Soil Moisture Availability as a Factor Affecting Valley Oak (*Quercus lobata* Neé) Seedling Establishment and Survival in a Riparian Habitat, Cosumnes River Preserve, Sacramento County, California[1]

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Abstract

The lack of valley oak (*Quercus lobata* Neé) regeneration throughout much of its historical range appears to be related to both habitat destruction and soil moisture availability. The water relations, growth and survival of greenhouse potted seedlings, field-planted and natural seedlings were monitored through the growing season, 1989. The age structure of the valley oak population of a riparian forest at the Cosumnes River Preserve was determined. The history of fluvial events of the Cosumnes River was ascertained to determine whether such fluvial events are associated with past seedling establishment within the forest. Natural and non-irrigated field-planted seedlings exhibited considerable water stress, little stem growth and leaf loss, while greenhouse potted and irrigated field-planted seedlings displayed limited water stress. Irrigated field-planted seedlings grew vigorously. Past seedling establishment within the forest showed a positive relationship with historical fluvial events. These studies suggest that soil moisture availability is fundamentally important for successful establishment of valley oak seedlings. Significant recruitment of valley oak seedlings may be limited to years in which plentiful soil moisture is available into the growing season, i.e. with the natural flooding of unconfined riparian systems.

Introduction

The California endemic valley oak (*Quercus lobata* Neé) is found as a dominant species in riparian forests. Valley oak forests, woodlands and savanna are found on higher portions of the floodplain above riparian forests dominated by Fremont cottonwood (*Populus fremontii*) (Holstein 1984). The present extent of Great Valley riparian forests is only a remnant of what existed in the "pristine" valley. Because of the very rapid destruction of these forests, their original extent is very difficult to determine. Katibah (1984) estimated that 21,449 hectares of mature riparian forest is left in the Great Valley, most of which has been disturbed. The Cosumnes River Preserve encompasses one of the healthiest and most extensive remnants of mature valley oak riparian forest (Griggs 1987).

In addition to the loss of valley oak forests, woodlands, savannas and individuals, natural regeneration of the valley oak has been observed to be poor

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(Callizo 1983; Cavagnaro 1974; Griffin 1971, 1973a, 1976, 1977, 1980; Jepson 1910; Kirn 1982; McClaran 1983; Rossi 1980; Steinhart 1978; Stern 1977). This has prompted research on the factors considered to limit the successful establishment of seedlings. The effect of varying water regimes on growth and survival has been studied (McCreary 1989, Reynolds 1991), as have the water relations of mature trees at varying distances from a known water source (Griffin 1973b).

Since the first discovery of the valley oak, the abundance of growth of valley oaks associated with riparian forests, higher portions of floodplains, natural levees, well-watered valleys and other sites with high soil moisture availability or relatively high water tables has been reported (Canon 1914, Jepson 1910, Thompson 1961). Also reported is the demise of great numbers of valley oaks due to the pumping of ground water, water diversions, dams and flood control projects (Griggs 1990, Steinhart 1978). Studies focusing on the effects of water stress on valley oaks have been limited.

Knowledge of how water availability affects present seedlings and affected valley oak seedling establishment in the past will help to elucidate how limited water availability may be contributing to limited valley oak regeneration in California. Two main objectives were the subject of this research: 1) To determine and evaluate the water relations of greenhouse potted, field planted, and natural seedlings under differing water regimes to reveal the physiologic and growth responses of valley oak seedlings to water stress; and 2) To determine an age structure of the valley oaks in the eastern, relatively undisturbed riparian valley oak forest ("Tall Forest") at the Cosumnes River Preserve, and to determine if past seedling establishment is associated with historical fluvial events.

Methods

Study Area

The Cosumnes River Preserve is located in the central portion of California's Great Valley. The Cosumnes River flows through the Preserve and joins the Mokelumne River at the southwestern corner of the Preserve. The Cosumnes remains a major natural river system with regular flooding beyond its banks (Jones and Stokes 1974, US Army Corps of Engineers 1965). The Cosumnes River, sloughs, and backwaters of the Preserve are all affected by tidal activity. With the elevation of the land at the Preserve averaging less the 10 ft above sea level, this activity combined with high flows of the Cosumnes, ensures regular flooding at the Preserve.

Water Relations

In order to find the degree to which valley oak seedlings are dependent on the availability of soil moisture for establishment and growth in their first season, the effects of water stress on their physiology and growth was examined.

A greenhouse potted seedling study was conducted. Germinated acorns were planted in 300 1 gal plastic pots in January, 1989. The planted pots were randomly assigned to one of two groups: 1) "well-watered" group, watered every other day to saturation; and 2) "stressed" group, watered every four days to saturation. The pots were watered with a drip irrigation system.

The field-planted seedling study was conducted in the "savanna-ranch" area of the Cosumnes River Preserve adjacent to a slough. The germinated acorns were planted in January, 1989, in rows, each seed 1 ft from the next with 2 ft between rows. Three plots of five rows each with 30 seeds in each row were planted. Rigid plastic mesh seedling protection tubes were placed over each seed. The exclosure was fenced with hog wire fencing and chicken wire buried at the base of the hog wire. Field-planted seedlings were watered with a drip irrigation system with water pumped from the adjacent slough. The first plot of 150 sites, "Plot A," was watered for ½ hr twice per month from April, 1989 through August. The second plot, "Plot B," was watered for ½ hr once per month from April through August. The last plot, "Plot C," was given no supplemental water.

A population of naturally occurring seedlings growing in a young stand of valley oak in the forest of the Preserve was identified. Fifty seedlings from this population were tagged for growth measurements. Seedlings used for xylem potential and leaf conductance measurements were taken at random.

Seedlings were monitored for xylem potential and leaf conductance diurnally through the growing season (April through August) of 1989. Xylem potential was measured with a pressure bomb (Scholander and others 1965). Pressure-volume curves for the determination of osmotic potential were constructed from measurements at the end of the season in August 1989. Pressure-volume curves were constructed from measurements as per Tyree and Hammel (1972). The measurement of leaf conductance was made with the use of a stomatal diffusion porometer (Kanematsu and others 1969).

Seedling growth measurements were also made through the growing season of 1989. Leaf number increase/month and stem height added/month (cm) were recorded for all three studies. Total leaf area and root/shoot ratio measurements were made in August for the potted greenhouse seedlings. Seedlings were removed from the pots and leaves removed for leaf area measurements. Leaf area was determined by optical planimeter and root/shoot ratios were determined by measuring the dry mass of the roots and shoots.

Valley Oak Age Structure

The age structure of the valley oak trees of the Preserve's eastern riparian "Tall Forest," 45.5 hectares in extent, was determined by ring-counts of cores taken from the trees. Using an aerial photograph, the forest area was broken down into major visually distinct types, or strata, so that the valley oak population of the forest could be inventoried with a stratified random sample (Freeze 1962). The strata were further subdivided into substrata depending on location within the forest area (*fig. 1*). Plots, 809.4 square meters in size and comprising 10 percent of the total forest area that was studied, were randomly selected within each substratum by the proportional allocation method (Freeze 1962). One valley oak tree from each quadrant of each plot was cored at 1 ft above ground with an increment borer, except in substratum B1 Plots 1 and 2 and substratum C1 Plot 1 wherein all valley oak trees were cored. As annual rings of each core were counted, the boundaries between annual rings were determined using criteria described for Engelman oak (*Quercus engelmannii*) by Lathrop and Arct (1987).

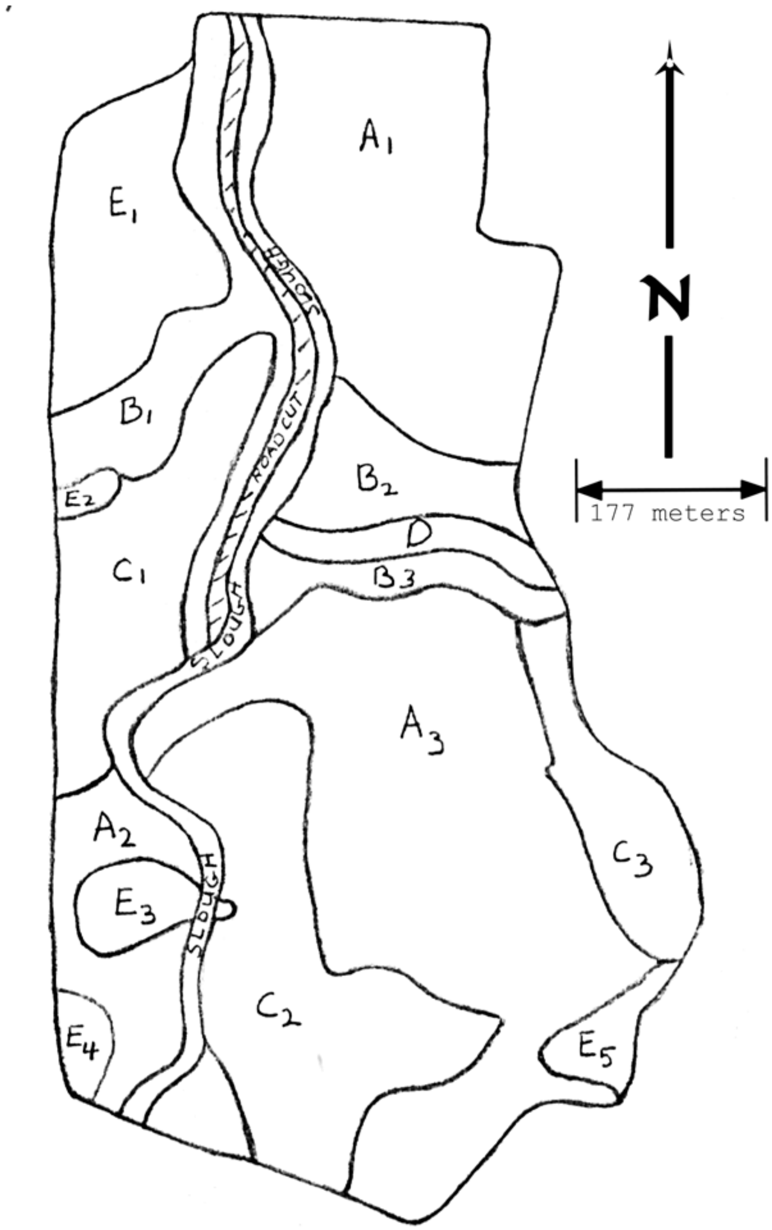

Figure 1—Map of the "Tall Trees" forest at the Cosumnes River Preserve, divided into visually distinct strata for sampling. A: tall forest, with mixed riparian trees, B: young, monospecific valley oak forest and woodland, C: forest of mostly valley oak with Oregon ash and cottonwood, D: ditch and willow thicket, E: open, with scattered old valley oak.

For fluvial event dating on the Cosumnes River, discharge records were obtained from the U.S. Geological Survey Water Resources Division for the Michigan Bar gauging station, approximately 30 mi upstream from the Preserve.

The number of trees established each year from 1915 through 1973 was graphed with discharge parameters as recorded at the Michigan Bar gauging station. The establishment year for each tree was estimated as 1989 minus the ring-count of the core sample minus 1 yr. A comparison was made between the proportion of trees established within 1 yr after a flood event (>800 cfs mean annual discharge) and the proportion of years-within-1-yr-after-a-flood event. The frequency distributions of the ages of trees sampled for ring-counts were analyzed by stem-and-leaf plots for the forest as a whole and for each of the strata (Velleman and Hoagland 1981).

Results

Water Relations

In the greenhouse study, no significant difference in mean xylem potentials or osmotic potentials was found between well-watered and stressed potted seedlings (*table 1*). The xylem potential in both treatments decreased significantly at mid-day only in August, and both treatment groups were able to recover overnight xylem potential to high pre-dawn means (*table 2*). The mean leaf conductance of the well-watered seedlings was significantly higher than that of the stressed seedlings (*table 1*). For both treatments, daily mean leaf conductances decreased through the season (*table 3*). By August, the well-watered seedlings were slightly but significantly taller, had more total leaf area and smaller root/shoot ratio than the stressed seedlings (*table 4*). Thus, the stressed seedlings reacted to the water stress by adding more root mass rather than above-ground growth.

In the field-planted seedling study, the mean xylem potentials in Plots A and B were not significantly different for the season overall, but the xylem potential of Plot C seedlings, which received no supplemental watering, was much lower than those of the seedlings in the other two plots (*table 1*). Plot C seedlings experienced a significant amount of water stress, with increasingly lower xylem potentials as the season progressed (*table 2*). The pre-dawn xylem potential of Plot C seedlings was very low (-2.08 Mpa) by the end of the season, that is, they showed no overnight recovery. There were no significant differences found between the three groups of seedlings in osmotic potential (*table 1*). Leaf conductance was highest in Plot A and lowest in Plot C for the season overall, and the leaf conductance continually decreased in Plot C seedlings over the course of the season (*table 3*). By season's end in August the mean total leaf number and stem height were also much lower in Plot C seedlings, and experienced a 9 percent mortality compared with a 4 percent mortality of Plot B seedlings and no mortality of Plot A seedlings (*table 4, fig. 2*).

Table 1—*Mean conductances, xylem potentials and osmotic potentials of greenhouse potted, field-planted, and natural valley oak seedlings for growing season, 1989.*

Seedlings	**Conductance** (cm/s)	**Xylem potential** (MPa)	**Osmotic potential** (MPa)
Greenhouse potted			
Well-watered	0.24[1]	-0.68	-1.96
Stressed	0.21[1]	-0.74	-1.52
Field-planted			
Plot A	0.21	-1.56	-1.16
Plot B	0.20[1]	-1.63[1]	-1.53
Plot C	0.16[1]	-2.40[1]	-1.46
Natural	0.15	-1.81	-1.48

[1] Denotes a significant difference down columns at $P<0.05$.

Table 2—*Mean xylem potentials (MPa) of greenhouse potted, field-planted and natural seedlings, 1989.*

		Seedlings:					
		Greenhouse		Field-planted			
Month	**Time**	**Well-watered**	**Stressed**	**Plot A**	**Plot B**	**Plot C**	**Natural**
April	0400	-0.43	-0.24	------	------	------	-0.48
	1200	-0.88	-0.79	------	------	------	-1.64
May	0400	-0.22	-0.32	-0.41	-0.44	-0.49	-0.71
	1200	-1.13	-1.00	-2.02	-2.34	-2.78	-2.18
June (E)	0400	-0.33	-0.16	------	------	------	-0.62
	1200	-0.57	-0.86	------	------	------	-1.84
June(L)	0400	-0.22	-0.24	-0.44[2]	-0.55[2]	-1.56[2]	-1.20
	1200	-0.85	-1.17	-3.03[2]	-1.23[2]	-2.10[2]	-1.34
July	0400	-0.33	-0.30	-0.42[2]	-0.57[2]	-1.86[2]	-2.34
	1200	-0.58[1]	-1.30[1]	-2.22[2]	-2.61[2]	-4.14[2]	-2.50
August	0400	-0.34	-0.35	-0.22[2]	-0.26[2]	-2.08[2]	-2.95
	1200	-2.32	-2.47	-1.55	-2.12	-2.66	-3.39

[1] Denotes a significant difference between means of groups of greenhouse study at $P<0.05$.
[2] Denotes a significant difference between means of groups of field-planted study at $P<0.05$.

Table 3—*Mean leaf conductances (cm/s) of greenhouse potted, field-planted and natural seedlings, 1989.*

	Seedlings:					
	Greenhouse		Field-planted			
Month	**Well-watered**	**Stressed**	**Plot A**	**Plot B**	**Plot C**	**Natural**
April	0.36[1]	0.31[1]	-------	------	-------	0.28
May	0.30	0.26	0.24[2]	0.18[2]	0.21	0.18
June (E)	0.22	0.23	-------	------	------	0.21
June (L)	0.22[1]	0.17[1]	0.22[2]	0.22[2]	0.16[2]	0.10
July	0.20[1]	0.14[1]	0.20[2]	0.19	0.15[2]	0.08
August	0.16	0.14	0.20[2]	0.20[2]	0.14[2]	0.07

[1] Denotes a significant difference between means of groups greenhouse study at $P<0.05$.
[2] Denotes a significant difference between means of groups of field-planted study at $P<0.05$

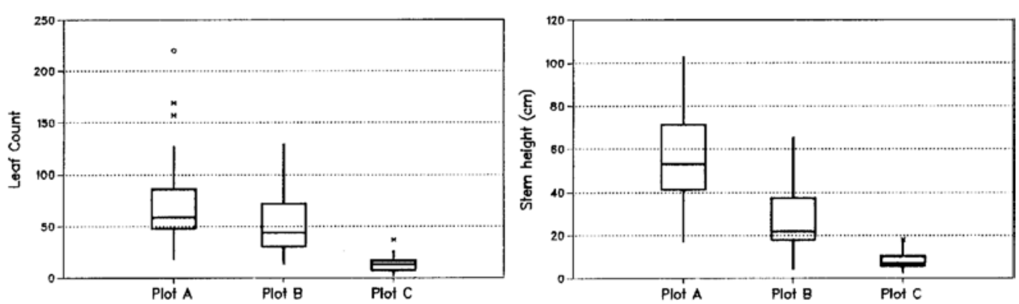

Figure 2—Leaf count and stem height distributions of field-planted valley oak seedlings in August 1989, Cosumnes River Preserve. Horizontal bars indicate median; vertical bars indicate range; * and o denote outliers.

Table 4—*Mean growth (total leaf number, total stem height, leaf area, and root/shoot) and growth rates (leaf number added/month and stem height added/month) of greenhouse potted seedlings, field-planted seedlings and natural seedlings, 1989.*

	Seedlings:					
	Greenhouse		Field-planted			
Month	**Well-watered**	**Stressed**	**Plot A**	**Plot B**	**Plot C**	**Natural**
Total leaf #	11[1]	8[1]	72[2]	52[2]	13[2]	------
Total stem height (cm)	14.0[1]	10.0[1]	56.5[2]	27.5[2]	8.0[2]	------
Leaf area (cm^2)	9.06[1]	6.73[1]	------	------	------	------
Root/shoot	7.28[1]	9.85[1]	------	------	------	------
Leaf added per month	2	1	14[2]	11[2]	3[2]	2
Stem height added per month	2.5	1.5	11.5[2]	5.5[2]	1.5[2]	1.2

[1] Denotes a significant difference between means of groups of greenhouse study at P<0.05.
[2] Denotes a significant difference between means of groups of field-planted study at P<0.05.

The natural seedlings, as with the unwatered field-plot seedlings, had increasingly lower xylem potential as the season progressed, with July and August pre-dawn xylem potentials approaching the mid-day values (*table 2*). The osmotic potential of August was similar to that found in the other studies. Leaf conductances of the natural seedlings decreased over the course of the season also, with a slight recovery in early June after a June 4 thunderstorm (*table 3*). The natural seedlings tagged for growth measurements averaged 2 yrs in age. In April the tagged seedlings had a mean of 10 leaves and were an average of 21.5 cm in height. By August there was a net increase of one leaf per seedling and an increase in stem height of 5.5 cm (*table 4*).

By examining all three studies together, patterns of stress emerge. High pre-dawn xylem potentials were maintained throughout the season by the greenhouse and Plots A and B seedlings, while the pre-dawn xylem potentials gradually decreased in Plot C and the natural seedlings. Both the unwatered Plot C field-planted seedlings and the natural seedlings were under continuing water stress as the season progressed. The greenhouse, Plot C and natural seedlings all displayed a continuing decrease in conductance as the season progressed as well. Plot C and natural seedlings experienced "flatter" diurnal curves of conductance in August, but even this response did not enable these seedlings to recover xylem potential; they were unable to draw enough water from the soil. The greatest growth rates were recorded for the field-planted Plots A and B seedlings. Plot C and natural seedlings all showed very little growth from April through August.

Valley Oak Age Structure

The forest area is bounded by the Cosumnes River at the south, a previously agricultural field to the west and north, and an agricultural field to the east. A slough traverses through the forest from the river. As described above, the forest was broken down into five major strata of visually distinct types and substrata using an aerial photograph (*fig. 1*). Stratum A is tall forest of mixed riparian species. Stratum B is woodland, with almost exclusively young valley oak. Stratum C is forest of mostly valley oak). Stratum D is a single strip along a branch the slough apparently completely cleared and now consisting of willow-scrub. Stratum E represents the areas of the forest that are presently open, apparently cleared and now are composed of annuals, grasses and scattered saplings of valley oak and very old, remnant valley oak trees.

From the graphs of the number of trees established in each year and the discharge parameters, a tendency for more trees to become established in years with a higher discharge can be discerned (*fig. 3*), especially in the years 1952 and 1956. In contrast, fewer trees became established in years with low discharge. The comparison between the proportion of trees established within one year after a flood event of >800 cfs mean annual discharge and the proportion of years-within-one-year-after-a-flood event revealed a significant difference for the forest as a whole and for Stratum B (*table 5*).

Stem-and-leaf analysis of the ring-counts of all 155 trees sampled for core age in the forest shows 52 percent of the counts between 30 and 49 years (*table 6*). Trees samples in Stratum A were medium-aged, with a mean of 46 years, those of Stratum B were youngest with a mean of 32 years, and the trees of Stratum C were oldest with a mean of 50 years (*table 7*).

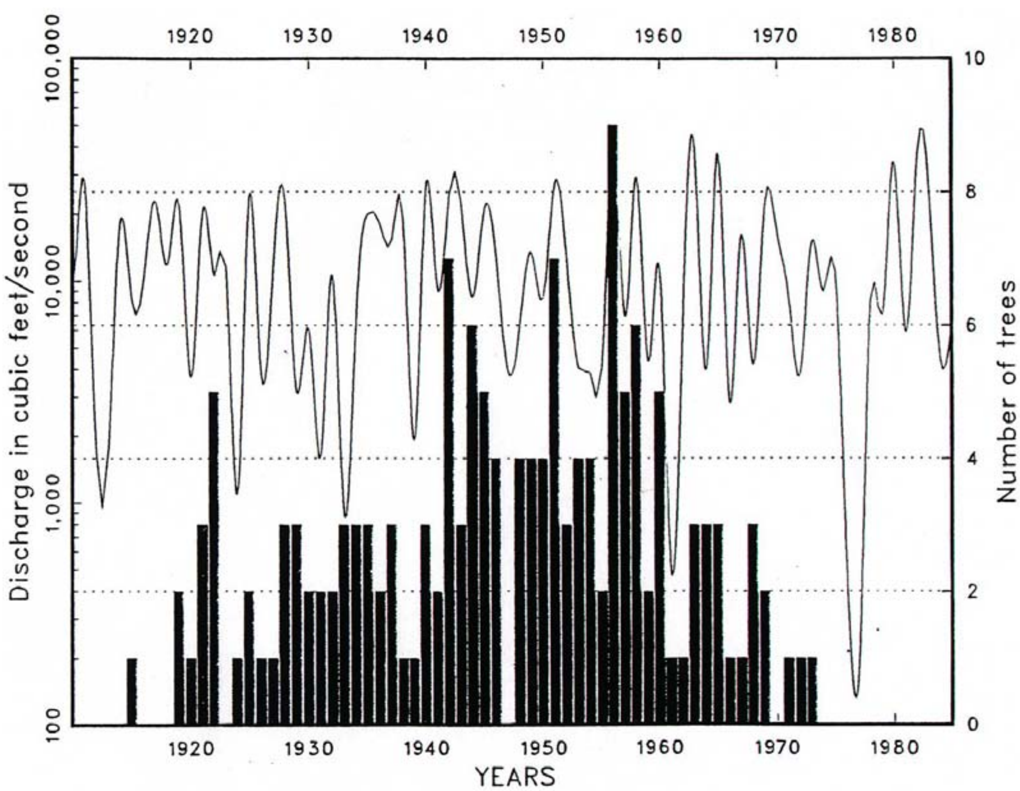

Figure 3—Number of valley oak trees established each year in the “Tall Trees” forest at the Cosumnes River Preserve, and the peak discharge (cubic ft/sec, cfs) recorded each year at US Geological Survey Michigan Bar gauging station, 1910-1985.

Table 5—*Comparison of the proportion of trees established in the "Tall Trees" forest at the Cosumnes River Preserve, within one year after a flood (>800 cfs mean annual discharge) and the proportion of years-within-a-year-after-a-flood, as recorded at the USGS Michigan Bar gauging station on the Cosumnes River.*

	Total years	Trees		Years	
		n	pct within 1 yr	n	pct within 1 yr
Forest	1915-73	155	22[1]	59	15[1]
Stratum					
A	1921-65	35	14	45	16
B	1931-73	63	36[1]	43	21[1]
C	1915-69	55	13	55	16

[1] Denotes a significant difference across rows at P>0.05.

Table 6—*Stem-and-leaf[1] age distribution of the population of valley oaks of the "Tall Trees" forest at the Cosumnes River Preserve, 1989.*

Forest
n = 155
Leaf Unit = 1.0 year

5	1	56799
16	2	00012333444
29	2	5556778888899
54	3	0000001111122222222334444
76	3	5555666777777888899999
(19)	4	0000222233333444444
60	4	555666666677888
45	5	011122333444
33	5	555667788999
21	6	000112334
12	6	66666777899
1	7	3

Stratum A
n = 35
Leaf Unit = 1.0 year

2	2	34
4	2	57
5	3	4
11	3	567789
16	4	02344
(4)	4	5678
15	5	2344
10	5	555688
4	6	01
2	6	77

Stratum B
n = 63
Leaf Unit = 1.0 year

3	1	569
11	2	00012344
20	2	556788899
(21)	3	000000111122222223344
22	3	55677788999
11	4	2234
7	4	668
4	5	01
2	5	57

Stratum C
n = 55
Leaf Unit = 1.0 year

1	1	9
2	2	3
3	2	8
6	3	124
11	3	56789
21	4	0002333444
(8)	4	55666678
22	5	67999
17	6	0012334
10	6	666667899
1	7	3

[1] Left column of each display is depth of leaf, or count at each stem; center column is stem of plot, i.e. the first digit of each value of the ring count; right column is leaf of plot, or second digit of each value of the ring count of same stem, e.g. 56799 leaf of stem 1 arranges values of 15, 16, 17, 19 and 19 ring counts. The parenthesis in the first column denotes the leaf with the median value of the ring count of the plot.

Table 7—*Age structure of sampled valley oak trees of the "Tall Trees" forest at the Cosumnes River Preserve, and of each of the strata of the forest, 1989 (n= number).*

	Age	
	mean	**n**
Forest Stratum	42	155
A	46	35
B	32	63
C	50	55
E	32	3

Discussion and Conclusions

Water Relations

Evidence of considerable water stress was found in both unwatered first-season field-planted seedlings and in natural valley oak seedlings growing in the forest of the Preserve. Since neither of these groups received irrigation, the stress evidenced in water relations measurements and in the very slight growth during the growing season may represent stress of natural seedlings under canopy cover and in the open.

Osmotic potentials between groups of greenhouse and field-planted seedlings suggest no osmotic adjustment, that is, no decrease in cell osmotic potential for intake of water by passive diffusion. Unlike valley oak, blue oak seedlings show decreased osmotic potentials through the growing season with osmotic adjustment and this was important for seedling survival (Menke, no date; Momen and others 1994). If osmotic adjustment does not occur in water-stressed valley oak seedlings, their ability to deal with water stress successfully would be limited.

Most striking is the abundant growth of the field-planted seedlings that were irrigated in Plots A and B. Greenhouse, natural and non-irrigated Plot C seedlings all grew very little during the season. Non-irrigated Plot C seedlings had the advantages of the other field-planted seedlings (unencumbered root growth and lack of competition), but still did not grow significantly more or faster than the natural seedlings. This suggests that these advantages can be translated into increased growth rates only when sufficient soil moisture is available. Cell growth has been shown to be very sensitive to water stress, more sensitive than either stomatal opening or carbon assimilation (Salisbury and Ross 1985). Thus, growth is affected by water stress before transpiration is decreased. Valley oak seedlings may be more limited than the seedlings of other California oaks in their ability to survive and grow during the summer drought. As a deciduous oak with thin leaf cuticle, valley oak continues to lose water through cuticular transpiration after stomata are completely closed (Rundel 1987). Though valley oak seedling roots grow quickly, they lack the drought-resistant characteristics of other deciduous oaks, such as blue oak.

Age Structure

The positive relationship between years of high mean annual discharge and valley oak tree establishment supports the conclusion reached in the population structure study conducted at the Bobelaine Sanctuary on the Feather River: more valley oak seedlings and saplings survived in more mesic habitats (Knudsen 1987). The increased tendency for tree establishment to occur in years of high mean annual discharge was most pronounced in Stratum B of the forest at the Preserve. This area of the forest had been without tree cover since 1937. The canopy of this substratum is comprised almost entirely of valley oak trees. From the age distribution (Table 5), it is seen that the valley oak stand of Stratum B was more even-aged that the stands of the other forested strata. The composition of the other forested areas (Strata A and C) is of mixed trees, including obligate phreatophytes such as Fremont cottonwood and willows (Barbour 1987). From this composition, it may be presumed that the land of these strata was more frequently inundated by flood waters and that the establishment of valley oak would be less dependent upon unusual fluvial events within these strata. In fact, the ages of the valley oak trees in these strata were mixed. In Stratum B, the establishment of the more even-aged stand of valley oak appears to have been facilitated by the high flows of the Cosumnes River in the 1950's and inundation by flood waters. Stratum B is located farther from the river than the strata with mixed riparian species. This distribution fits the patterns described by previous studies (Barbour 1987, Conard and others 1980, Holland and Roye 1989, Holstein 1984, McBride and Strahan 1984, Strahan 1984).

The stem-and-leaf plot analysis of the age distribution for the trees sampled in the forest as a whole shows the highest number of ages in the mid-range, 30 to 50 years *(table 6,* Forest). The age distribution for the trees of Stratum B is bell-shaped, whereas the distributions for the trees of Strata A and C are bimodal. Of the ages obtained, in the trees of the strata separately and as a whole, there is a tapering off in the number of trees in the younger age classes. This suggests that conditions optimal for valley oak establishment were present in each of the strata for a number of years and that subsequent establishment was suppressed or that the younger age-classes of trees were more susceptible to mortality. Thus, the age distributions of the different strata of the forest suggest that the establishment of valley oak in the forest tends to be episodic and not continuous.

The natural flooding events at the Preserve which were correlated with increased establishment of the valley oak in the forest may have also drowned small mammals that "are the major predators on acorns and oak seedlings" (Griggs 1990). The herbivory by small mammals, especially pocket gophers, has been implicated as a limiting factor of native oak seedling establishment in many studies (Adams and others 1987; Borchert and others 1989; Griffin 1971, 1973, 1976, 1980; Knudsen 1987). Thus, the natural flooding processes of unconfined river systems may provide a combination of reduced acorn and seedling predation and high soil moisture levels into the growing season during high water years. This combination of factors may be necessary for successful valley oak establishment in areas not inundated on a yearly basis. Alternatively, high soil moisture may allow valley oak seedlings to grow at a rate fast enough that such seedling herbivory that did occur would not have as devastating an impact on overall seedling survival and establishment.

Conclusion

A number of problems exist in interpreting native California oak regeneration, including a dearth of documentation of past distribution and stand structure (Bartolome and others 1987). Because of the plethora of factors that may be causing the present patterns of seedling and sapling recruitment, and because these factors vary considerably in space and time, Muick and Bartolome (1987) considered these present patterns to be "highly species and site-specific." The pattern of more frequent recruitment and successful establishment of valley oak in more mesic sites and lower sites has been observed in previous studies (Knudsen 1987, McBride and Strahan 1984, Strahan 1984). The water relations findings of the present studies provide evidence that variations in soil moisture availability are a major factor in explaining this pattern.

The regeneration of riparian valley oak forests is dependent on the natural flooding processes of unconfined river systems. The periodic intense and sustained inundation almost certainly provides high soil moisture levels into the growing season and either drowns small mammal herbivores or provides sufficient moisture to allow fast enough growth rates to avoid devastating effects of herbivory.

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