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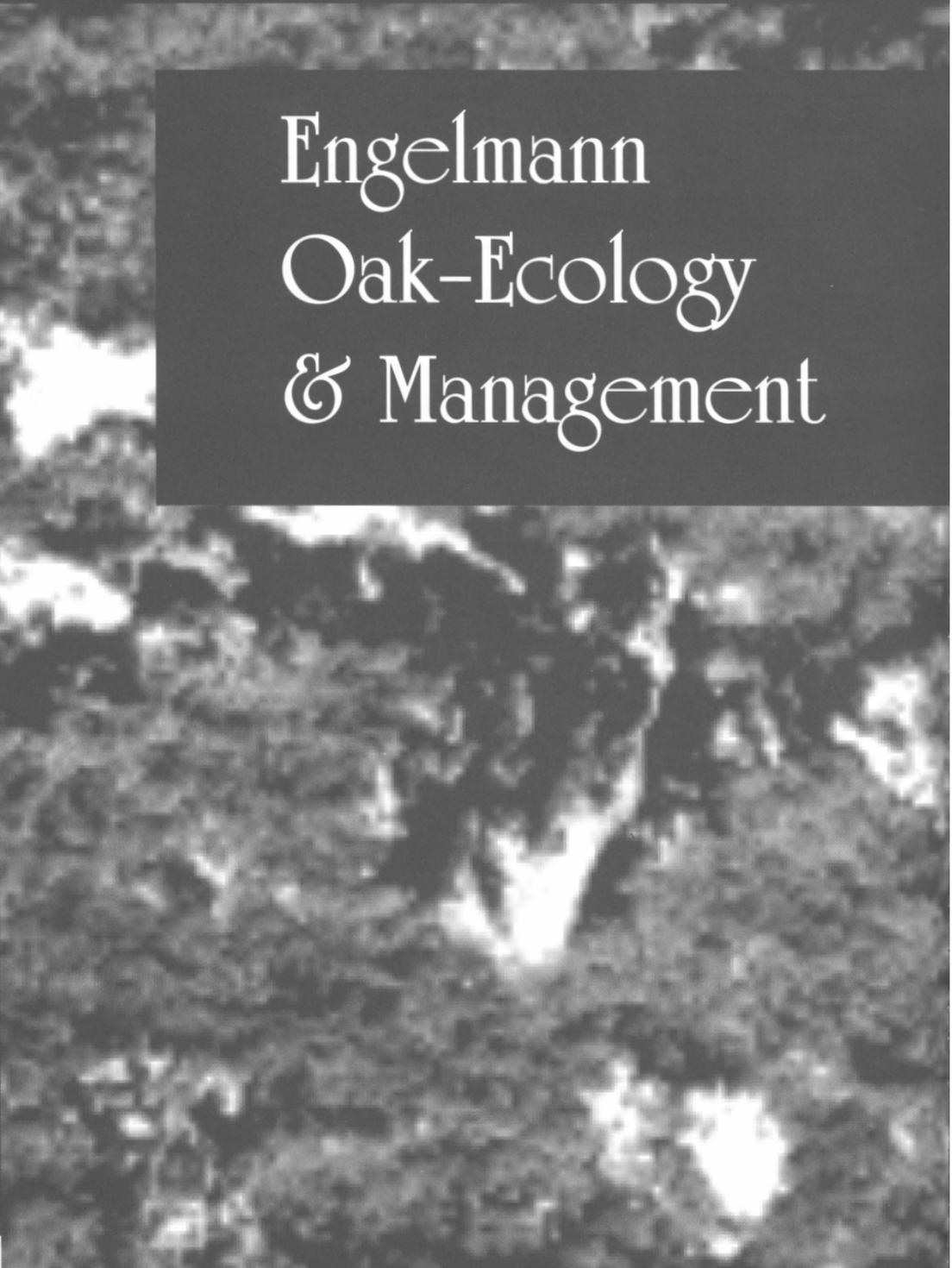


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The Distribution of Engelmann Oak (*Quercus engelmannii*) in California¹

Thomas A. Scott²

Abstract: Engelmann oaks (*Quercus engelmannii*) only occur in the foothills of San Diego (93 pct of extant stands), Riverside (6 pct), Orange (0.5 pct), and Los Angeles (<0.1 pct) counties, covering the smallest range of any oak species in California. The overall distribution of the species covers approximately 31,500 hectares of woodlands, although they are subdominant (contributing <50 pct of canopy area) to coast live oak (*Quercus agrifolia*) over about 52 pct of that area. Individual stands across the species range were mapped at 1:24,000 scale into a geographic information system (using 1:20,000 scale aerial photographs). Stands were separated into 6 classes of Engelmann oak canopy dominance: (one) 0 to 5 pct of canopy area; (two) >5 to ≤25 pct; (three) >25 to ≤50 pct; (four) >50 to ≤75 pct; (five) >75 to ≤95 pct; and (six) >95 to ≤100 pct. All areas were field checked for accuracy in boundary and canopy classification. There are approximately 7,300 ha of woodlands in categories five and six; 14,000 ha in categories three and four; and 9,200 ha in categories one and two. Combining these data with USGS Digital Elevation Models suggests that Engelmann oaks are most concentrated on 0° to 10° slopes with southwestern aspects between the elevations of 700 m to 1250 m above sea level. They tend to occur at higher elevations and slightly steeper slopes (5° to 10°) than coast live oaks, but there are no differences in the distribution of the two species relative to slope-aspect. The largest landholder of Engelmann oak stands is the Cleveland National Forest (24 pct of all stands), followed by Spanish Land Grants (29 pct; unbroken large land holdings), Native Americans (7 pct; on Indian Reservations), and the US Marine Corps (6 pct; Camp Pendleton). A large number of small private parcels control the remaining 31 pct of Engelmann oak stands.

This study was undertaken to define the distribution of the Engelmann oak (*Quercus engelmannii*). It is the first step in conserving and managing this oak resource in a rapidly urbanizing part of California. Wieslander and Jensen (1946) mapped part of the Engelmann oak range in the 1940's; if it were not for the rapid conversion of wildland habitats and the increased interest in woodland, these maps probably would have been sufficient to typify the species distribution. The U.S. Forest Service maps (Anderson 1969) are more up to date and at a finer

scale than the Wieslander maps, but still did not provide the data for private lands outside the Cleveland National Forest. Bolsinger (1986) provided the best estimates of Engelmann oak area, but these data were neither location specific nor retrievable by geographic unit.

The goals of this paper are threefold: (1) to define the extent of Engelmann oak woodlands, (2) to make broadscale predictions on the occurrence of the species relative to topographic features, and (3) to outline the ownership, administration, and management control of Engelmann oak woodlands.

METHODS

Photographic Imagery

I used 1980 color imagery at 1:20,000 scale to map the woodlands. Areas with rapidly changing (urbanizing) landscapes in the northern half of the species range were mapped with 1989 color infrared imagery at 1:20,000. Engelmann oak woodlands in the aerial photographs were traced onto 46 USGS 7.5 minute topographic maps using a zoom transfer scope or drawn directly onto maps using stereoscopic glasses and stereo-paired photographs. Engelmann oaks in aerial photographs were separated from other trees by: (1) the open canopy and growth form of *Q. engelmannii* and (2) lighter green color of *Q. engelmannii* in infrared imagery. Oak woodlands that did not contain Engelmann oaks (i.e., pure stands of coast live oak) were not mapped.

Woodland Mapping

Polygon boundaries were drawn by connecting the canopies of oaks on woodland perimeters; woodland areas with less than 10 mature oaks per hectare (10 to 30 pct canopy cover) were not mapped. When woodlands were interdigitated with or bisected by other vegetation, I followed two conventions: (1) if the distance between two canopies exceeded 75 m, the space between was not mapped as woodland, and (2) stands smaller than 0.5 ha were not mapped unless they occurred in isolated areas (greater than 3 km from nearest stand) or they occurred along the edge of the species range. We used the GIS ARC/INFO to calculate the area and perimeter of each polygon.

¹Presented at the Symposium on California's Oak Woodlands and Hardwood Rangeland, October 30 - November 1, 1990, University of California, Davis.

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Categorization of Woodlands

A releve method was used to classify woodlands containing Engelmann oaks into six categories of species dominance. The dominance of Engelmann oak within polygons was ranked into six categories: (one) 0 to 5 pct of canopy area was Engelmann oaks; (two) >5 to ≤25 pct; (three) >25 to ≤50 pct; (four) >50 to ≤75 pct; (five) >75 to ≤95 pct; and (six) >95 to ≤100 pct. A specific woodland was subdivided into separate polygons only when a clear division could be drawn between two dominance categories. I did not attempt to separate woodland areas into canopy cover-density classes (oak canopy area/total area), because this categorization clouded comparison between live and Engelmann oak. Categorization of the woodlands was done in the field during the spring and summer months of 1987 through 1989. Stands of hybrid *Quercus engelmannii* x *dumosa* and *Q. engelmannii* x *cornellius-mullerii* were not mapped unless they contained single stemmed trees with predominantly Engelmann oak leaf and bark characteristics (Scott 1990).

Overall Topographic Distribution of Woodlands

Engelmann oak woodland polygons were overlaid onto topography to calculate the distribution of woodland areas among elevation, slope, and aspect. Categories of dominance were maintained so the relative distribution of live oak and Engelmann oak dominated woodlands could be calculated for each of the variables. I used Digital Elevation Models (DEMs) created from United States Geological Survey (USGS) data files for twenty-five 7.5-minute quadrangle data. These data were available for approximately 70 pct of the distribution of *Q. engelmannii*, but did not cover some stands in the southern and eastern portion of the species distribution. The DEM data were divided in the following manner to maximize computer efficiency: (1) elevation was divided into 25 m intervals; (2) slope data was divided into 5° intervals; (3) slope-aspect data was divided into 45° intervals. The Very Important Points (VIP) program of the GIS ARCO/INFO was needed to reduce the number of points in the DEM data set.

Land-Use Boundaries

The distribution of Engelmann oak woodlands was overlaid onto a coverage of the boundaries and county, state, and federally administered lands (take from USGS quadrangle maps and County of San Diego base maps). These categories were used to divide woodland areas into private, county, state, and federal holdings. Federally owned parcels smaller than 2.5 km² (1 mi²) were not mapped.

Deviations from Random Distributions

I compared the observed topographic distribution of woodlands against random distributions in nine of the 46 quadrangles where Engelmann oaks occur (figure 1). Because the computer time required to calculate DEM data limited the number of quadrangles that could be used, I selected nine representative quadrangles: three from the northern end, four from the central portion, and two from the southern end of the Engelmann oak distribution. DEM data were calculated for the entire surface of each quadrangle and the frequency distributions of elevation, slope, and aspect were calculated to describe the available landscape in the sampled area. I then measured the deviation in the observed woodland elevation, woodland slope, and woodland aspect from the distributions that would be expected if woodlands were randomly distributed across the nine quadrangles.

Statistical Analyses

The majority of data presented in this paper are derived from GIS map polygons. In nearly all cases the spatial areas (measured in hectares) of these polygons have been grouped in categories and their summed values among these categories were then compared against an expected (random) distribution. At present, there are no statistical techniques for calculating the significance of the differences in two distributions of summed (rather than enumerated) categorical data. Although the tests used here represent trends, they cannot be compared to standard tests of statistical significance. To be conservative, I used average woodland polygon size (15 hectares) as the operational geographic (sample) unit (Crovello 1981) rather than my unit of measurement, which was the hectare. Summed data in categories were divided by this geographic unit to approximate sample size for estimating the appropriate critical values in Kolmogorov-Smirnov comparisons (P_{est}) summed values within cells were divided by the geographic unit to approximate the frequency values for Chi-square comparisons.

RESULTS

Overall Distribution of Woodlands

I recorded 31,512 ha of woodland containing Engelmann oaks in 2,150 GIS polygons. These stands were concentrated in the cis-montane foothills of San Diego and southwestern Riverside counties (figure 1) (for general description of distribution see Scott 1990). The western edge of the species range averages

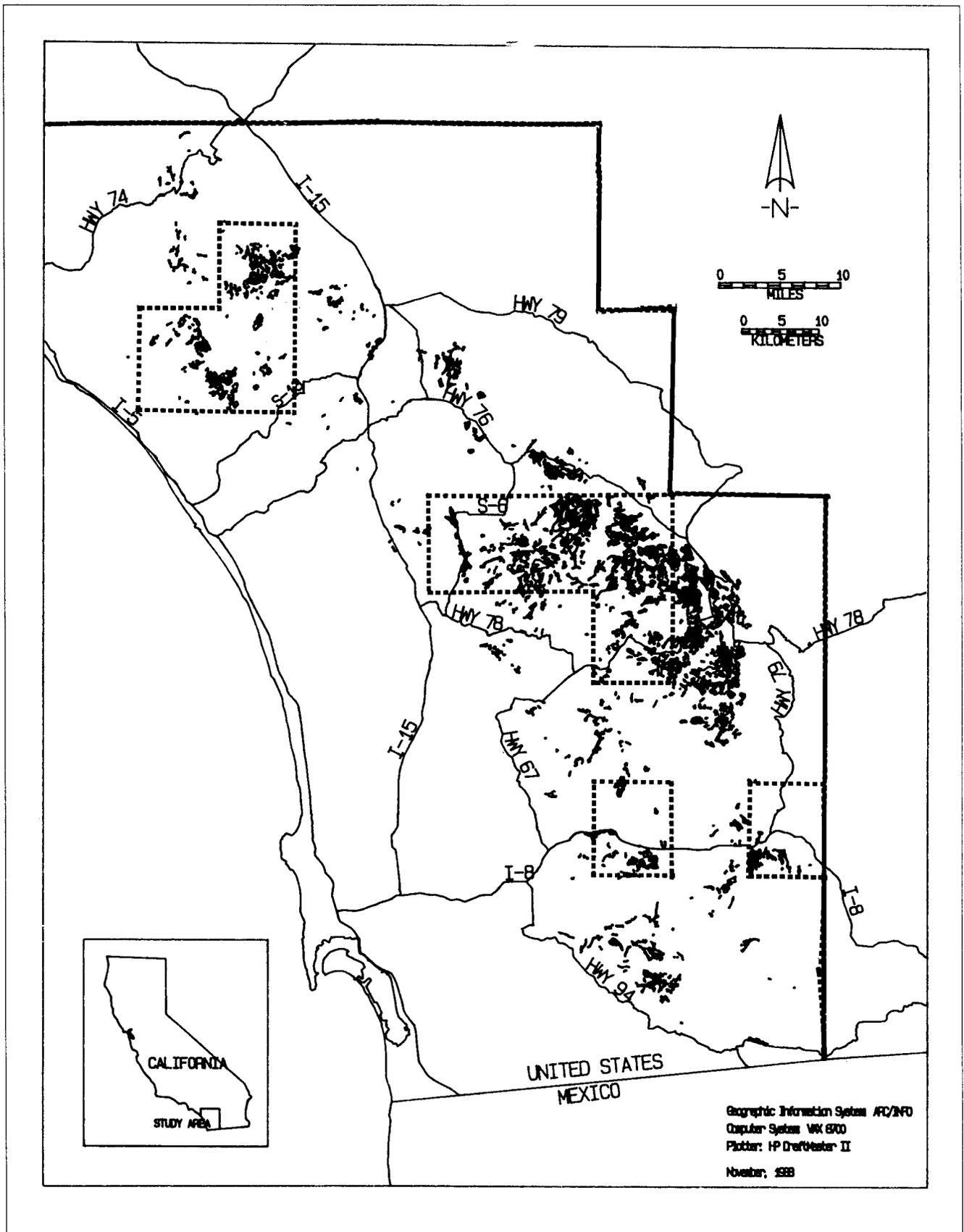


Figure 1—The geographic distribution of Engelmann oak (*Quercus engelmannii*). The dark line represents USGS quadrangles where topographic data was collected on woodlands; the dashed line outlines quadrangles where topographic data was collected for both woodland and landscape.

22.0 ± 1.6 km (13.7 ± 1 mi) (measured on 50 polygons at 2.5 km north/south intervals) from the coastline; the species range comes within 7 km (4.5 mi) of the coast at Camp Pendleton (north end of the range) but is 30 km (19 mi) from the coast at the Mexican border. The east-west width of the species range is 20 km (12.5 mi) at the Mexican border and reaches a maximum width of 40 km (25 mi) between the cities of Escondido and Julian (33° 7' latitude); north of this latitude the range splits into a narrow western (20 km; 12.5 mi) band in the Santa Ana Mountains and a diffuse pattern of small (0.2 to 1 ha) stands across the Perris Plain and the foothills of the San Jacinto Mountains. I found only scattered Engelmann oaks south of the Mexican Border and north of California State Highway 74. The proportion of USGS (7.5 minute) quadrangle area covered by Engelmann oaks varied from 2 pct of quadrangles at the western fringe of the species distribution to 29 pct of quadrangles in the center of the species distribution. Engelmann oak woodland area averaged 8.1 ± 7.6 (SD) pct of quadrangle area in the 18 contiguous quadrangles where the majority of the species distribution occurred.

Distribution Among Woodland Types

Only 1.6 pct of the woodland area was classified as pure stands of Engelmann oak woodland (category six) (table 1). A slight majority of woodlands (52 pct) occurred in stands where Engelmann oaks were subdominant to live oak. There were no strong patterns of spatial segregation among the different categories of woodlands other than the elevational differences (see beyond).

Polygon Size and Shape

Polygons averaged 15.9 ± 49 ha, with a wide range of averages among woodland categories (table 2). The high variance to mean ratios in all six woodland categories indicates that the pattern of a few large woodlands and a large number of small woodland stands is consistent across all categories of Engelmann oak woodlands. Woodlands in categories four and five had the largest average woodland areas, measuring 20.3 ± 53 ha and 20.1 ± 76 ha, respectively. Pure stands of Engelmann oaks averaged 9.1 ± 18 ha. About 22 pct of the woodlands had area/perimeter ratios of less than 0.125, which approximates the ratio for a linear or strongly interdigitated woodland.

Elevational Range

Engelmann oaks in the sample quadrangles ranged from 50 m (160 ft) to 1,375 m (4500 ft) (a.s.l.), with 60 pct of woodland area occurring between 475 m (1,640 ft) to 1075 m (4,000 ft) (a.s.l.). The distribution was bimodal, with peaks occurring at 600 m (1,950 ft) and 1075 m (3,500 ft) (figure 2).

The elevational distribution of Engelmann oak deviated strongly from the elevational distribution of the nine sample quadrangles. In general, there were more hectares of Engelmann oak woodland between 700 m (2,300 ft) and 1,275 m (4,200 ft) than would be predicted by random distribution (Kolmogorov-Smirnov test; $P_{est} < 0.01$) (figure 3) across the nine quadrangles; conversely, there were fewer hectares of woodland above and below this range than would have been predicted.

Woodlands dominated by Engelmann oak showed a strong tendency to occur at higher elevations than woodlands dominated

Table 1—Total area of Engelmann oak woodland in hectares.

CATEGORY ¹	PRIVATE PARCEL ²	LAND GRANT	NATION FOREST	INDIAN RESERV	MILITARY BASE	STATE/COUNTY	TOTAL
SOLITARY TREES	2354	937	1441	378	145	20	5273
SCATTERED GROUPS	2003	440	1025	275	254	5	4001
SUB-DOMINANT	2140	2624	1244	426	190	2	6626
CO-DOMINANT	2137	2062	1546	939	657		7341
DOMINANT	2254	1939	2088	140	269		6690
PURE STAND	141	258	38	41	2		481
TOTAL	11029	8260	7382	2198	1516	27	30412

¹The ratio of Engelmann oak (*Quercus engelmannii*) canopy area to coast live oak (*Quercus agrifolia*) canopy area within these 6 woodland categories are; Scattered trees, 0 to 0.05; Scattered groups, >0.05 to ≤0.25; Sub-dominant, >0.25 to ≤0.5, Co-dominant, >0.5 to ≤0.75, Dominant, >0.75 to ≤0.95; Pure stands, >0.95 to 1.00.

²Includes Nature Conservancy property.

Table 2—The mean and standard deviation of woodlands (polygons) containing Engelmann oaks.

CATEGORY ¹	PRIVATE PARCEL ²	LAND GRANT	NATION FOREST	INDIAN RESERV	MILITARY BASE	STATE/COUNTY	TOTAL
SOLITARY TREES	10.80 ³	12.49	18.71	12.59	8.51	4.60	12.49
	8.63	27.46	55.90	20.22	12.24	4.70	30.42
SCATTERED GROUPS	11.64	8.62	16.27	14.45	11.04		12.18
	18.13	13.36	34.34	19.15	18.32		29.44
SUB-DOMINANT	13.38	24.76	13.82	9.90	10.54		15.89
	20.94	99.61 _≤	18.89	12.53	11.80		53.08
CO-DOMINANT	16.31	32.21	15.01	22.91	28.56		20.28
	27.14	99.32	34.73	54.31	38.49		3.16
DOMINANT	14.09	26.57	31.64	10.77	12.79		20.09
	27.26	83.55	139.72	10.05	22.92		76.50
PURE STAND	6.72	12.89	7.63	6.87	2.32		9.07
	8.64	26.83	10.83	8.43	0.00		18.15

¹The ratio of Engelmann oak (*Quercus engelmannii*) canopy area to coast live oak (*Quercus agrifolia*) canopy area within these 6 woodland categories are: Scattered trees, 0 to 0.05; Scattered groups, >0.05 to ≤0.25; Sub-dominant, >0.25 to ≤0.5; Co-dominant, >0.5 to ≤0.75; Dominant, >0.75 to ≤0.95; Pure stands, >0.95 to 1.00.

²Includes Nature Conservancy property.

³Data are presented as mean (top) and standard deviation (bottom) for each category and land-use type.

by live oak (figure 4). Over 45 pct of live oak dominated woodlands occurred below 525 m (1,700 ft), while only 5 pct of Engelmann oak dominated woodlands occurred below this area. These two types of woodlands have similar patterns of distribution above 1,150 m (3,900 ft); only 4 pct of live oak dominated woodlands and 6 pct of Engelmann oak woodlands occur above this elevation.

Slopes

Approximately 62 pct of Engelmann oak woodlands occur on slopes of less than 10° inclination, and approximately 94 pct occur on slopes of less than 20° inclination (figure 5). The Chi-

square comparison (test for contingency; $P_{est} < 0.01$, 3 d.f.) suggests that more woodlands occurred in areas with 0° to 10° slope than would be predicted by a random distribution across slope categories; approximately 68 pct of the woodlands occurred on slopes of 0° to 10°, while only 54 pct of the landscape area had slopes of less than 10°.

Slope-Aspect

Engelmann oaks occurred throughout slope-aspect categories, but showed a trend towards southwestern aspects (225° to

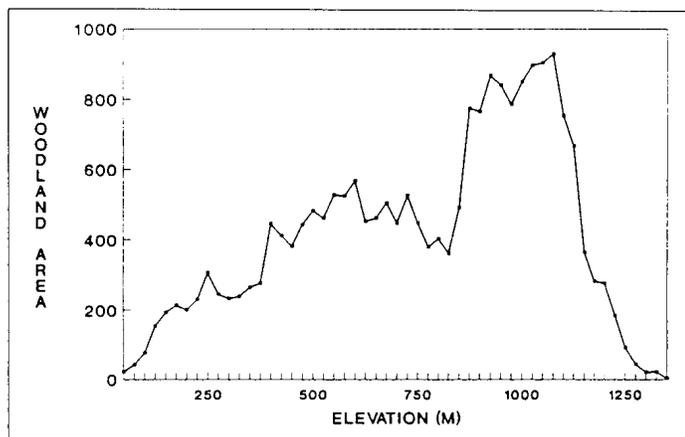


Figure 2—The elevational distribution of Engelmann oak woodland area.

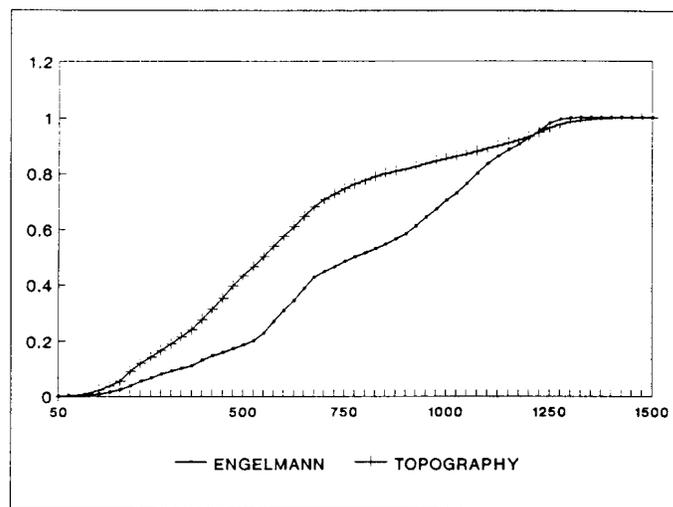


Figure 3—Cumulative frequency (0 to 1.0) of Engelmann oak woodland area (.) and landscape area (+) across elevation (m).

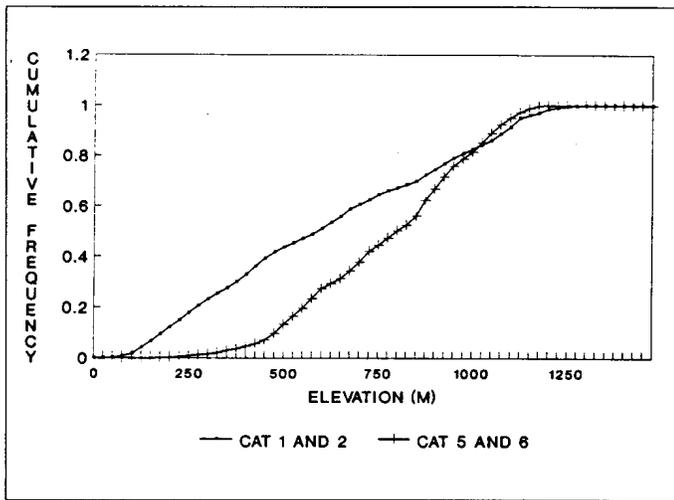


Figure 4—Cumulative frequency (0 to 1.0) of coast live oak (*Quercus agrifolia*) dominated woodland area (category 1 and 2) and Engelmann oak (*Quercus engelmannii*) dominated woodland area (category 5 and 6) across elevation (m).

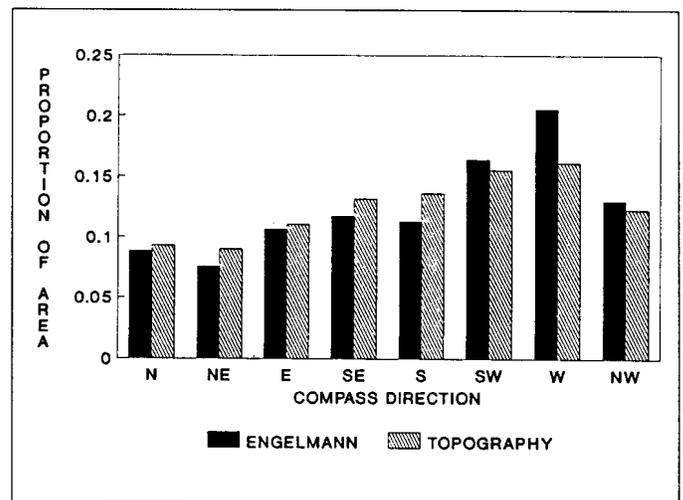


Figure 6—The proportion of Engelmann oak woodland area (ENGELMANN) and landscape area (TOPOGRAPHY) among 45° compass divisions.

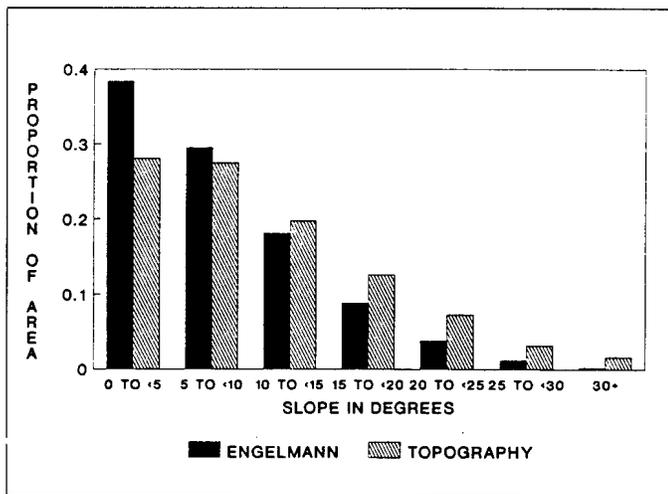


Figure 5—The proportion of Engelmann oak woodlands area (ENGELMANN) and landscape area (TOPOGRAPHY) among 5° slope categories.

315° azimuth) (figure 6). The distribution of Engelmann oak woodlands among slope-aspect categories deviated from what would be predicted by random distribution across the nine quadrangles (Chi-square test for contingency; $P_{est} < 0.05$, 5 d.f). Even though the difference was consistent in direction, Engelmann oak woodland area varied no more than 6 pct from the area that would be predicted by distribution of slope-aspects in the sample nine quadrangles. The distribution of woodland categories is equivocal and suggests no pattern between Engelmann oak dominated and live oak dominated woodlands (figure 7).

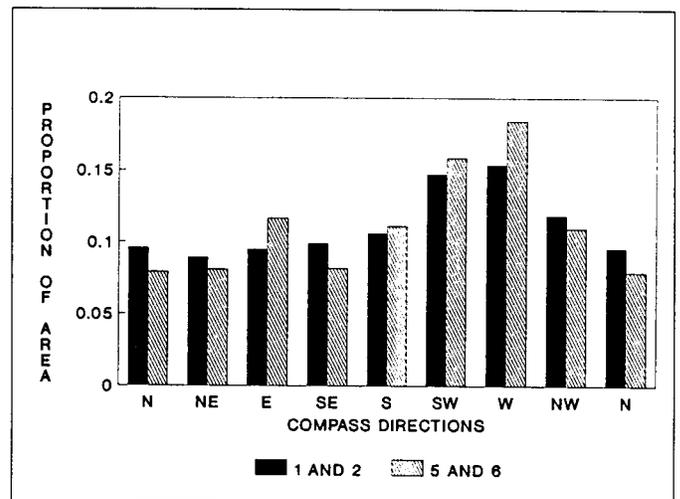


Figure 7—The proportion of coast live oak (*Quercus agrifolia*) dominated woodland area (category 1 and 2) and Engelmann oak (*Quercus engelmannii*) dominated woodland area (Category 5 and 6) among 45° compass divisions.

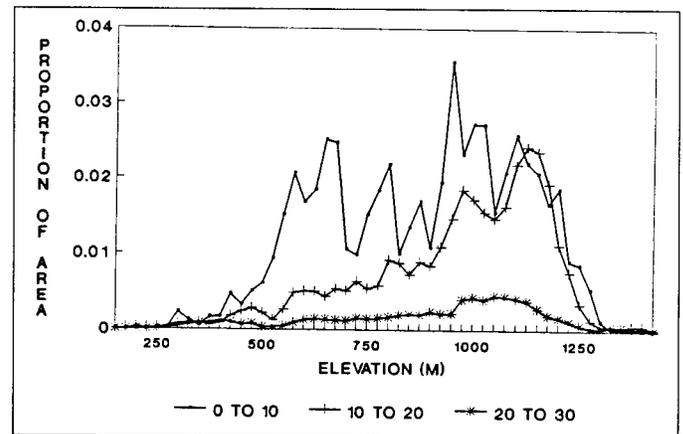


Figure 8—The elevational distribution of landscape area among slope categories: 0 to $\leq 10^{\circ}$ (.), $> 10^{\circ}$ to $\leq 20^{\circ}$ (+); and $> 20^{\circ}$ to $\leq 30^{\circ}$ (*) intervals and elevation.

Confounding Effect of Slope on Elevational and Aspect Data

The area within specific slope categories was not evenly distributed across elevational categories. A recalculation of elevation distribution, corrected for slope area within each elevation category (figure 8), suggests that variable pattern in elevation may be attributable in part to the availability of 0° to 10° slopes (figure 9). No differences were found when the aspect analysis was run on data grouped by slope category: aspect distributions were not significantly different among 10° slope intervals (0° to ≤10°; 10° to ≤20°; and 20° to ≤30°).

Aspect and Elevation

The distribution of woodlands among aspect categories showed no gradients across topographic elevation. Instead, the tendency of woodlands to occur on south facing slopes was relatively uniform from 50 m to 1250 m of elevation (figure 10), and did not vary significantly from what would be predicted by the elevational distribution of aspects in the landscape. This relationship did not change when the data was re-analyzed using only slopes greater than 10°.

Distribution Among Counties and Ownerships

Approximately 93.5 pct of Engelmann oak woodland areas occur in San Diego; approximately 6.0 pct occur in Riverside County and 0.4 pct occur in Orange County. The extant woodland areas in Los Angeles County account for less than 0.1 pct

of the species distribution. Less than 0.5 pct of Engelmann oak woodland areas occur in any incorporated cities (only Poway and Escondido).

The Cleveland National Forest controls the largest area of Engelmann oak woodlands (table 1). However, the largest proportion (57 pct) of the species distribution falls under the administration and land-use planning of the County of San Diego as private lands (including land grants). Approximately 60.5 pct of the Engelmann oak dominated woodlands (categories four, five, and six) are administered by the County, while the National Forest administers approximately 25.7 pct. The remaining lands are administered primarily by Native Americans (7.7 pct; Indian Reservations) and the U.S. Marine Corps (6.4 pct; Camp Pendleton).

The largest polygon areas occurred in category five woodlands on the National Forest (31.6 ± 139 ha) and category four woodlands on Land Grants (32 ± 99 ha). Category four woodlands were larger, on average, than category five woodlands in all land-use types except for the National Forest lands. Pure stands had the largest average area (12.9 ± 26 ha) on Land Grants.

DISCUSSION

Geographic Distribution

The area covered by Engelmann oaks is the smallest reported for any species of oak tree in California. The estimate of 15,000 ha (36,900 ac) is relatively close to Bolsinger's (1987) estimate of 39,000 ac of Engelmann oak woodlands; the 9 pct

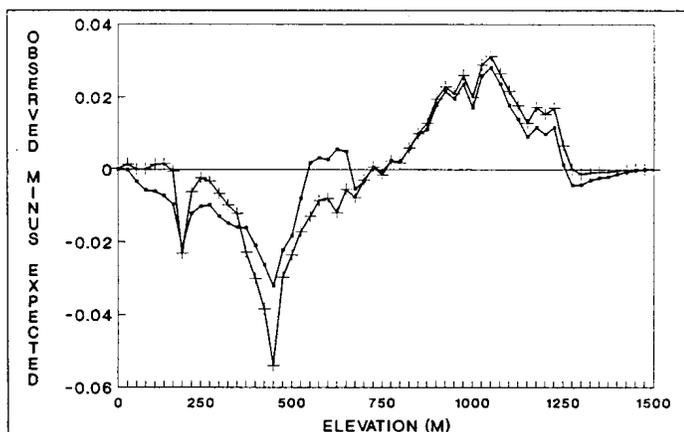


Figure 9—The difference between the distribution of Engelmann oak (*Quercus engelmannii*) woodlands and the distribution expected if these woodlands were randomly distributed across the landscape. The points (.) denote the distribution differences at 25 m elevation intervals; the crosses (+) denote the differences when the expected distribution is adjusted to include only areas with slopes < 10°.

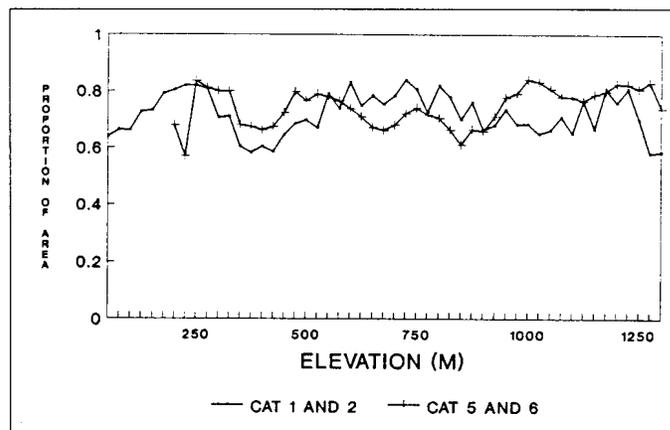


Figure 10—The proportion of oak woodland area on south facing (90° to 270° azimuth); coast live oak (*Quercus agrifolia*) dominated woodland area (category 1 and 2)(.); and Engelmann oak (*Quercus engelmannii*) dominated woodland area (Category 5 and 6) (+).

difference is attributable to methods used to divide Engelmann and live oak woodlands and to methods of mapping. The results of this study do not significantly alter his conclusions, but indicate a greater intergradation of Engelmann oak and live oak than could be detected at the statewide scale that Bolsinger was required to use.

Engelmann oak woodlands occupy a small portion of the overall range of the species; in general, stands are widely scattered and often small in area. The only regions where they contribute over 10 pct to vegetation cover-types are the Santa Rosa Plateau in Riverside County, and mountain region of San Diego County from Palomar Mountain to Cuyamaca Peak. A quarter of Engelmann oak woodland area occurs as linear or interdigitated woodlands. These areas, found on the western edge of the species distribution, are typically dominated by live oaks. The small average size of Engelmann oak woodlands, their scattered distribution, and the linearity of woodland polygons suggests that these stands are strongly effected by adjacent conditions and human activities, perhaps more so than the larger tracts of oak woodlands in western Sierra Nevada Mountains and central Coast Ranges.

Topographic Distribution

Engelmann oaks are most concentrated on low angle slopes, on southwestern aspects, and between elevations of 700 m and 1,250 m. While these data provide a general model of Engelmann oak occurrence, the variance in woodland distribution across elevation and aspect suggest other factors strongly influence the species distribution.

Engelmann oak woodlands occurred primarily in areas of less than 10° slope. Although Engelmann dominated woodlands tend to occur on steeper slopes than live oak dominated woodlands, the majority of both types of woodlands occur on slopes of less than 10°.

The upper elevational limit of Engelmann oak woodlands was far more abrupt than would have been predicted by the landscape. Temperature decreases (both average annual and daily minimum) and rainfall increases (annual precipitation) are the primary climatic condition associated with elevational increase in southern California mountains (Major 1988); it appears that 1275 m of altitude produces low enough temperatures to severely reduce Engelmann oak establishment and persistence.

The lower elevational limit of Engelmann oak distribution is far less abrupt, but appears to be tied to precipitation. A comparison of woodland occurrence to estimates of rainfall distribution (California Department of Water Resources, 1980) suggests that Engelmann oaks are concentrated in areas with over 45 cm (18 in) of annual precipitation and are nearly absent from areas with less than 35 cm (14 in). Rainfall in the region is controlled in part by orographic conditions (unpublished data³).

It appears that the elevations where rainfall typically exceeds 35 cm (350 m) approximate the elevations where Engelmann oak concentrations occur (400 m). The two depressions located in the lower elevations of figure 9 represent large areas of valley where rain shadows may alter precipitation more than elevation (Major 1988).

Engelmann oak woodlands showed a slight tendency to occur on south facing slopes through its elevational range, in part reflecting the slightly southern orientation of aspects across the landscape. The data indicates that Engelmann oak woodlands were not concentrated on either south-facing slopes at high elevations or on north-facing slopes at lower elevations. It appears that either (1) the species tends to occur on south facing slopes; however, light and temperature are contributing rather than critical elevation factors in the species distribution; or (2) the low angle slopes do not provide sufficiently different light and temperature conditions to change the aspect distribution of Engelmann oak stands at high and low elevations.

Distribution of Woodlands Among Land-Use Types

The U.S. Forest Service has the largest tracts of Engelmann oak woodlands under one management, and provides the best opportunity for comprehensive planning for the conservation and management of the species. Land Grants, particularly those which have not been divided into subunits, provide the next largest group of undivided woodland areas. In some cases, these large tracts of lands will remain as buffers, separating Forest Service lands from urbanizing areas. In other cases, the pressures and incentives to develop large tracts of private lands suggests that some Engelmann oak woodlands may have to be protected through land purchase and donation to conservation agencies.

At present, very little of the distribution of the Engelmann oak is protected in parks or preserves. Cuyamaca Rancho State Park has approximately 0.1 pct of the species distribution. The Nature Conservancy and the County of Riverside are attempting to acquire the Santa Rosa Plateau, which contains approximately 5 pct of all Engelmann oak woodlands. U.S. Marine Corps and Native American lands provide de facto nature preserves because of their low levels of land development. However, these areas should not be considered as preserves because their charters and management goals do not necessarily protect woodlands.

The greatest challenge in Engelmann oak conservation occurs in the small parcels which share 36 pct of all Engelmann oak woodlands. Maintenance of community woodlands through the management actions of individual landowners will require a combination of education and creative policies by the counties of San Diego and Riverside. Most woodlands occur on slopes of less than 10°, and are likely to be developed as the population of southern California expands into foothill areas.

³Unpublished data on file, Geography Research Library, Department of Earth Sciences, University of California, Riverside, CA 92521.

ACKNOWLEDGMENTS

This work was funded by the Integrated Hardwood Range Management Program. Elaina Misquez and Arle Montalvo helped with the mapping; Barbara Pitzer helped with field surveys. Elaina Misquez created the GIS overlays; Keith Palmer, Jean Power, and Mathew Rossano helped to create the DEMs. Thomas Oberbauer let me use his vegetation maps of San Diego County as a starting point in woodland mapping. Thomas White provided Forest Service maps and photographs.

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Germination Characteristics of Engelmann Oak, and Coast Live Oak from the Santa Rosa Plateau, Riverside County, California¹

Gerald E. Snow²

Abstract: Over 2,000 acorns of *Quercus agrifolia* (coast live oak) and over 500 acorns of *Q. engelmannii* (Engelmann oak) were collected in the Jim Knight pasture area of the Santa Rosa Plateau. These were used to test for temperature and moisture conditions on germination of viable acorns in the laboratory under controlled environmental conditions. At 24°C *Q. engelmannii* had almost 90 percent germination after 6 days, while *Q. agrifolia* had about 20 percent (96 percent after 20 days). At 14°C completeness and speed of germination of *Q. engelmannii* was reduced to about 80 percent after 36 days, while *Q. agrifolia* had over 90 percent at 30 days. At 4°C *Q. engelmannii* had about 60 percent germination at 72 days, while *Q. agrifolia* had over 90 percent at 72 days. At varying degrees of moisture stress from field capacity to -100 bar atmosphere (at 20°C) *Q. engelmannii* had at least 70 percent germination of viable acorns after 36 days, while *Q. agrifolia* did not germinate in a -100 bar atmosphere, reached complete germination in a -10 bar PEG-vermiculite mixture after 60 days and took 132 days for complete germination under 100 percent relative humidity conditions. Drying (20°C, 45 percent RH) acorns for up to 3 weeks with 24 percent moisture loss had no effect on *Q. engelmannii* but *Q. agrifolia* lost 42, 58 and 75 percent of their initial moisture after 1, 2 and 3 weeks drying and all the seeds were dead after 2 weeks. The "self-rooting" of *Q. engelmannii* is also discussed. These germination characteristics are related to the distribution of these two oak species in the field.

The two major oak species in southern oak woodlands are Engelmann oak (*Quercus engelmannii* Greene) and coast live oak (*Q. agrifolia* Née), the former often growing in open savannas called the "Engelmann oak phase" and the latter growing in denser more widespread woodlands termed the "coast live oak phase" (Griffin 1977). Some of the factors influencing the establishment and distribution of these two species on the Santa Rosa plateau in the Santa Ana Mountains were the greater fire resistance of Engelmann oak seedlings compared to coast live oak (Snow 1980), the inhibition of seedling establishment by cattle in open areas and the concentration of coast live oak around rock outcrops (especially in cracks and the north side) due to ground squirrel transport and the apparently higher moisture requirements for germination (Snow 1973).

¹ Presented at the Symposium on Oak Woodlands and Hardwood Rangeland Management, October 31 - November 2, 1990, Davis, California.

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The only study as extensive as this one on oak germination was Korstian's (1927) study on germination and early survival in certain eastern white oaks (subgenus *Lepidobalanus*) and black or red oaks (subgenus *Erythobalanus*). Although *Q. engelmannii* is in the white oak group and *Q. agrifolia* in the black oak group, only general comparisons can be made due to the markedly different conditions under which these western "Mediterranean" climatic type oaks have developed. Also *Q. agrifolia* acorns mature in one season and have no dormancy (U.S. Forest Service, Woody-Plant Seed Manual, 1948) which are characteristics typical of white oaks rather than black oaks. In spite of these differences these two western white and black oaks show many of the same differences Korstian found in the eastern white and black oaks.

This paper focuses on the germination response to temperature and moisture conditions of these two southern oak woodland species. The temperature and moisture conditions used are assumed to cover the full range for these conditions found in the field.

METHODS

Over 2,000 acorns of *Q. agrifolia* and over 500 acorns of *Q. engelmannii* were collected from the ground under trees in the Jim Knight pasture area of the Santa Rosa plateau and air shipped to Corvallis, Oregon. After arrival the acorns were stored at 4°C and 95 ± 5 percent RH for three weeks before germination tests were begun.

For temperature germination tests wooden flats filled with wet vermiculite were maintained at 4, 14 and 24 ± 1°C in constant temperature chambers. Sixty *Q. agrifolia* and 50 *Q. engelmannii* were randomly assigned to each of the temperature chambers. Acorns were planted at least 2 cm deep and maintained at field capacity with distilled water. Germination (2 mm of radicle extending beyond the pericarp) was checked one and two days after planting and then every two days for 90 days or until germination was complete. All ungerminated acorns were tested for viability by removing the pericarp and planting the seed in wet vermiculite at 20°C for up to 30 days. A germination value which varies directly and proportionally with the speed of germination, total germination or both (Czabator 1962) was calculated for each germination curve.

In preliminary experiments, *Q. agrifolia* showed little or no germination under limited moisture conditions while *Q. engelmannii* did not appear to be affected by these conditions. In order to determine more precisely the germination-moisture response, the following moisture conditions for germination at 20 ± 1 °C were used: (I) vermiculite maintained at field capacity with distilled water; (II) 100 percent RH atmosphere; (III) vermiculite saturated with a -10 bar polyethylene glycol solution; (IV) -100 bar atmosphere. For moisture conditions I and III, the acorns were packed in vermiculite inside a vertically placed glass tube (7 cm diameter and 60 cm long) with vented rubber stoppers top and bottom. For moisture condition II an approximately 100 percent RH atmosphere was obtained by placing vermiculite saturated in distilled water over the bottom of a flat, round, clear plastic, six-liter germination chamber sealed with stopcock grease. Acorns were supported above the bottom in open glass petri dishes. For treatment III a -10 bar osmotic potential polyethylene glycol solution was added daily to the vermiculite to maintain this osmotic potential. The solution was made fresh each week and the vermiculite changed to avoid possible inhibitory effects reported for stored solutions (Greenway and others 1968). For moisture condition IV, a -100 bar atmosphere was maintained by using one liter of a saturated sodium sulfate solution (O'Brien, 1948) in a two-liter glass dish, 10 by 20 by 10 cm. Acorns were supported above the saturated salt solution in open glass petri dishes.

The use of the -10 bar polyethylene glycol osmotic solution with vermiculite may not exactly simulate the same matric potential in soil, even though identical in free energy status (Bonner and Farmer 1966). But the work of Parmar and Moore (1968) suggested that polyethylene glycol may simulate the soil rather closely in terms of the effects of water stress on total germination. Kaufmann and Ross (1970), in comparing soil and solute systems, found that for studying total germination polyethylene glycol may be satisfactory but when germination rate is important the solute system does not adequately represent the more normal soil conditions because germination in the soil system is much slower.

Thirty acorns of each species were assigned to each of the four moisture conditions. All the acorns were surface sterilized by being placed in a 2.6 percent solution of sodium hypochlorite for one minute. Germination was checked every two days for 90 days or until germination was complete, except for *Q. agrifolia* in the 100 percent RH test which continued for 132 days until germination was complete. All ungerminated acorns were tested for viability as described before.

The percent moisture on a dry weight basis of subsamples from stored and germinated acorns of the temperature and moisture tests were determined. Acorns were weighed to the nearest 0.01 g with and without the pericarp (shell), then oven dried at 95°C for 48 hours and weighed again.

The relationship between germination, water uptake and moisture content was determined more specifically using 20 *Q. agrifolia* and 10 *Q. engelmannii* randomly selected acorns, half of which had their pericarps removed. All were planted together in a single vermiculite flat as described before and maintained at field capacity for 30 days. At 12, 24 and subsequently every 24

hours, each seed and acorn was weighed to the nearest 0.01 g. After germination dry weights were obtained as described before and the percent moisture determined for the various time intervals.

The effects of drying acorns for different lengths of time on their subsequent germination were also determined for a few sound, unmarred acorns selected from a single tree of each species. Fifteen *Q. agrifolia* acorns were divided into three groups of equal size and weight to be dried at 20 ± 1 °C and 45 \pm 5 percent RH for one, two and three weeks. Ten *Q. engelmannii* acorns were divided into two groups of equal size and weight to be dried under the same conditions for one and three weeks. Each group was weighed as a unit every 24 hours. Following the drying period for each group, they were planted in vermiculite as described before and maintained at field capacity for 30 days to test for germination. After germination or 30 days, the dry weights were obtained as described before and the percent moisture determined for the various time intervals.

After five months under the storage conditions described before, 20 *Q. agrifolia* were tested for viability. Since this test indicated 100 percent viability, 50 acorns were randomly selected and divided into two groups to determine the percent moisture which would kill approximately 50 percent of the seeds. This was done by drying one group for three and one-half days and the other for seven days at 20 ± 1 °C and 50 \pm 5 percent RH and then testing them for viability. A subsample of five acorns from each group was individually weighed and dry weights determined after each drying period.

The phenology of shoot development from mid-germination until the first leaves were expanded at 14 and 24°C was determined for both species by observations recorded for the acorns in the 14 and 24°C germination test. A 14-hour photo period at 2000 foot candles was used at each temperature.

An index of the self-rooting ability of each species was obtained. The distance to the base of the shoot from the radicle emergence point on the acorn after the leaves expanded was measured for seedlings grown at 14 and 24°C from acorns used in germination tests at these temperatures. Twenty acorns of *Q. agrifolia* and 15 of *Q. engelmannii* at each temperature were measured.

RESULTS

The results of the germination of the two species at 4, 14, and 24°C in vermiculite at field capacity are presented in figure 1. *Quercus engelmannii* had a germination value (26.8) about five times larger than *Q. agrifolia* (5.4) at 24°C. At 14°C their germination values were about the same (3.8 and 4.4 in the same order). At 4°C *Q. engelmannii* (0.9) was almost half that of *Q. agrifolia* (1.6). *Quercus engelmannii* showed a marked reduction in both speed and completeness of germination with decreasing temperatures while *Q. agrifolia* showed only a reduc-

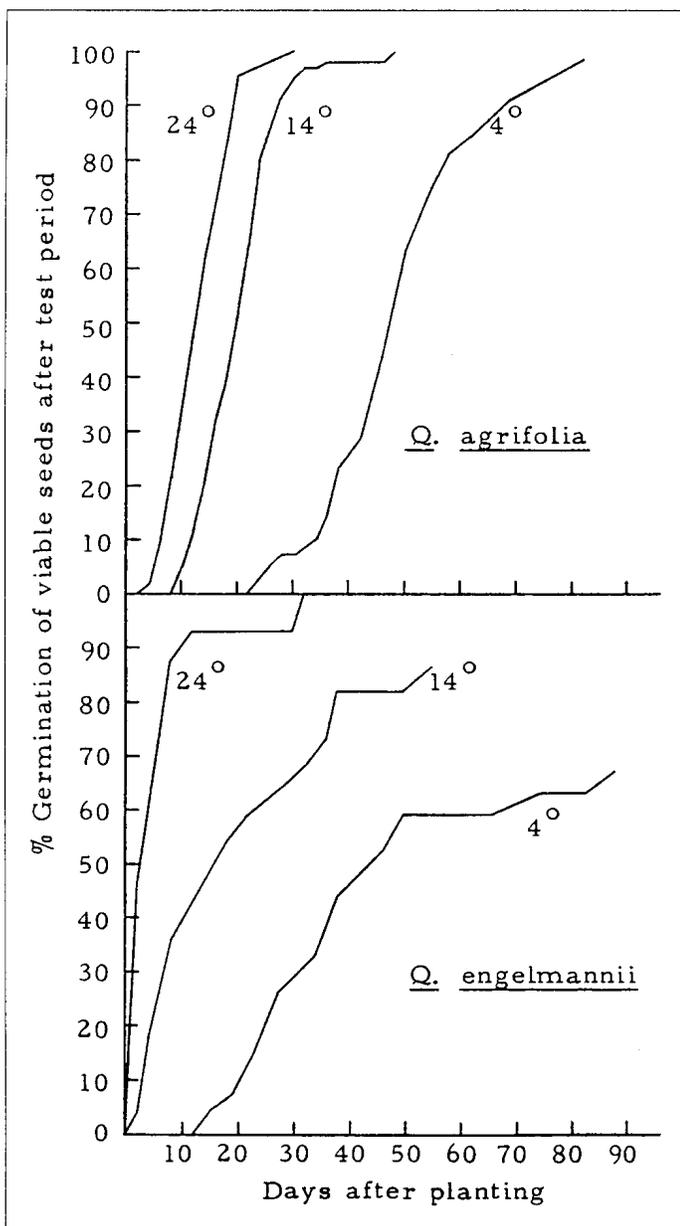


Figure 1—Germination of *Q. agrifolia* and *Q. engelmannii* at 4, 14, and 24°C. Sixty acorns of *Q. agrifolia* were planted for each temperature and 50 of *Q. engelmannii* for each temperature.

tion in its speed of germination.

The results of the germination of the two species under increasing degrees of moisture stress are presented in figure 2. *Quercus engelmannii* showed little influence from any of the moisture treatments with its germination values ranging between 1.9 and 2.4. After 36 days the percent germination for *Q. engelmannii* ranged between 67 and 75 percent for all four treatments. *Quercus agrifolia* showed a marked depression in germination by the increasing moisture stress. Germination values for the vermiculite at field capacity, the -10 bars polyethylene glycol (PEG) solution and vermiculite, the 100 percent RH atmosphere and the -100 bars atmosphere respectively are: 4.8, 2.5, 0.4 and 0.0. After 36 days the percent germination for

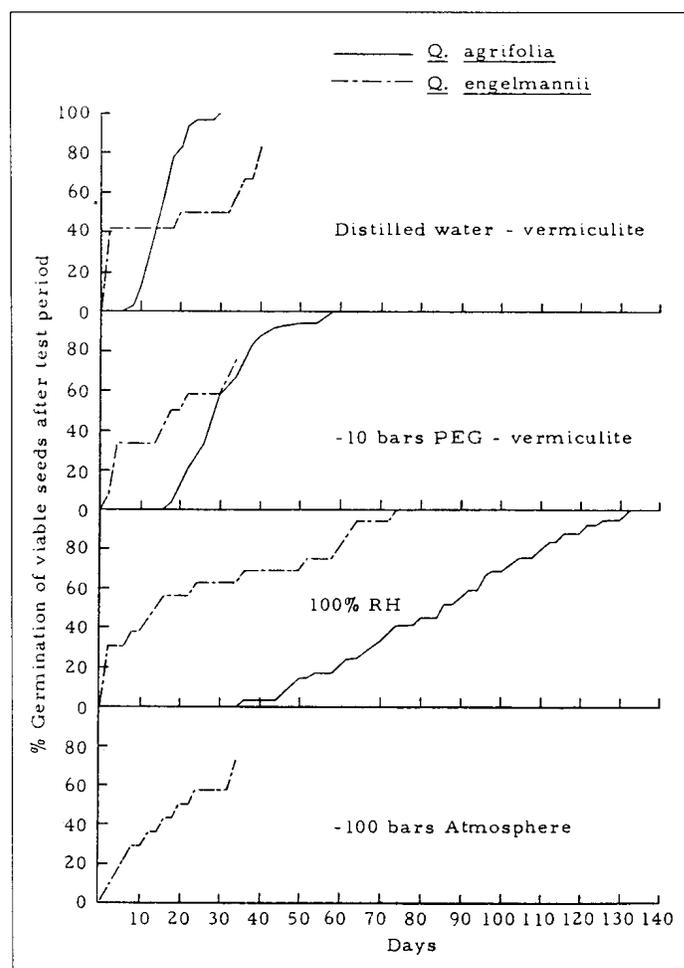


Figure 2—Germination of *Q. agrifolia* and *Q. engelmannii* under increasing degrees of moisture stress at 20°C. Thirty acorns of each species were used in each of the four moisture levels.

Q. agrifolia in the same series was 100, 76, 3 and 0 percent.

The moisture content (percent of dry weight) of the seeds of the two oak species from the field and various germination conditions is summarized in table 1. The percent moisture content of *Q. engelmannii* seeds field collected and stored for nine days was 10 to 15 percent higher than *Q. agrifolia*. The range of percent moisture content for germinated seed under various conditions was very broad for *Q. engelmannii* (54-120 percent moisture) but much narrower for *Q. agrifolia* (57-78 percent moisture). Another difference between the two species indicated in the table is the ability of *Q. engelmannii* to germinate in the -100 bars atmosphere at the same moisture content as the field collected and stored seeds and lack of germination in *Q. agrifolia* under these same conditions. Apparently *Q. engelmannii* can germinate without any additional water uptake from the field and storage conditions while *Q. agrifolia* requires additional uptake for germination.

Drying for one and three weeks had no effect on subsequent germination in *Q. engelmannii*. After losing 15 percent of their initial moisture content after one week and 24 percent after three weeks of drying, all the acorns germinated from both periods.

Table 1— The percent moisture (dry weight) of *Q. agrifolia* and *Q. engelmannii* seeds from the field and various germination conditions.

Condition	<i>Q. agrifolia</i> ^a		<i>Q. engelmannii</i> ^b	
	No. sampled	Pct moisture and range	No. sampled	Pct moisture and range
Field collected and stored for 9 days at 4°C and 95 pct RH	10	51(40-58)	10	61 (55-66)
Germinated at mean temperature of 14 °C	30	67(60-75)	10	79(63-120)
Germinated in wet vermiculite at 20°C	28	69(61-77)	7	77(64-118)
Germinated at 100 pct RH atmosphere at 20°C	28	65(57-71)	5	68(56-78)
Germinated in vermiculite at -10 bars and 20°C	18	68(62-78)	0	
Germinated in -100 bars atmosphere at 20°C	5 ^c	51(47-57)	5	58(54-62)

^aAcorns are 2 pct less than the values for seeds.

^bAcorns are about 10 pct less than the values for seeds.

^cNone of these germinated.

The *Q. agrifolia* lost 42, 58 and 75 percent of their initial moisture content after the one, two and three week drying periods. After one week of drying it had 40 percent germination but after two and three weeks of drying all the seeds were dead.

Based on the above experiment and the experiment to determine the percent moisture content which would kill 50 percent of the *Q. agrifolia* seeds, it was found that a moisture content of seeds between 26 and 34 percent (for whole acorns between 25 and 31 percent) or about 30 percent less than the field and storage conditions would kill about 50 percent of the seeds. Any acorns with a moisture content of 20 percent or less were dead. This point was not determined for *Q. engelmannii* due to lack of acorns.

As expected, both species took longer to develop shoots and leaves at the cooler temperature. *Quercus engelmannii* required almost twice as much time as *Q. agrifolia*. At 24°C *Q. agrifolia* took 35 days from mid germination until the first leaves were expanded while *Q. engelmannii* took 56 days. At 14°C *Q. agrifolia* took 59 days and *Q. engelmannii* took 103 days.

An illustration of the more rapid shoot development in *Q. agrifolia* and the self-rooting mechanism of *Q. engelmannii* is seen in figure 3. The *Q. agrifolia* on the left had been growing for 13 days after germination and had a shoot more than twice as long (1.5 cm) as the *Q. engelmannii* on the right which has been growing for 16 days (its shoot is 0.7 cm). Also note that the petioles of the cotyledons of the *Q. engelmannii* have elongated downward so that the shoot base is about 2.5 cm below the radicle emergence point on the acorn. There is no downward elongation of the petioles of the cotyledons in the *Q. agrifolia* so that its shoot arises from the same point at which the radicle emerged from the acorn. The distance from the shoot base to the radicle emergence point on the acorn for *Q. engelmannii* showed

no significant difference between 14 and 24°C. The mean distance for 30 acorns measured was 1.4 cm and ranged from 0.5 to 2.5 cm.

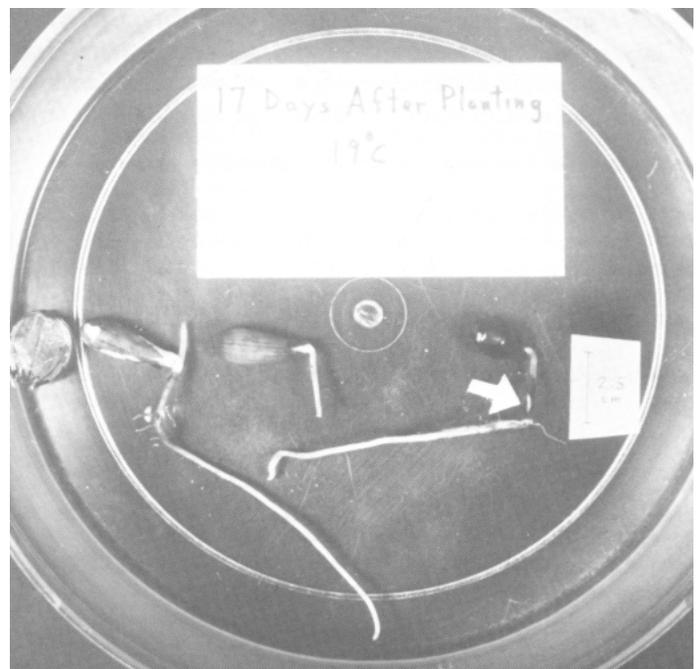


Figure 3—An illustration showing the degree of development and shoot origin in the two oak species 17 days after planting at 19°C. From left to right are the following: a *Q. agrifolia* 13 days after germination with its pericarp removed, an intact *Q. agrifolia* three days after germination, and an intact *Q. engelmannii* 16 days after germination. The arrow points to the cotyledonary node. The cotyledonary node is at the tip of the acorn in *Q. agrifolia*.

DISCUSSION

These two western white and black oaks show many of the same differences Korstian (1927) found in the eastern white and black oaks. For example, the white oaks have a higher initial moisture content than the black oaks and their acorns often germinate as soon as they are shed while the black oaks germinate later. Thirty percent of the field collected *Q. engelmannii* collected for this study had already germinated while less than 5 percent of the *Q. agrifolia* had done so and I have found *Q. engelmannii* cached in a hollow tree trunk germinating in the fall before any rains had come.

The general characteristics of the germination curves in figure 1 at 24°C for *Q. engelmannii* and *Q. agrifolia* are very similar to the warmer temperatures tested for the eastern white and black oaks (Korstian, 1927). Both *Q. engelmannii* and the eastern white oaks show very rapid initial germination rates while *Q. agrifolia* and the eastern black oaks show an initial delay in germination and sigmoid germination curves. This delay in *Q. agrifolia* is mainly due to the time required for water uptake in order to bring the seed to the moisture content required for germination.

At 4°C *Q. engelmannii* shows a marked depression in speed and completeness of germination while *Q. agrifolia* mainly shows a greater delay in the onset of germination probably mainly due to slower water uptake at this low temperature. Field temperatures may get this low, especially overnight in winter months. The eastern white and black oaks showed little or no

germination at 4°C (Korstian, 1927).

Matsuda and McBride (1987) planted three species of California white oaks and three species of California black oaks, including *Q. agrifolia*, at three elevations in the Sierra Nevada and the Santa Lucia ranges. Two of the white oaks, including *Q. douglasii* germinated soon after planting at all elevations, while the black oaks germinated 1 to 3 months later. *Q. agrifolia* germinated up to 2 months later than the faster germinating white oaks.

The lack of or poor germination of *Q. agrifolia* under low moisture conditions and the insensitivity of *Q. engelmannii* to these conditions again reflects on their initial moisture content. *Q. engelmannii* requires little or no increase in moisture content and begins germination within the first day or two, whereas *Q. agrifolia* requires an increase in moisture content to effect germination by exposure to moist conditions for from one to five weeks (table 1 and figure 2). Korstian (1927) found the eastern white oaks tested had better germination in drier soil than the black oaks he tested but both had poor germination in soil a little drier than the wilting coefficient. Bonner (1968) reported little germination for stresses greater than 10 atm using a sucrose osmotic solution for the eastern black oak, *Q. palustris* Muenchh.

The eastern white oak whole acorns in Korstian's (1927) study showed more rapid and greater water uptake than the black oak acorns which also appears true for the two western species studied here (figure 4). Both species in this study showed a more rapid water uptake with the pericarps removed which was also true for four eastern black oak species studied by Bonner (1968).

Since *Q. agrifolia* has a tougher, thicker pericarp enclosing the seed much more tightly than *Q. engelmannii*, the additional water uptake by *Q. agrifolia* might be required in order to crack the pericarp and allow the radicle to grow out. The results of the relationship between water uptake, moisture content and germi-

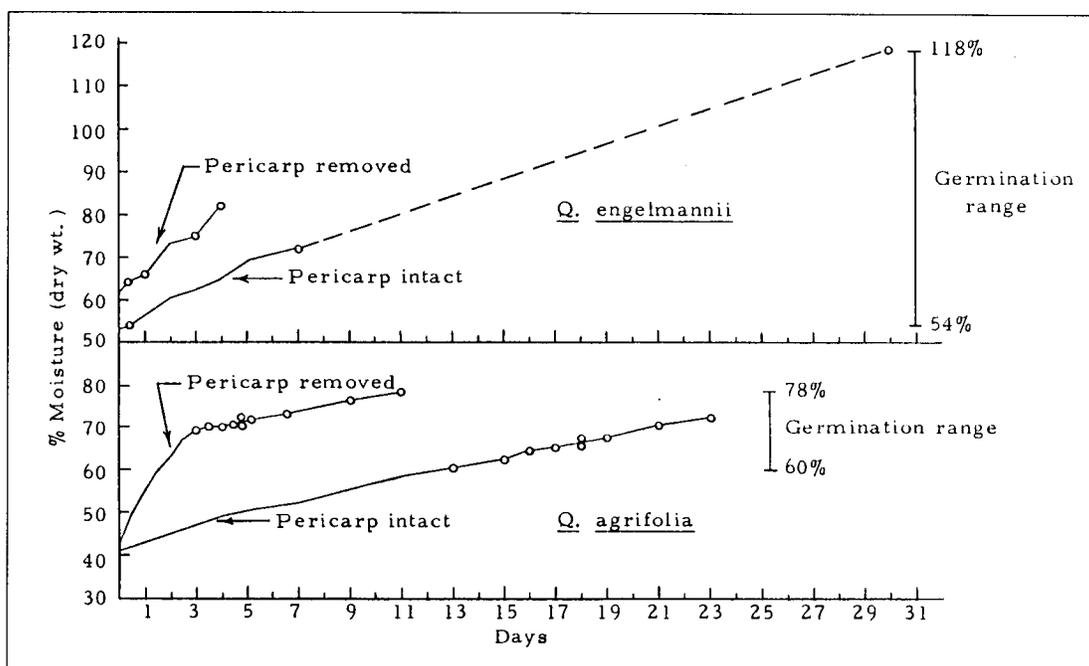


Figure 4—Water uptake and germination of *Q. agrifolia* and *Q. engelmannii* at 20°C. Circles indicate germination of individual acorns.

nation of seeds with and without the pericarp presented in figure 3 do not support that view. Even with the pericarp removed, *Q. agrifolia* seeds required a substantial increase in moisture content (from 45 percent to almost 70 percent moisture) before germination began (figure 3). Again it can be seen that *Q. engelmannii* can begin germination with little or no increase in moisture content. The typical delay in the beginning of germination in *Q. agrifolia* seen in figures 1, 2, 3 and 4 is at least in part due to the reduced rate of water uptake (figure 3) when the pericarp surrounds the seed in the typical acorn.

Krajicek (1968) found that *Q. falcata* var. *pagodaefolia* Ell. (an eastern black oak) lost moisture and viability very rapidly on air drying at room temperature. *Q. agrifolia* did not lose moisture or viability as fast as this species but it did lose moisture more rapidly than *Q. engelmannii*. Griffin (1971) air-dried in an unheated room acorns of two species of central California white oaks for 60 days with no gross effect on viability. Some of the acorns germinated during this storage.

The 50 percent loss of viability on drying for *Q. agrifolia* falls in about the same range as for the eastern black oaks in Korstian's (1927) study (moisture content between 21 and 33 percent). The eastern white oaks' 50 percent loss of viability occurred between a moisture content of 32 and 50 percent which may be similar to *Q. engelmannii* but none of them in this study got very far into this critical range.

Matsuda and McBride (1986) found that *Q. agrifolia* began to develop shoots significantly sooner after germination than the central California white oak, *Q. douglasii*, grown under the same conditions. Similar results were found in this study with much longer delays in shoot development in *Q. engelmannii* as compared to *Q. agrifolia*. This may allow *Q. engelmannii* more time for root development before moisture stresses are imposed by transpiring leaf surfaces. It would seem that this mechanism might have an adaptive advantage in establishment in more open exposed habitats where *Q. engelmannii* is normally found.

The self-rooting mechanism seen in *Q. engelmannii* in the elongation of the cotyledonary petioles carrying the radicle and plumule out of the acorn and down into the soil has also been described for the genus *Marah* (Cucurbitaceae) especially *Marah oreganus* (Torrey and Gray) Howell (Schlising 1969). Engelmann (1880) and Coker (1912) have noted this phenomenon in other oaks, especially white oaks. This pattern of germination and seedling establishment for these and a few other dicotyledonous plants occurs mainly in areas of hot and dry habitat that are generally referred to as having Mediterranean climate (Schlising 1969).

This study has shown that *Q. engelmannii* may be better adapted for establishment in more open exposed habitats than *Q. agrifolia* because it is less sensitive to moisture loss on air drying, will germinate with little or no additional water uptake, is self-rooting and has delayed shoot development. *Quercus agrifolia* may need more protected, moist habitats for initial establishment like the north side of rocks or in cracks in rock outcrops (where it is usually found on the Santa Rosa plateau) because of its greater sensitivity to moisture loss on air drying, its requirement for water uptake for from one to five weeks to effect germination (depending on temperature and moisture

conditions), its lack of a self-rooting mechanism and its more rapid shoot development after germination.

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Influence of Fire on Oak Seedlings and Saplings in Southern Oak Woodland on the Santa Rosa Plateau Preserve, Riverside County, California¹

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Abstract: One wildfire and two prescription burns were monitored at 15 oak seedling/sapling regeneration sites and at four non-burned comparison sites to study the effect of fire on seedlings and saplings of *Quercus engelmannii* (Engelmann oak) and *Q. agrifolia* (coast live oak). The number of initial top-killed seedlings and saplings, initial survivors, postburn resprouts and total survivors at the end of the study were compared between fire study sites and the non-burned comparison sites. The initial top-kill rate was higher in the burn sites than in comparison sites. Although top-killed seedlings and saplings in burned sites resprouted at a higher rate than top-killed seedlings and saplings in unburned sites, the differences were not statistically significant. Total overall survival of test seedlings and saplings at the end of the study was slightly higher in burned sites than in non-burned sites. Resprouting after fires may compensate for the high initial top-kill rate of fire in oak woodlands and contribute to the early recovery and total survivorship of the young oak population following fires.

This study reports the influence of three burn experiments monitored in 1988 and 1989—one wildfire and two planned prescription burns on seedlings of *Quercus engelmannii* Greene (Engelmann oak). *Q. agrifolia* Née (coast live oak) occurs as a co-dominant with *Q. engelmannii* in the "Engelmann oak phase" of southern oak woodland (Griffin 1977). Of the total seedling and sapling oak samples (N=791) in the 15 burn test sites, 699 were *Q. engelmannii*, the focus of this study, and 92 were *Q. agrifolia*. Snow (1980) reported on the differential response of *Q. engelmannii* and *Q. agrifolia* seedlings to prescription fires. He states that buds of *Q. engelmannii* are better protected and/or more resistant to fire and heat than those of *Q. agrifolia*. The few *Q. agrifolia* oak samples in our burn sites were included in the total analysis.

Wildfires can be very destructive to the mature oak trees, depending on the season, climatic conditions and fuel properties. Wildfires may burn at high intensity (104-132 °F) and may kill surface or subsurface permiating buds (Lathrop and Martin 1982b). However, prescription burns are typically light-intensity (98 °F) mosaic fires initiated when fuel moisture, humidity,

and wind velocity make the fires controllable. Studies have shown that burning initially involves a major disturbance to vegetation, but tends to generate new and fresh plant growth (Sugihara and Reed 1987, Lathrop and Martin 1982a,b). Sugihara and Reed state that periodic low intensity burning can result in long-term preservation of one of California's threatened oak woodland types. The vulnerability of above ground parts of shrubs or saplings to fire is due to the thin bark (surrounding their trunks) and damage to the cambium. Low or light-intensity fires cause little apparent injury to trees, except where heavy fuel has built up directly under or adjacent to canopies. Seedlings and saplings less than 5 cm diameter breast height (DBH) will be top-killed by most fires, including light intensity mosaic burns (Plumb 1980).

This paper reports on the number of oak seedlings and saplings at field test sites which survived or were top-killed as a direct result of the three fires studied, subsequent resprouting of destroyed above ground parts, and total survivors at the end of the study period.

STUDY AREA

The 1255 hectare (ha) Santa Rosa Plateau Preserve (SRPP), located on the Santa Rosa Plateau in the southeastern part of the Santa Ana Mountains of the Peninsular Ranges (Lathrop and Thorne 1978,1985a, 1985b) is a complex mosaic of vegetation communities: southern California grassland; riparian woodland; southern oak woodland; chaparral; and vernal pool ephemeral. Among management objectives of the prescribed burns on the SRPP, conducted by the California Division of Forestry (CDF) in cooperation with the California Nature Conservancy, were to: 1) reduce mulch layer 50-75 pct; 2) remove non-native grasses; 3) reduce shrub fuel load below the canopy and adjacent to *Quercus engelmannii* by 50-75 pct; and 4) reduce chaparral shrub canopy by 75 pct. This was part of an effort to restore native plants to the SRPP, and to increase species richness. The prescribed burns also reduce fire hazard, improve wildlife habitat, and increase water runoff (without running the risk of erosion) to enhance stream flow.

¹Presented at the Symposium on Oak Woodlands and Hardwood. Rangeland Management, October 31-November 2, 1990, Davis, California.

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METHODS

Prior to the burns, 15 study sites were selected at given *Quercus engelmannii* trees which had naturally occurring oak seedlings (basal stem diameter <1 cm) and saplings (basal stem diameter ≥ 1 cm - <10 cm dbh) under the canopy and in the immediate vicinity surrounding the tree. Three of these sites were fortuitously set up in an area subsequently burned by wildfire. The sample number (N) was determined as the number of live (with green stems and leaves) sample seedlings and saplings at all study sites prior to the wildfire and prescription burns. Each oak seedling or sapling was flagged and tagged with 3/4 inch numbered metal tags at each study site. Seedlings and saplings at sites within the prescription burns and the wildfire were counted prior to and within a short time after the fires to determine the number of survivors (S) and those which were top-killed (Tk) by the fire. Survivorship rate was determined as a function of the initial number of live oak samples (N) which survived the fire. Resprouts (Rs) were those seedlings and saplings which were initially top-killed by fire but subsequently produced new above ground growth. Total survivorship (TS) was determined as the number survivors at the last interval plus resprouts (Rs) minus secondary top-killed (STk) specimens. Desiccation (Des) and browsing (Brw) by small rodents (i.e: *Peromyscus* sp. [deer mouse], *Spermophilus beecheyi* [California ground squirrel], *Perognathus californicus* [jumping mouse], and *Thomomys bottae* [California pocket gopher]) were the usual cause of secondary top-kill following fire. Oak samples were considered to have sustained top-kill if there were blackened remains, above-ground parts completely destroyed by

contact with flames, or if leaves and stems were brown from being heat-killed. It is well known that most oak species vigorously resprout (Rs) from root crowns and at the below-ground bud zone (Plumb 1980). The *Quercus engelmannii* and *Q. agrifolia* seedlings that were top-killed by fire or heat may still have remained alive at their roots, below-ground buds, and stem buds and thus, may have retained the ability to resprout from these buds.

Burnt wire flag markers were replaced with new flags and the metal specimen number tags were left in place for each seedling/sapling sample in the test population at the first postfire monitoring. We conducted postburn measurements at all test sites each fall and spring seasons, usually in November and May because these times of the year correspond to the greatest periods of regrowth and mortality. Postburn data collected were: 1) number of secondary top-killed (STk) seedling and saplings; 2) resprouts (Rs) of original fire damaged samples; and 3) number of total survivors (TS). Following fire, renewal of seedlings and saplings may take place by resprouting. However, many resprouted seedlings die-back and resprout several times. The frequency of resprouting of *Quercus engelmannii* seedlings, however, tends to diminish with age and may cease altogether before reaching the more stable sapling stage.

The wildfire of August 31, 1988 burned over grassland and oak woodland, mainly on the north slope and top of Mesa de Colorado on the SRPP (table 1). The two prescription fires burned through valleys and gentle slopes on November 16, 1988 (four sites) and June 13, 1989 (eight sites), respectively (table 1). Four comparison sites, containing a total N of 703 seedlings and 38 saplings of *Quercus engelmannii* and 14 *Q. agrifolia* seedlings in adjacent non-burned oak woodland on the SRPP, were monitored over approximately the same seasons as the burn sites to compare recovery and frequency of resprouting between burn and non-burn sample seedlings and saplings (table 2).

Table 1—Description of fire conditions and area of burns in hectares (ha) of one wildfire and two prescription burns on the Santa Rosa Plateau Preserve. S= number of study sites; N= total number of preburn seedlings (sdl) and saplings (spl). W spd.= wind speed; RH= relative humidity; high intensity fire= 104-132°F; low intensity fire= 98°F.

Fires	N Sdl	N Spl	Conditions	Type
WILDFIRE				
August 1988 121 ha, 3 sites			Temp. 85°F W spd. 15/mi/hr RH semi-dry	Moderately high intensity Fire carried by ground/shrub cover
<i>Q. agrifolia</i>	2	1		
<i>Q. engelmannii</i>	79	43		
PRESCRIPTION BURN 1				
November 1988 109 ha, 4 sites			Temp. 68°F W spd. 1-2/mi/hr RH 45 pct	Medium intensity Fire carried by ground cover
<i>Q. agrifolia</i>	62	5		
<i>Q. engelmannii</i>	132	9		
PRESCRIPTION BURN 2				
June 1989 170 ha, 8 sites			Temp. 70°F W spd. 3-5/mi/hr RH 27 pct	Low intensity Fire carried by ground cover
<i>Q. agrifolia</i>	22	0		
<i>Q. engelmannii</i>	436	0		

Table 2—Overall breakdown of total number (N), total number initial top-killed (Tk), total initial survivors (S), total resprouts (Rs), total secondary top-killed (STk), and total survivors (TS) of seedlings (A) and saplings (B) at each of the 15 burn sites and four comparison sites from Fall 1988 - Spring 1990 on the Santa Rosa Plateau Preserve.

Sites	Wildfire			Prescribed 1				Prescribed 2							Comparison				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
A. SEEDLINGS																			
NUMBER																			
N	25	38	18	113	2	19	60	69	38	142	30	26	54	50	49	47	123	335	212
Tk	15	35	18	88	2	14	50	69	35	136	30	24	54	50	49	8	14	48	70
S	10	3	0	25	0	5	10	0	3	6	0	2	0	0	0	39	109	287	142
Rs	13	24	4	75	0	8	29	48	26	96	19	11	29	14	15	0	10	15	51
STk	6	4	1	10	0	3	5	5	1	6	0	0	0	2	3	5	67	122	78
TS	17	23	3	90	0	10	34	43	28	96	19	13	29	12	12	34	52	180	115
B. SAPLINGS																			
N	14	30	0	0	7	0	7	0	0	0	0	0	0	0	0	0	0	5	3
Tk	11	30	-	-	0	-	7	-	-	-	-	-	-	-	-	-	-	0	0
S	3	0	-	-	7	-	0	-	-	-	-	-	-	-	-	-	-	35	3
Rs	7	28	-	-	0	-	7	-	-	-	-	-	-	-	-	-	-	0	0
STk	0	0	-	-	0	-	0	-	-	-	-	-	-	-	-	-	-	7	0
TS	10	28	-	-	7	-	7	-	-	-	-	-	-	-	-	-	-	28	3

The chi-square goodness of fit test (Zar 1984) was used to test the null hypotheses that initial top-kill, resprouts, and long term survival rates do not differ between comparison and burn sites and between *Quercus agrifolia* and *Q. engelmannii*.

RESULTS

The initial top-kill for the wildfire (table 1) was 109 individuals out of 125 (tables 2, 3). Of this number, 11 *Quercus engelmannii* seedlings and five *Q. engelmannii* saplings survived. All three of the *Q. agrifolia* samples (two seedlings and one sapling) were top-killed. Sixty-eight *Q. engelmannii* seedlings out of 81 (83.9 pct) sustained top-kill, as did 40 *Q. engelmannii* saplings out of 45 (88.9 pct; table 3). However, 72 individuals (66 pct of top-killed specimens) resprouted by May 1989 (10 months postburn), plus three surviving stems (three stems perished) make 68 pct of the original preburn N of 125 (table 3). Only six resprouts died in the next year. Thus the seedling and sapling population at the wildfire test sites remained at or near 81 through the monitoring period (tables 2, 3).

The second fire examined was a prescription burn of November 1988 (table 1). One hundred sixty-one of the 208 preburn sample seedlings and saplings (78.3 pct) were top-killed by the fire (tables 2, 4). Sixty seven of the 208 samples specimens were *Quercus agrifolia* (62 seedlings and five saplings). Of the *Q. agrifolia* samples, 59 seedlings (88.0 pct) were top-killed by fire. Ninety-five of the 132 *Q. engelmannii* seedlings and seven of nine saplings did not survive the fire (tables 2, 4). By May 1989 resprouts of *Q. agrifolia* (32) and of *Q. engelmannii* (80)

the previous winter season brought the total live stems back to 40 for *Q. agrifolia* and to 116 (including three top-kills by desiccation) for *Q. engelmannii*. Total survivors by the end of the study (May 1990) was 32 samples of *Q. agrifolia* out of the initial N of 67 (47.7 pct) and 110 live stems of *Q. engelmannii* out of the original N of 141 (78.0 pct; table 4). This recovery was due in part to continued survival of most of the fire escapees and from resprouting of top-killed seedlings and saplings in the test population.

Table 3—Response and subsequent recovery of *Quercus engelmannii* and *Q. agrifolia* seedlings and saplings to wildfire. N= total number of live preburn oak samples at test sites within the burn area; Tk= number top-killed by fire; S= initial fire survivors; Rs= resprouts from fire-killed samples; STk= post burn secondary top-killed samples; TS=survivors of last interval plus resprouts (Rs) minus secondary top-killed (STk); Des= desiccation; Brw= browsing.

Monitoring date	Pct secondary						
	N	Tk	S	Rs	STk	TS	Tk Des Brw
WILDFIRE Aug.'88							
<i>Quercus agrifolia</i>	3	3	0	—	—	0	— —
<i>Quercus engelmannii</i>	122	106	16	—	—	16	— —
POST BURN							
May 1989							
<i>Quercus agrifolia</i>	—	—	1	0	1	—	—
<i>Quercus engelmannii</i>	—	—	71	3	84	100	—
Sep. 1989							
<i>Quercus agrifolia</i>	—	—	0	0	1	—	—
<i>Quercus engelmannii</i>	—	—	2	8	78	88	12
May 1990							
<i>Quercus agrifolia</i>	—	—	0	0	1	—	—
<i>Quercus engelmannii</i>	—	—	2	0	80	—	—

Table 4—Response and subsequent recovery of *Quercus engelmannii* and *Q. agrifolia* seedlings and saplings to prescription burning. See legend table 3.

Monitoring date	Pct secondary Tk							
	N	Tk	S	Rs	STk	TS	Des	Brw
PRESCRIBED BURN 1								
Nov. 1988								
<i>Quercus agrifolia</i>	67	59	8	—	—	8	—	—
<i>Quercus engelmannii</i>	141	102	39	—	—	39	—	—
POST BURN								
May 1989								
<i>Quercus agrifolia</i>	—	—	32	0	40	—	—	—
<i>Quercus engelmannii</i>	—	—	80	3	116	100	—	—
Sep. 1989								
<i>Quercus agrifolia</i>	—	—	1	11	30	100	—	—
<i>Quercus engelmannii</i>	—	—	5	7	114	100	—	—
May 1990								
<i>Quercus agrifolia</i>	—	—	6	4	32	100	—	—
<i>Quercus engelmannii</i>	—	—	4	8	110	100	—	—

Table 5—Response and subsequent recovery of *Quercus engelmannii* and *Q. agrifolia* seedlings and saplings to prescription burning. See legend table 3.

Monitoring date	Pct secondary Tk							
	N	Tk	S	Rs	STk	TS	Des	Brw
PRESCRIBED BURN 2								
June 1989								
<i>Quercus agrifolia</i>	22	21	1	—	—	1	—	—
<i>Quercus engelmannii</i>	436	426	10	—	—	10	—	—
POST BURN								
Sep. 1989								
<i>Quercus agrifolia</i>	—	—	1	0	2	—	—	—
<i>Quercus engelmannii</i>	—	—	74	6	78	100	—	—
Apr. 1990								
<i>Quercus agrifolia</i>	—	—	10	0	12	—	—	—
<i>Quercus engelmannii</i>	—	—	173	11	240	73	27	—

The fire at the second prescription burn of June 1989 (table 1) top-killed 97.6 pct of the total test seedlings (n=458; tables 2, 5). There were no saplings in any of the eight test sites. Twenty one *Q. agrifolia* seedlings out of 22 were top-killed by the burn (table 5). Only 10 *Q. engelmannii* seedling out of the preburn N of 436 were not top-killed by the fire (table 5). By September 1989, there was one resprout of *Q. agrifolia* and 74 resprouts of *Q. engelmannii* seedlings in the test sites, which brought the total live population from 11 after the burn to 80 (tables 2, 5). By April 1990, heavy resprouting of seedlings over the winter, brought the population up to 252, or 55.0 pct of the pre-fire value (tables 2,5).

The non-burn comparison sites (table 2, sites 16-19) were used to measure seedling and sapling recovery from fire as opposed to non-burned seedlings and saplings. The initial top-kill rate was higher in burn sites (90.6 pct, N= 791) than in comparison sites (18.5 pct, N= 755) where $X^2= 809.96$, $df= 1$, and $P= <0.001$. Although the resprout rate was higher in burn sites (63.2 pct, N= 717) than in comparison sites (54.3 pct, N= 140), it was not statistically significant ($X^2= 3.55$, $df= 1$, $P= 0.059$). Likewise, burn sites showed a higher long term survival rate (60.8 pct) than comparison sites (54.6 pct; $X^2= 5.91$, $df= 1$, $P= 0.015$).

The initial top-kill rates from fire were the same for both *Quercus agrifolia* (90.2 pct, N= 92) and *Q. engelmannii* (90.7 pct, N= 699; $X^2=0.0$, $df= 1$, $P= 1.0$), and there were no significant differences in the resprout rates during the study period for *Q. agrifolia* (55.4 pct, N= 92) and *Q. engelmannii* (59.8 pct, N= 699; $X^2=0.47$, $df= 1$, $P= 0.49$). However, the long term survival rate during the study period was greater for *Q. engelmannii* (61.5 pct, N=699) than for *Q. agrifolia* (48.9 pct, N=92; $X^2=4.87$, $df= 1$, $P= 0.027$).

DISCUSSION

Our data show that resprouting may occur several years following the initial demise of a particular seedling. Although there is an upsurge of top-kill to seedlings and saplings with fire, strong resprouting was noted to occur in all burns. Chi-square tests indicate significant differences in both initial top-kill rates and long term survival rates between burn and comparison sites. However, there were no significant differences in subsequent resprout rates between burn and non-burn sites.

Comparison of preburn and postburn data demonstrate the effect of the fire on the young oak seedlings and saplings (tables 2-5). Although the initial top-kill rates were essentially the same for both *Quercus agrifolia* and *Q. engelmannii*, long term survival from the fire was generally less for *Q. agrifolia* compared to *Q. engelmannii*. The mature *Q. engelmannii* and *Q. agrifolia* trees at the burn sites were not noticeably affected by the fires. However, each of the three fires studied destroyed several large and small trees where fuel build up was high beneath their canopies; for the most part only the lower canopy leaves and twigs were fire-scorched. New bud growth for twigs and leaves of partially burned trees were evident within a few months after the fires. Stump sprouts of destroyed saplings were noticed within weeks or days, particularly following the wildfire. Most oak seedlings in the path of the fire were top-killed directly by the fire or indirectly by the heat. Fire causes higher initial top-kills to oak seedlings and saplings, but ultimately enhances long term survival and recovery of the reproductive population.

MANAGEMENT RECOMMENDATIONS

Top-killed seedlings and saplings in burned sites apparently fared better than those top-killed by desiccation and browsing. The eventual success of the increased resprouting frequency following any fire may be influenced by the season of the burn. For example, the initial upsurge of resprouting of *Quercus engelmannii* and *Q. agrifolia* seedlings and saplings after fire will have a better chance of surviving their first season if burns occur in late summer or fall. This permits the newly regenerated oaks to avoid the summer drought. Regenerated oak seedlings, following our late summer and fall prescription burns, had relatively good survival during the ensuing winter months (tables 3, 4). Our study indicates that prescription burns intended to enhance regeneration in oak woodland might be better if conducted in late summer or early fall to permit better survival of fresh resprouts, without first having to withstand the summer drought, as a spring burn would entail.

ACKNOWLEDGMENTS

The authors wish to thank Gary Bell, manager of the Santa Rosa Plateau Preserve, and the California Division of Forestry and Fire Protection, Riverside Ranger Unit, for their helpful cooperation during the burning experiments. Special thanks goes to James R. Griffin for sharing his extensive knowledge of California oak ecology with the senior author. Graduate students Obed Rutebuka and Floyd Hayes have given invaluable assistance with field work and data analysis, for which we are grateful. This study was made possible by a research grant to the senior author (NO: IHRMP-86/2) from University of California, Berkeley.

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