as recruitment because dead individuals had been recruited to the sapling stage before they died. The total number of dead saplings and the number of plots containing only dead saplings were small enough that excluding dead saplings from the outcomes would not have yielded substantially different results. There were also too few dead saplings to construct separate models for sapling mortality.

Plots with nearly closed or closed canopies appear to be generally unfavorable for sapling recruitment, which is consistent with our finding that few saplings were found under tree canopy (Swiecki and others 1993, these proceedings). Muick and Bartolome (1987) reported that only 16 percent of the blue oak saplings (1 to 10 cm DBH) in their survey were located under canopy. Mature blue oaks have long been considered intolerant of shade (Sudworth 1908).

The strong positive association between canopy gaps and sapling recruitment (*tables 2, 4*) is typical of species that regenerate from persistent seedlings ("advance regeneration") located in the understory (Oliver and Larson 1990). For blue oak, we believe that small persistent seedlings in the understory, typically less than 15 to 20 cm tall, constitute advance regeneration. These small seedlings can survive in the understory for periods of at least 3 to 15 years despite repeated loss of their above-ground shoots due to desiccation or herbivory (Allen-Diaz and others 1990, Griffin 1971, Phillips and others 1996, Swiecki and others 1990). These seedlings exhibit tolerance of understory conditions, which is typical of advance regeneration, whereas blue oak saplings do not (Swiecki and others 1993).

In the absence of any recent gap, plots with little or no tree canopy were unlikely to have saplings (*tables 2, 4*). We seldom observed blue oak saplings in old (>42 years) cleared fields or other old clearings within our study areas. White (1966) reports similar observations. Several studies have shown that most blue oak seedlings become established under or very close to tree canopy (Muick and Bartolome 1987, Swiecki and others 1990, White 1966), presumably because of the combination of a favorable microclimate under tree canopy and relatively low rates of long-range acorn dispersal. Although it is difficult for first-year seedlings to establish in open sites (Gordon and others 1989; Muick, these proceedings), established advance regeneration is able to compete successfully in new canopy gaps.

Grazing and browsing variables were negatively associated with recruitment in within-location models for all currently grazed locations (*table 2*) and in the all-location model (*table 4*). From these results and our field observations of browsing damage (Swiecki and others, these proceedings), we conclude that browsing by livestock is a major constraint to both blue oak sapling recruitment and the regeneration of other woody species at many locations. Other studies (Bernhardt and Swiecki, these proceedings; Borchert and others 1989; Hall and others 1992) have also documented strong adverse effects of cattle on the growth and survival of oak seedlings and saplings in California. Livestock may inhibit blue oak sapling recruitment by both depleting the understory stock of seedling advance regeneration and adversely affecting sapling survival.

In the two nongrazed locations, there was a positive association between browsing and saplings (*table 2*). In these areas, browsing damage was caused by deer, which may have been attracted to areas with saplings because of the accessible browse they provided. On the basis of our field observations, we believe that deer browsing damage usually has little impact on blue oak sapling survival, but may tend to prolong the sapling stage by slowing height growth.

McClaran and Bartolome (1989) have suggested that fire favors sapling recruitment, but studies involving direct observation of burned areas have not shown any positive effect of fire on blue oak seedling or sapling establishment or survival (Allen-Diaz and others 1990, Haggerty 1991). Fire is clearly not requisite for sapling recruitment, because two locations with significant amounts of recruitment had no recent fires (*table 1*). Topkilled saplings normally revert to a smaller size class upon resprouting, so fire is likely to prolong the sapling stage of development. This could account for the positive association between OneFire30 and sapling presence in the all-location model (*table 4*). Fires may also open new canopy gaps by killing decadent blue oaks or other competing tree species in the overstory, thereby favoring sapling recruitment.

The associations between environmental and soil variables and recruitment in the models indicate that xeric site conditions generally do not favor blue oak sapling recruitment. Blue oak is a dominant tree in many xeric habitats and should have a competitive advantage in xeric locations because of its ability to withstand severe drought. However, saplings in xeric locations are likely to grow slowly, and the negative effects of factors such as livestock grazing or repeated fires may be of greater significance at such locations. Among the most xeric locations in this study, moderate recruitment was observed only at Pinnacles, which has not been grazed for more than 60 years (*table 1*).

Microsite conditions that seem to favor blue oak sapling recruitment in xeric locations are those that support faster growth because of greater soil moisture availability and/or reduced evaporative demand. Northerly aspects, patches of deeper soil, and topographic positions that receive runoff are more likely to have blue oak saplings in xeric locations. However, in more mesic locations, these factors are often associated with dense tree canopy cover which reduces blue oak sapling recruitment.

We observed no evidence of a direct interaction between shrubs and blue oak saplings, even though shrubs and blue oak saplings were often present in the same plots. Many of the factors related to blue oak sapling recruitment could have similar positive or negative effects on other woody species, including shrubs. At every location where we observed moderate numbers of blue oak saplings, regeneration of other woody species was also present. Conversely, with the exception of Henry W. Coe State Park, locations with little or no blue oak recruitment also had little or no regeneration of other woody species in the understory (Swiecki and others 1993, these proceedings). The failure of blue oak to regenerate is not a unique phenomenon, but appears to be part of the overall suppression of woody plants in the understory of many oak woodlands.

Blue oak sapling recruitment is a multistep process that may require many years or decades to complete. Because sapling recruitment is affected by a number of factors interacting over time, the elimination or modification of a single constraining factor will not necessarily increase the rate of recruitment. For example, eliminating livestock browsing may have little or no effect on sapling recruitment if canopy cover levels are unfavorably high or low. If seedling advance regeneration has been depleted or eliminated, factors that favor the recruitment of saplings from advance regeneration, such as gap formation, will not result in sapling recruitment.

Because colonization of old, open rangeland clearings by blue oak is uncommon under prevailing conditions, the conversion of blue oak woodland to grassland is not likely to be an easily reversible process. If blue oak is to be managed as a sustainable resource, efforts must be made to favor natural regeneration. Recruitment may be favored by altering grazing practices to reduce browsing impacts on seedlings and saplings of blue oak and other woody species. Greater attention should also be paid to the status of advance regeneration before, during, and after wood harvesting or other canopy or understory manipulations.

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